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Long-term effects of fire on Arctic tundra vegetation in Western Siberia

Ramona J. Heim[1]*, Anna Bucharova[1], Daniel Rieker[1], Andrey Yurtaev[2], Johannes Kamp[1], Norbert Hölzel[1]

[1] Institute of Landscape Ecology, University of Münster, Heisenbergstraße 2, 48149 Münster, Germany

[2] Institute of Environmental and Agricultural Biology (X-BIO), Tyumen State University, 6 Volodarskogo Street, Tyumen, Russia

*corresponding author: E-Mail: ramona.heim@uni-muenster.de, Tel.: +49 251-83 30 114

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Summary

Wildfires are a naturally rare phenomenon in subarctic tundra ecosystems. Climate change triggers feedback loops that probably increase fire frequency and extent in those regions. Fire can change ecosystem properties of the Arctic tundra. However, long-term effects of fire on vegetation dynamics are still poorly understood.

We studied soil and vegetation patterns of three fire scars (>44, 28 and 12 years old), situated at the northern border of the forest tundra ecozone within the Yamalo-Nenets Autonomous Okrug in Western Siberia, Russia.

Lichen cover was lower on burnt compared with unburnt plots, while bryophyte and shrub cover was higher. Those effects were still apparent more than four decades after fire.

Betula nana showed enhanced growth of individual plants after burning, indicating increased vitality and growth potential, due to modified ecosystem processes after fire: While the active layer and soil temperatures returned to levels comparable with unburned plots after 44 years, shrub growth was still enhanced. This reveals a strong fire legacy effect and can reinforce shrub encroachment with far reaching impacts on the ecosystem.

Keywords: active layer, *Betula nana*, permafrost, plant traits, Russia, shrub encroachment, soil temperature, vegetation cover

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1. Introduction

Fire drives ecosystem patterns and processes across biomes and climatic zones (Bond & Keeley, 2005; Bond *et al.*, 2005; Bowman *et al.*, 2009; Turner, 2010). Wildfire patterns are governed by, and in turn affect, climate and land use (Pechony & Shindell, 2010; Archibald *et al.*, 2013). Fire frequency, extent and severity are predicted to increase with global warming (Flannigan *et al.*, 2009), which might affect ecosystem functioning (Moritz *et al.*, 2012). An ecosystem with predicted strong increases in fire frequency is the subarctic tundra, where the effect of global warming is particularly strong compared to other parts of the world (Pachauri *et al.*, 2014; Hu *et al.*, 2015). Here, fires are naturally rare, cool and small compared to other biomes (Viereck & Schandelmeier, 1980; Archibald *et al.*, 2013). However, a strong increase in extent is predicted e.g. for Alaskan tundra (Hu *et al.*, 2015) and Arctic fires are already getting a lot of attention as a highly actual and relevant topic in media (Amos, 2019; Watts, 2019).

Tundra fires occur most frequently during dry and warm periods (Hu *et al.*, 2015; Masrur *et al.*, 2018). This suggests that climate warming will increase probability of ignition in subarctic regions (Higuera *et al.*, 2008; Bowman *et al.*, 2009; Moritz *et al.*, 2012; Young *et al.*, 2016). Fire regimes vary regionally regarding fire frequency. In Arctic Alaska, cooler and moister locations burnt less frequently than drier and warmer zones that reached a fire frequency similar to that of boreal forests (Higuera *et al.*, 2011; Rocha *et al.*, 2012). Tundra vegetation has strong effects on fire patterns through fuel availability and quality as past fire regimes show: fire frequency was higher in shrub than in herb tundra (Higuera *et al.*, 2009).

Disturbance by fire changes vegetation structure and influences vegetation dynamics of the Arctic tundra (Narita *et al.*, 2015). Plant cover is directly affected by fire through the combustion of living and dead biomass (litter) (Bliss & Wein, 1972). Changes in plant cover and biomass induce shifts in ecosystem processes such as nutrient cycles or ecological interactions (Myers-Smith *et al.*, 2011; Jiang *et al.*, 2015). The removal of living plant biomass and litter alters surface albedo and energy fluxes (Chambers *et al.*, 2005; French *et al.*, 2016). Cryptogams, vascular plants and litter insulate against extreme temperatures and thereby buffer temperature fluctuations, a loss of cover therefore results in increased soil temperature during summer (Chambers *et al.*, 2005; Jiang *et al.*, 2015). That can cause permafrost thaw, which means an increase in active layer (surface layer above permafrost) depth, and increased soil microbial activity, which enhances decomposition of organic matter and nutrient cycling (Jiang *et al.*, 2015; Zhang *et al.*, 2015; Baets *et al.*, 2016; Aaltonen *et al.*, 2019).

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Vascular plants and cryptogams react differently to fire (Racine, 1981; Bret-Harte *et al.*, 2013). While fire reduces lichens and bryophytes (Jandt *et al.*, 2008; Joly *et al.*, 2009; Turetsky *et al.*, 2012; Abdulmanova & Ektova, 2015; Ektova & Morozova, 2015; Narita *et al.*, 2015), the growth of grasses and shrubs is enhanced (Racine, 1981; Landhausser & Wein, 1993; Barrett *et al.*, 2012; Narita *et al.*, 2015). This can result in a dominance of shrubs over lichens and bryophytes that may last decades after a fire event (Racine, 1981; Landhausser & Wein, 1993; Barrett *et al.*, 2012; Narita *et al.*, 2015). Fire might therefore enforce the shrub expansion that has been observed in many regions across the tundra, and has often been attributed to global warming (Racine *et al.*, 2004; Myers-Smith *et al.*, 2011; Arefiev SP, 2016; McLaren *et al.*, 2017). An increase in shrub cover in Arctic regions may induce permafrost thaw through two mechanisms. Shrubs can retain more snow during winter than open tundra vegetation (Myers-Smith & Hik, 2013). This causes a better insulation and warmer soil temperatures during winter, as well as to a bigger amount of meltwater in spring and thus a better thermal conductivity, resulting in permafrost thaw (Johansson *et al.*, 2013). The second mechanism is that taller shrubs promote surface albedo decrease, followed by soil warming, which is evoked by shrub stems sticking out of the snow in spring (Lawrence & Swenson, 2011).

To assess changes in ecosystem properties after fire, such as successional pathways, we need a better understanding of the environmental factors that shape vegetation structure in the tundra ecosystem (Bjorkman *et al.*, 2018). An important tool to study successional pathways after fire are plant functional traits (Keeley *et al.*, 2011; Casals *et al.*, 2018), as they link plant physiology and environmental processes (Cornelissen & Makoto, 2014) and thus improve the understanding of global change impacts on tundra ecosystems (Myers-Smith *et al.*, 2019). Warming mobilizes belowground nutrient resources (Hobbie *et al.*, 2002) and enhances plant growth (Arft *et al.*, 1999; Bjorkman *et al.*, 2018). Local warming in the tundra biome can result in increasing height, specific leaf area (SLA) and decreasing leaf dry matter content (LDMC) (Bjorkman *et al.*, 2018). Whether such warming-induced principal growth effects on tundra vegetation can also be related to warmer soil conditions after fire, remains poorly understood, but is of great importance for future models estimating the effect of fire and climate change impacts on tundra ecosystems.

The impacts of fire on plant functional traits in the tundra has rarely been investigated. This is unfortunate, as a more comprehensive understanding of fire-plant trait interactions might provide insight into the drivers of changes in ecosystem properties. There is a general need

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for long-term studies on tundra fire effects (Liljedahl *et al.*, 2007; Jiang *et al.*, 2017), as ecosystem processes in the Arctic are rather slow (Dunbar, 1973; Dahl, 1975). There is also a substantial geographical bias: While almost all studies on tundra fires have been performed in Alaska (e.g. Racine *et al.*, 1987; Barrett *et al.*, 2012; Bret-Harte *et al.*, 2013), there is very little information for the extensive area of the Russian Arctic and tundra ecosystems, apart from few exceptions (e.g. Loranty *et al.*, 2014; Abdulmanova & Ektova, 2015).

Here we present the first comprehensive study on long-term effects of fires in tundra ecosystems in the north of Western Siberia. Using a space-for-time approach across a series of large burns (>44, 28 and 12 years old) we studied post-fire succession using vegetation structure and plant functional traits. We hypothesise that:

1. Fire has long-term effects on tundra vegetation structure: vascular plants on burnt plots will grow higher and have higher cover values, while lichens and bryophytes will grow smaller and have lower cover values.
2. Structural changes in vegetation induced by fire will increase soil temperatures and depth of the active layer.
3. Fire-related changes in soil temperature will lead to higher values in growth-related plant functional traits (mean aboveground cover, height, blade length, leaf thickness, SLA and LDMC).
4. Measurable fire effects on vegetation will weaken with years since fire.

2. Material and Methods

2.1. Study area

The study area is situated on the northern border of the forest tundra ecozone in Western Siberia within the Yamalo-Nenets Autonomous Okrug (Region) between the rivers Pur and Taz, north of the Arctic Circle (centre of the study area at 67° 1'19.59"N, 79° 1'53.53"E, total study area size ca. 70 km²). The region has a subarctic climate with a mean annual temperature of -8.1 °C, a mean January temperature of -26.2 °C and a mean July temperature of 14.4 °C (Kazakov, 2019). Annual precipitation amounts to 482 mm with a maximum in August. The vegetation period lasts from mid-June to early September (Kazakov, 2019). Our study area is situated in transition between the forest tundra to the south and the shrub tundra to the north (Yurkovskaya, 2011). Vegetation is dominated by reindeer lichens (mostly *Cladonia* spp.), and shrubs such as *Betula nana, Vaccinium uliginosum* and *Ledum palustre*.

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The largely open landscape is sparsely dotted with larch trees (*Larix sibirica)*. With the exception of depressions and small streams, the study region is well-drained and comparatively dry in comparison with other tundra areas. Soils are characterized as Crysols (IUSS Working Group WRB, 2015) developed in silty, loess-like parent material. Naturally, fires in the region are mainly induced by lightning (Kornienko, 2018). However, with a recent increase in transport and settlement infrastructure in the area (due to oil and gas exploitation) the number of human-induced fires has increased in recent years (Vilchek & Bykova, 1992; Mollicone *et al.*, 2006; Yu *et al.*, 2015).

2.2. Sampling design and data collection

We compared vegetation and environmental parameters at three large, non-overlapping burnt areas (fire scars) and adjacent unburnt control sites. Fire scars were selected opportunistically in an area that was accessible via tarmac roads, and based on the availability of scars of various age in close vicinity to facilitate efficient sampling. Fire scars were visually detectable by comparing annual Landsat images in Google Earth Timelapse (Gorelick *et al.*, 2017): areas appeared pale due to a high lichen cover in the year before the fire, but black (due to removed lichen cover) in the year of fire. Fire scars were easily distinguished from other features with similar spectral properties by their irregular shape, and the location of their borders that generally followed meandering water courses (where the moving flames were often stopped).

The youngest fire scar (542 ha) burnt in 2005, a medium-aged scar (ca. 12,500 ha) burnt in 1990, and an old scar (3,500 ha) was already present on the first satellite image we used (from Landsat 1) from 1973, downloaded via USGS earth explorer (band combination 7,5,4, to make it comparable to the timelapse tool). Field sampling took place in July 2017 (areas burnt before 1973 and in 2005) and July 2018 (area burnt in 1990). Time since fire was therefore 12, 28 and at least 44 years for the three scars. As the tundra ecosystem is rather stable with low inter-annual variability in environmental conditions (Dahl, 1975), the fact that data was collected in two subsequent years is not expected to bias the results considerably.

On each of the three fire scars, we selected 10 sampling locations along the fire border, which were located at least (300) 400-500 m from each other. At each location vegetation and environmental parameters were recorded at two plots of 10 x 10 m, one inside and one - as a reference - outside the burnt area. The plots of each pair were placed as close to each other

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as possible, but at least 100 m apart, because we always kept 50 m distance from the fire border to both sides to avoid edge effects.

On each plot, we estimated total vegetation cover, and the cover and growth height of different functional plant groups (lichens, bryophytes, herbs, grasses, dwarf shrubs, shrubs). For the most abundant dwarf shrub and shrub species, *Vaccinium uliginosum* L. and *Betula nana* L., we measured six functional plant traits that are related to plant growth (Hudson *et al.*, 2011; Perez-Harguindeguy *et al.*, 2016; Bjorkman *et al.*, 2018): Mean aboveground cover for plant individuals (calculated as: (*longest diameter + orthogonal diameter) / 2*), plant height, blade length, leaf thickness, specific leaf area (SLA) and leaf dry matter content (LDMC) (Suppl. 1). Apart from dry weights for SLA and LDMC, and leaf area, all measures were taken in the field. For SLA analysis, we placed at least four leaves per plant on an illuminated plate and took photographs in the field. We also considered two more species for trait sampling (*Petasites frigidus* and *Carex globularis*), which were infrequently found on the sample plots and are thus not considered in analyses.

On all plots, we measured soil temperature in 12 cm depth and active layer depth by using a thermometer and a metal stick. Both measurements were repeated five times per plot and the mean was calculated.

2.3. Statistical analysis

To test hypothesis 1 (fire has long-term effects on tundra vegetation structure) we subtracted the cover and trait values of the control plots from those of the paired plots within the fire area to obtain a difference. We then modelled the difference in vegetation cover and height between fire and control plots as a function of the vegetation recovery time (years since fire event) using linear mixed effects models in a Bayesian framework. Difference in cover and height were the response variables. Functional vegetation group and years since fire event were factorial explanatory variables. Both factors and their interaction were fitted as fixed effects. Plot was included as a random effect to account for the repeated sampling of vegetation groups on each plot. We used the R-package lme4 (Bates *et al.*, 2015). In the model with cover as dependent variable, the variance of the random factor was 0. Therefore, we excluded the random factor plot.

In order to obtain the posterior distributions, we used improper priors (Korner-Nievergelt *et al.*, 2015) and simulated 2000 values from the joint posterior distribution using the sim function from the R-packages arm (Gelman & Su, 2007) and the package blmeco (Korner-

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Nievergelt *et al.*, 2015). We present the mean values and the 95% credible interval (CrI) of the simulated posterior distribution. We calculated the posterior probabilities of the hypothesis 1 being true by using the proportion of simulated values of the posterior distribution being > 0 and based our conclusions on those values.

For testing hypothesis 2 (structural changes in vegetation induced by fire will increase soil temperatures and depth of the active layer) we subtracted the soil temperature and active layer depth values of the control plots from the paired plots within the fire area. Afterwards, we fitted linear mixed effects models with difference in soil temperature and difference in active layer depth as dependent numeric variables and years since fire event as independent variable. Plot was considered as random effect. We calculated the posterior probabilities of the hypothesis 2 as described above in the analysis for hypothesis 1.

Hypothesis 3 (fire-related changes in soil temperature will lead to higher values in growth-related plant functional traits) was tested by modelling the differences in six different plant traits between the fire and control plot as a function of time since fire, for *V. uliginosum* and *B. nana*. We used linear mixed effects models with difference in trait value (traits: mean aboveground cover, plant height, blade length, leaf thickness, SLA, LDMC) as dependent variable, species and years since fire event and their interaction as fixed effects, and plot as random effect. The posterior probabilities were calculated as described before.

For testing the hypothesis 4 (measurable fire effects on vegetation will weaken with years since fire) we repeated the analysis that was used to test hypothesis 1 and 3 but with the years since fire as a continuous independent variable. We calculated the posterior probabilities of the model used to test hypothesis 4 by using the proportion of simulated values of the posterior distribution for the slopes being > 0. We could not date the oldest fire event exactly as no satellite images from the years prior to 1973 were available. We therefore performed a sensitivity analysis. We re-run the model to test hypothesis 4 (Scenario1) assuming that the oldest fire scar was created 100 years ago (instead of 44 as in the models above) (Scenario2) and compared the results.

To separate direct and indirect effects of fire on vegetation and soil properties, we used a piece-wise structural equation model (SEM) implemented in the piecewiseSEM-package in R (Lefcheck *et al.*, 2016). This approach can be used for a relatively small sample sizes and allows to correct for spatial autocorrelation by including random factors (Lefcheck, 2016). We focused on the plant traits of the dominating shrub species, *B. nana*. As we included fire plots

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as well as control plots, we could not use the variable Years since fire event, but included the variable Fire instead (two levels: burnt/unburnt). Variables that were included in the initial multilevel model were chosen based on the results of the regression analyses described above, and based on relationships between ecosystem compartments from the literature (see introduction). SEMs contain multiple predictor and response variables, organized in component models. Each component model of the initial multilevel model was set up by a linear mixed effects model with pair (paired plots) nested in site (sites of the three different fire events) as random factor using the nlme-function in package nlme in R (Pinheiro *et al.*, 2018). All component models were added to a list and a piece-wise SEM was fitted. The initial multilevel model included nine response variables (Suppl. 2). We reduced the number of variables of the initial model via stepwise backward selection to obtain a smaller and more robust final model by using the sample size-corrected Akaike information criterion (AIC_C) and the Bayesian information criterion (BIC) together, excluding variables from the initial model until both, AIC_C and BIC, stopped improving (Suppl. 3).

Model assumptions for all described analyses were graphically assessed with Tukey-Anscombe- and QQ-plots. All statistical analyses were performed in R, Version 3.5.3 (R Core Team, 2019). The following R-packages were used for creating the figures: ggplot2 (Wickham, 2009) and cowplot (Wilke, 2019).

3. Results

3.1. Influence of fire on soil temperature and active layer depth

Fire strongly influenced soil temperature and active layer depth. Twelve and 28 years after the event, burnt plots showed a higher soil temperature and a deeper active layer than control plots, so that hypothesis 2 (structural changes in vegetation induced by fire will increase soil temperatures and depth of the active layer) was accepted (Fig. 1, Table 1). Four decades after fire, the differences were no longer apparent, indicating that soil temperatures and active layer depth have returned to levels comparable with unburned plots.

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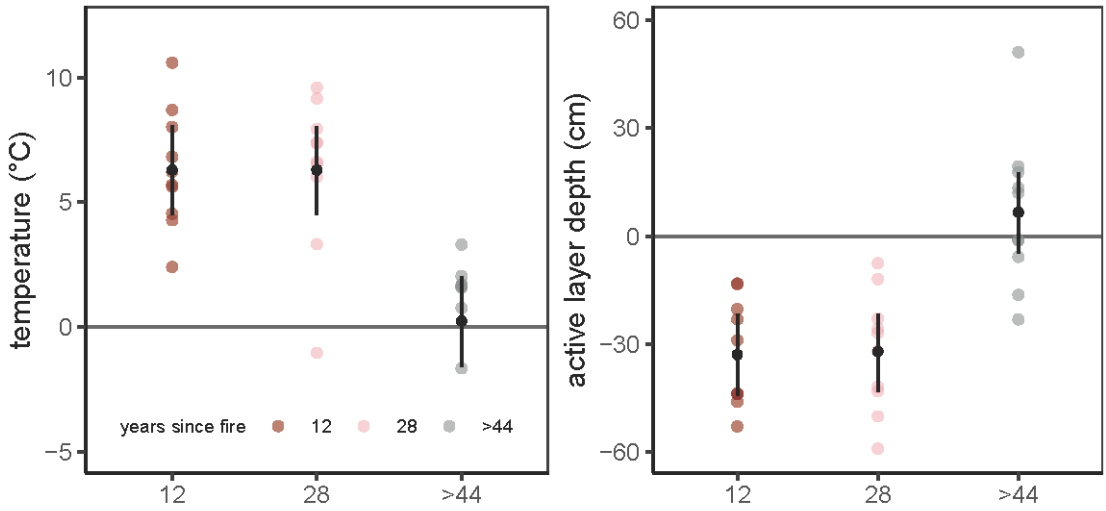

Fig. 1: Difference in soil temperature (12 cm depth) and active layer depth 12, 28 and >44 years since fire. Difference = value on burnt plot minus value on control plot. Coloured dots are differences calculated from the raw data, black dots are predicted mean values and lines 95% credible intervals (CrIs). CrIs not overlapping zero imply a consistent difference between burnt and control plots.

3.2. Influence of fire on vegetation cover and height

Lichen cover was found to be generally lower on burnt plots compared to unburnt plots, while bryophyte cover was higher (Fig. 2, Table 2). Those relationships were also found more than 44 years after fire. Lichen cover was 55% lower on burnt plots, even four decades after fire. The cover of shrubs and dwarf shrubs was similar on burnt and unburnt plots 12 years since fire. Twenty-eight years since fire, dwarf shrub and shrub cover were higher on burnt plots. Thus, hypothesis 1 (fire has long-term effects on tundra vegetation structure: vascular plants on burnt plots will grow higher and have higher cover values, while lichens and bryophytes will grow smaller and have lower cover values) was confirmed for lichens, grasses, dwarf shrubs and shrubs, but not for bryophytes and herbs.

Vegetation height was also influenced by fire: shrubs were found to be taller on sites that burnt 28 and >44 years ago and the height of the lichen carpet was predicted to be lower on burnt compared to unburnt plots. The effect on lichen height was no longer evident four decades after fire.

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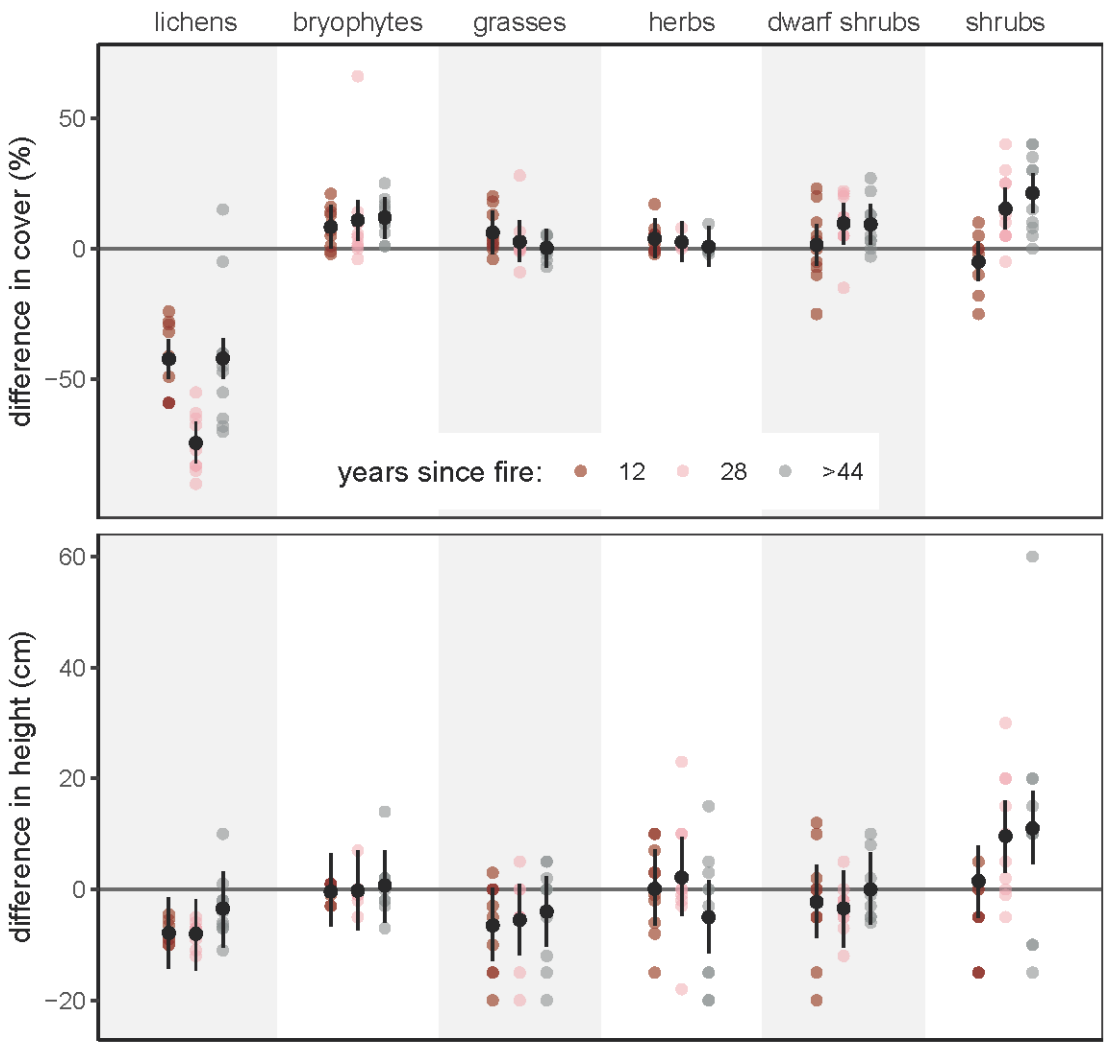

Fig. 2: Differences in cover and height for plant functional groups, 12, 28 and > 44 years since fire. Difference = value on burnt plot minus value on control plot. Coloured dots are differences calculated from the raw data, black dots are predicted mean values and lines 95% credible intervals CrIs). CrIs not overlapping zero imply a consistent difference between burnt and control plots.

3.3. Influence of fire on plant traits

Trait values of the dwarf shrub species *V. uliginosum* did not differ strongly between burnt and unburnt plots in contrast to our hypothesis. However, for the shrub species *B. nana* there was strong evidence for the long-term impact of fire on traits (Fig. 3, Table 3), like hypothesized. In this species, the mean aboveground cover was bigger on burnt plots compared to control plots. A similar pattern was found for height, blade length and SLA, which all exhibited much higher values on plots that burnt 44 years ago than on control plots and

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hypothesis 3 (fire-related changes in soil temperature will lead to higher values in growth-related plant functional traits) was partly accepted.

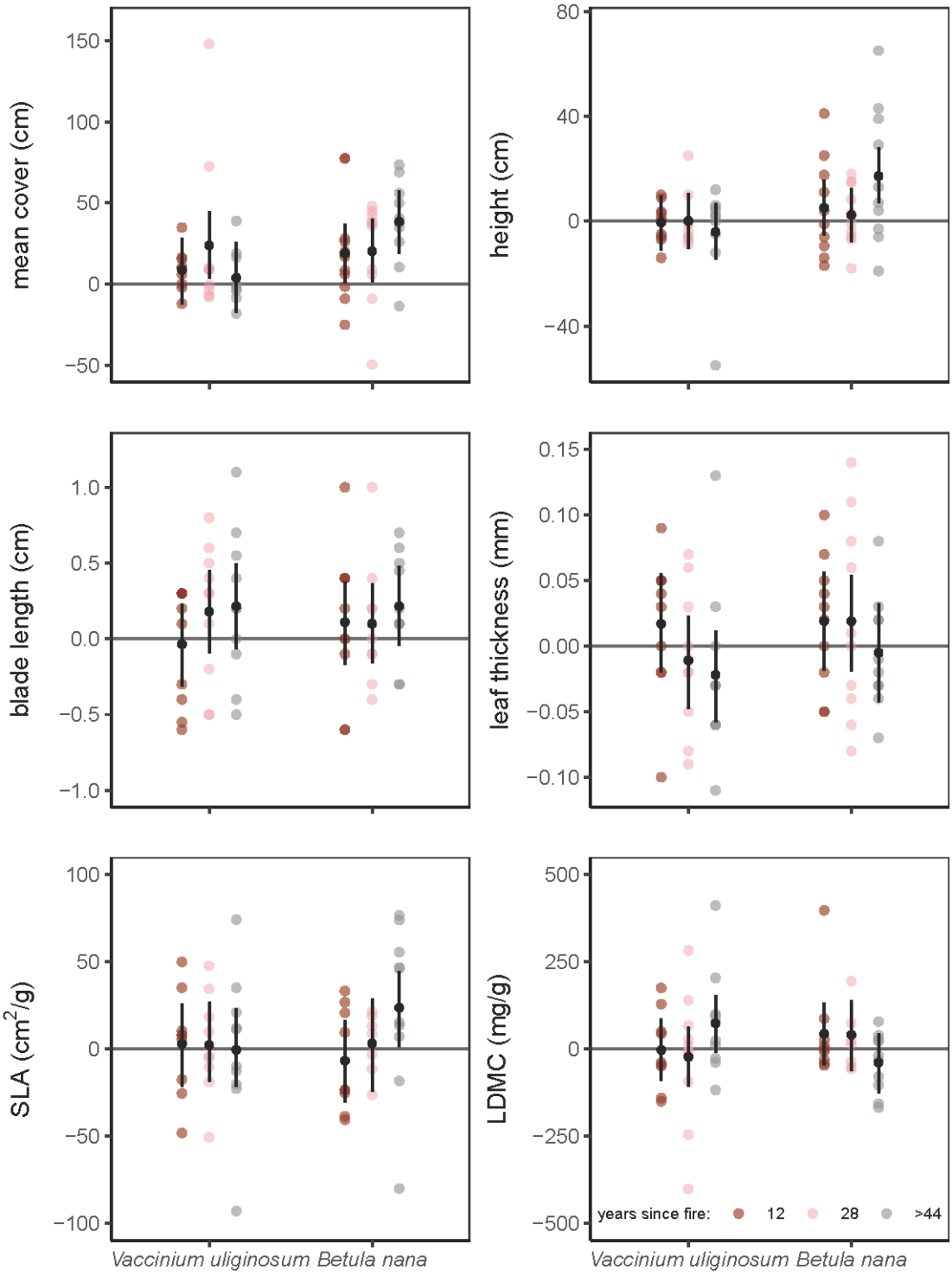

Fig. 3: Difference in functional plant traits of the shrub species *B. nana* and the dwarf shrub *V. uliginosum*, 12, 28 and >44 years since fire. Difference in functional plant trait = plant trait on burnt plot minus plant trait on control plot. Coloured dots are differences calculated from the

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raw data, black dots are predicted mean values and lines 95% credible intervals CrIs). CrIs not overlapping zero imply a consistent difference between burnt and control plots.

3.4 Vegetation recovery with time since fire

The difference in shrub cover and height between burnt and unburnt plots increased with increasing time since fire. The results were robust regarding uncertainty in the time of the oldest fire, as model results for both scenarios, 44 and 100 years since the last fire, suggested a steep increase of shrub cover and height (Fig. 4, Table 4). Therefore, hypothesis 4 (measurable fire effects on vegetation will weaken with years since fire) was accepted for cover and height of shrubs as well as for mean cover and SLA of *B. nana* individuals. We found mean aboveground cover and SLA to increase in difference with years since fire for *B. nana*, while differences for other traits and *V. uligonosum* showed no consistent increase or decrease. Those results were also robust regarding uncertainty in the year the oldest fire burnt (Fig. 4, Table 5).

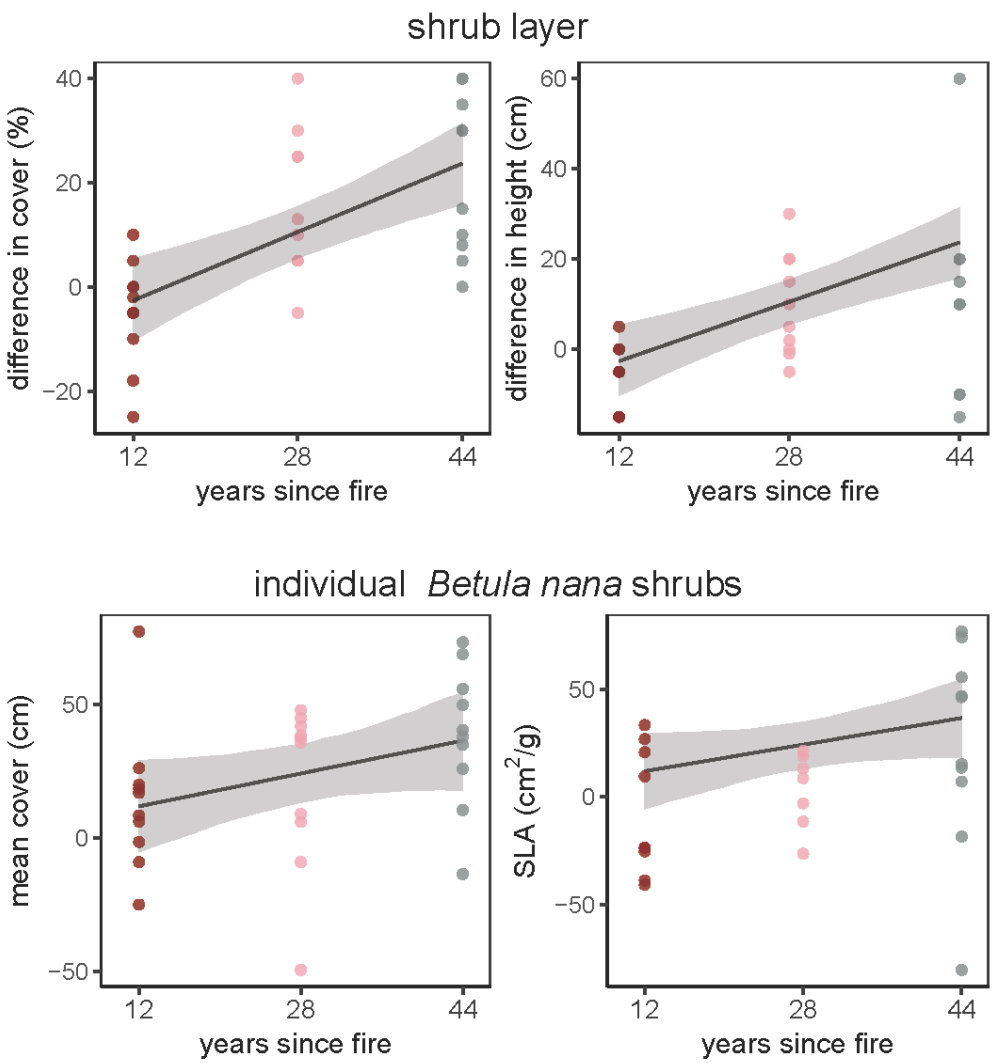

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Fig. 4: Predicted slope in functional plant traits (black line) with 95% CrI of the shrub layer and of plant traits of the species *B. nana* dependent on years since fire. Difference = value on burnt plot minus value on control plot. Coloured dots are differences calculated from the raw data.

3.5 Direct and indirect fire effects

Fire not only directly, but also indirectly affected soil and vegetation parameters. The final SEM contained six response variables and three predictor variables (Fig. 5). The global goodness of fit of the final model was Fisher's C = 34.0, P = 0.13 with 26 degrees of freedom (Suppl. 3). Fire had positive direct effects on soil temperature and plant traits of the shrub species *B. nana* and negative effects on total vegetation cover. Vegetation cover in turn negatively influenced soil temperature. While active layer depth was strongly positively influenced by soil temperature, there was no direct effect of fire or vegetation cover on active layer depth. Plant height of *B. nana* was negatively affected by higher soil temperature.

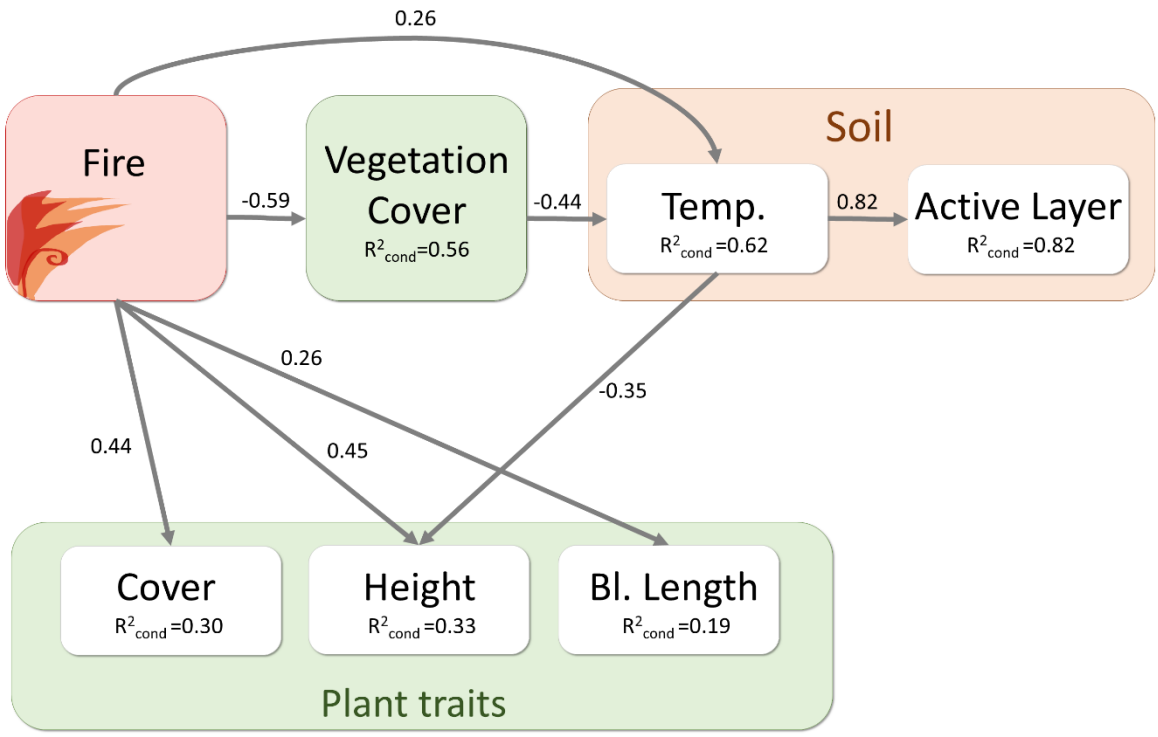

Fig. 5: Structural equation model showing direct and indirect effects of fire on the tundra ecosystem. Boxes represent included variables. Arrows with standardized estimates show the relationships between those variables.

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4. Discussion

Long-term fire impacts on soil temperature and active layer depth

Fire had strong impacts on soil temperature and active layer depth. Similar results were found in previous studies (Rocha *et al.*, 2012; Bret-Harte *et al.*, 2013; Narita *et al.*, 2015). Twelve and 28 years since fire, soil temperature was higher on burnt areas and the active layer reached deeper in comparison to unburnt areas, probably because of the missing insulating lichen cover, a lower albedo and a changed soil thermal conductivity regime (Jiang *et al.*, 2015). The increase of summer soil temperatures after fire has been described in previous studies for tundra soils (Chambers *et al.*, 2005; Jiang *et al.*, 2015) and is followed by permafrost thawing as well as an increase in active layer depth and can even lead to permafrost degradation (Jones *et al.*, 2015).

Soil temperature and active layer depth recovered several decades after fire to control plot levels. This finding confirms results for the Arctic tundra in Alaska, where the albedo was lower on a recently burnt area but gained again pre-fire levels after four to ten years (Rocha *et al.*, 2012; French *et al.*, 2016). This mechanism is probably the result of a restored vegetation cover (Narita *et al.*, 2015; Michaelides *et al.*, 2018), with a different composition regarding plant groups but a dense cover and similar albedo. During this process, organic material accumulates on the soil surface and soil temperatures as well as active layer depth can return to pre-fire levels (Michaelides *et al.*, 2018).

Long-term fire influence on vegetation

Fire had strong effects on tundra vegetation and even after more than 44 years since fire, vegetation on burned plots was far from being close to the vegetation at unburnt control plots. Long-term fire effects strongly influenced vegetation patterns: while lichens were negatively affected, shrubs generally benefited through enhanced growth. The long-lasting effects of fire on lichens might be driven by limited re-colonisation abilities in this group. As fire completely destroys all lichen biomass (Jandt *et al.*, 2008), re-establishment of lichens requires new establishment via dispersal. The most common species in the area, *Cladonia stellaris* and *Cladonia rangiferina*, disperse mainly through thallus fragments (Webb, 1998) and unless transferred by animals, the dispersal distances of lichens, growing on the ground, are relatively short (Heinken, 1999). The recovery of lichens on burnt areas is also affected by environmental conditions (Abdulmanova, 2010). An important factor is the substrate: fires on sandy substrate can burnout soil layers and make a primary succession inevitable, while more humid

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conditions with active peat formation lead to a preservation of lichen fragments and thus to a faster recovery (Abdulmanova, 2010). Additionally, the recovery of lichens can be influenced by vegetation, e.g. by shading shrubs, which hamper the establishment (Lambert & Maycock, 1968; Walker *et al.*, 2006). While lichens were limited in reaching pre-burn cover in our study, once established they grew generally well regarding thallus height on the burned sites and after four decades, lichen height on burnt plots reached nearly same mean values as on control plots. This is in line with the findings of Abudulmanova and Ektova (2015) who observed an increasing growth rate of *Cladonia* species with increasing time after fire.

Negative fire impacts on lichens are expected to interact with climate change effects, as climate change and fires induce favourable conditions for vascular plants and change fire frequency, leading to a reduction of total lichen cover in Arctic regions (Jandt *et al.*, 2008; Joly *et al.*, 2009). A depleted lichen cover after fire is often regarded as a problem for reindeer grazing, as animals do not find enough food during winter if extended areas of their forage range burnt (Viereck & Schandelmeier, 1980). Caribous avoid burnt tundra for more than a half century (Joly *et al.*, 2009). A general decline in lichens thus represents a threat for indigenous and rural people who depend on reindeer and caribou herds (Joly *et al.*, 2009).

In contrast to lichens, bryophytes benefited from fire in our study. Bryophytes are often the first plants that colonize burnt areas (Ryömä & Laaka-Lindberg, 2005), possibly because they establish from spores buried in the soil or colonize the area via aerial dispersal (Clymo & Duckett, 1986; Ross-Davis & Frego, 2004; Ryömä & Laaka-Lindberg, 2005; Hylander & Johnson, 2010). In Alaskan tundra ecosystems, bryophytes were found to take over bare ground after fire (Racine, 1981; Racine, Johnson, & Viereck, 1987), but one study reports that bryophytes cover decreased about five years since fire as vascular plant species recolonized (Racine et al., 1987). In our study, grasses or herbs did not dominate the vegetation after fire and thus, bryophytes could possibly benefit from overall low competition within vegetation on burnt areas.

Fire did not affect the cover of herbs and grasses on a longer time scale. This is surprising, as many studies report an increased cover of these functional types after a tundra fire event (Wein & Bliss, 1973; Racine *et al.*, 1987; Jones *et al.*, 2013; Narita *et al.*, 2015). One possible reason for this discrepancy might be the time-scale. Most studies collected data only in short periods since fire, and reported increased cover of grasses in the first years since fire (Wein & Bliss, 1973; Racine *et al.*, 1987). We did find an increase in grass height twelve years after the

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fire, but the differences between burnt and control plots later disappeared, a pattern that could not be found by other studies because of a shorter research period. Additionally, tundra is a highly heterogeneous habitat comprising many vegetation types. While we worked in rather dry tundra dominated by lichens, other studies focused on more moist or even boggy tundra with a higher dominance of grasses, for example in wet tussock tundra (Jones *et al.*, 2013; Narita *et al.*, 2015). The habitat type likely affects the post-fire recovery trajectory.

Shrubs benefited from fire, but the effect was detectable only after several decades. Twelve years after fire, shrub cover and height did not differ between burnt and control plots, in the older fire scars cover and height increased, and the pattern was more pronounced with increasing time since fire. Arctic shrubs generally benefit from fire (Racine *et al.*, 2004; Jandt *et al.*, 2008), which probably reinforces shrub encroachment (which is also caused by other global change-related processes) and significantly changes ecosystem functioning (Hallinger *et al.*, 2010; Myers-Smith *et al.*, 2011; Lantz *et al.*, 2013). This stays in contrast to other ecosystems such as savannahs or grasslands where fire can prevent shrub expansion (Naito & Cairns, 2011).

Fire can enhance shrub encroachment by two mechanisms. First, fire clears vegetation and thus, shrubs can better germinate and establish (Gough, 2006). Second, fire promotes re-growth of shrubs from parts that survived the fire, for example rhizomes (de Groot & Wein, 2004). While we do not have any information on seedling establishment, we documented a positive fire impact on growth-related traits, which indicates enhanced growth. Specifically individual plant cover and height as well as SLA in *B. nana*, the dominating vascular plant species of the tundra in our study region, increased. A similar pattern was shown for alder shrubs (*Alnus viridis subsp. fruticosa*) at the border between subarctic and Arctic (Lantz *et al.*, 2010).

The positive effect of fire on shrub growth is likely mediated via increased summer temperature, availability of nutrients and other ecological factors that change after fire (Chapin, 1983; Chambers *et al.*, 2005; Walker *et al.*, 2006; Myers-Smith *et al.*, 2015; Li *et al.*, 2016). High summer temperatures generally enhance photosynthesis, nutrient absorption and prolong the vegetation period (Chapin, 1983; Nielsen *et al.*, 2017). Higher temperatures additionally increase nutrient mineralization in the soil, making them better available for plants and thus, enhancing growth (Rustad *et al.*, 2001). While these factors affect all plants, *B. nana* poses further mechanisms that allow the species to benefit from post-fire elevated

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temperatures. This species can modify its physiology and develop bigger vessels that allow more efficient water transport (Nielsen *et al.*, 2017), and, in contrast to other tundra plants, use mycorrhiza to transfer belowground carbon (Deslippe & Simard, 2011). As a result, *B. nana* showed higher vertical growth and higher SLA, indicating increased nutrient availability (Kummerow *et al.*, 1987; Shaver *et al.*, 2001) on burnt plots.

The enhanced shrub growth and increased nutrient availability (as indicated by SLA) persisted over several decades, despite the active layer depth and soil temperatures returned to similar levels as in unburnt plots. This illustrates a strong fire legacy effect in shrub growth, possibly because individual shrub plants on burnt plots gained growth advantage over shrub plants on control plots during the time-limited phase when soil temperatures were higher and active layer deeper. The growth advantage remains also after the soil thermal regime went back to normal levels and shrubs on burnt plots grow with same progress as shrubs on control plots.

Interacting fire effects

Indirect fire effects on vegetation and soil play an important role in ecosystem dynamics and are sometimes even stronger than direct fire impacts on ecosystem components. We could show this for the active layer depth, which was strongly influenced by soil temperature. Regarding the impact of soil temperature on plant traits, our structural equation model could not capture the relationship (expected positive influence of soil temperature on plant traits) correctly. The fire legacy effect on shrub growth revealed that current shrub measures of traits may not mainly be related to the current soil temperature, but to soil temperatures years and decades ago. This relationship can thus explain the discrepancy between our model results regarding this path and our expectations following literature and emphasizes the importance of historical processes in regard to current ecosystem properties (Rhemtulla & Mladenoff, 2007).

Conclusions

The impacts of tundra fires on soil and vegetation are still visible after several decades. While soil thermal aspects seem to recover within decades, it is not clear, how long vegetation recovery takes, and whether it will recover to pre-fire levels at all.

A clear winner of tundra fires in Western Siberia is the shrub species *B. nana*, which shows enhanced growth of individual plants after burning. Whereas the active layer and soil temperatures returned to levels comparable with unburned plots after 44 years, we found shrubs to grow further. This indicates a strong fire legacy effect, with far reaching impacts on

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the whole ecosystem. Through higher shrub cover, an alteration in decomposition patterns is probable (McLaren *et al.*, 2017) and the changing fire regime in Arctic regions might be influenced as well.

With a space for time approach, we could unravel fire impacts on the soil thermal regime and vegetation and show connections between fire effects and plant traits. For a further understanding of links between ecosystem processes and fire impacts, more studies across the entire and so far largely unexplored northern Eurasian tundra belt are essential.

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Author Contributions

NH and RJH developed the idea and designed the study. AY, DR and RJH carried out the field work. RJH analysed the data with significant input of AB, JK and NH. RJH wrote the paper with considerable contributions of co-authors. All authors participated in the discussion regarding the results and contributed to the final version of the manuscript.

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References

Aaltonen H, Palviainen M, Zhou X, Köster E, Berninger F, Pumpanen J, Köster K. **2019**. Temperature sensitivity of soil organic matter decomposition after forest fire in Canadian permafrost region. *Journal of environmental management* **241**: 637–644.

Abdulmanova SY. **2010**. Zonal'nyye osobennosti dinamiki vidovogo sostava lishaynikov v khode pirogennykh suktsessyi [Zonal features of dynamics of species composition of lichens during pyrogenic successions]. *Ekologiya ot yuzhnykh gor do severnykh morey [Ecology from the southern mountains to the northern seas]*: 7–15.

Abdulmanova SU, Ektova SN. **2015**. Variations in the growth rate of Cladonia lichens during long-term postfire successions in the north of West Siberia. *Contemporary Problems of Ecology* **8**: 326–336.

Amos J. **2019**. *Arctic wildfires: How bad are they and what caused them?* BBC, [WWW document] URL https://www.bbc.com/news/world-europe-49125391?intlink_from_url=https://www.bbc.com/news/topics/ce2gz9mdde3t/wildfires&link_location=live-reporting-story. [accessed 2 August 2019].

Archibald S, Lehmann CER, Gómez-dans JL, Bradstock RA. **2013**. Defining pyromes and global syndromes of fire regimes. *Proceedings of the National Academy of Sciences of the United States of America* **110**: 6445–6447.

Arefiev SP. **2016**. The reaction of trees and shrubs in the eastern part of the Tazovsky Peninsula to climate warming. *Ecological monitoring and biodiversity*: 5–9 (in Russian).

Arft AM, Walker MD, Gurevitch J et al, Alatalo JM, Bret-Harte MS, Dale M, Diemer M, Gugerli F, Henry GHR, Jones MH. **1999**. Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. *Ecological Monographs* **69**: 491–511.

Baets S De, Weg MJ Van De, Lewis R, Steinberg N, Meersmans J, Quine TA, Shaver GR, Hartley IP. **2016**. Soil Biology & Biochemistry Investigating the controls on soil organic matter decomposition in tussock tundra soil and permafrost after fi re. *Soil Biology and Biochemistry* **99**: 108–116.

Barrett K, Rocha A, Van De Weg MJ, Shaver G. **2012**. Vegetation shifts observed in arctic tundra 17 years after fire. *Remote Sensing Letters* **3**: 729–736.

Bates D, Maechler M, Bolker B, Walker S. **2015**. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* **67**: 1–48.

bioRxiv preprint doi: https://doi.org/10.1101/756163; this version posted September 5, 2019. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Bjorkman AD, Myers-Smith IH, Elmendorf SC, Normand S, Rüger N, Beck PSA, Blach-Overgaard A, Blok D, Cornelissen JHC, Forbes BC. **2018**. Plant functional trait change across a warming tundra biome. *Nature* **562**: 57.

Bliss LC, Wein RW. **1972**. Plant community responses to disturbances in the western Canadian Arctic. *Canadian Journal of Botany* **50**: 1097–1109.

Bond W, Keeley J. **2005**. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution* **20**: 387–394.

Bond WJ, Woodward FI, Midgley GF. **2005**. The global distribution of ecosystems in a world without fire. *New Phytologist* **165**: 525–538.

Bowman DMJS, Bowman DMJS, Balch JK, Artaxo P, Bond WJ, Carlson JM, Cochrane MA, Antonio CMD, Defries RS, Doyle JC, *et al.* 2009. Fire in the earth system. *Science* **324**: 481–484.

Bret-Harte MS, Mack MC, Shaver GR, Huebner DC, Johnston M, Mojica CA, Pizano C, Reiskind JA. **2013**. The response of Arctic vegetation and soils following an unusually severe tundra fire. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **368**: 20120490.

Casals P, Valor T, Rios AI, Shipley B. **2018**. Leaf and bark functional traits predict resprouting strategies of understory woody species after prescribed fires. *Forest Ecology and Management* **429**: 158–174.

Chambers SD, Beringer J, Randerson JT, Chapin IS. **2005**. Fire effects on net radiation and energy partitioning: Contrasting responses of tundra and boreal forest ecosystems. *Journal of Geophysical Research D: Atmospheres* **110**: 1–9.

Chapin FS. **1983**. Direct and indirect effects of temperature on arctic plants. *Polar Biology* **2**: 47–52.

Clymo RS, Duckett JG. **1986**. Regeneration of Sphagnum. *New phytologist* **102**: 589–614.

Cornelissen JHC, Makoto K. **2014**. Winter climate change, plant traits and nutrient and carbon cycling in cold biomes. *Ecological Research* **29**: 517–527.

Dahl E. **1975**. Stability of tundra ecosystems in Fennoscandia. In: Fennoscandian tundra ecosystems. Springer, 231–236.

Deslippe JR, Simard SW. **2011**. Below-ground carbon transfer among Betula nana may increase with warming in Arctic tundra. *New Phytologist* **192**: 689–698.

Dunbar MJ. **1973**. Stability and fragility in arctic ecosystems. *Arctic* **26**: 179–185.

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Ektova SN, Morozova LM. **2015**. Rate of recovery of lichen-dominated tundra vegetation after overgrazing at the Yamal Peninsula (Short Communication). *Czech Polar Reports* **5**: 27–32.

Flannigan MD, Krawchuk MA, de Groot WJ, Wotton BM, Gowman LM. **2009**. Implications of changing climate for global wildland fire. *International journal of wildland fire* **18**: 483–507.

French NHF, Whitley MA, Jenkins LK. **2016**. Fire disturbance effects on land surface albedo in Alaskan tundra. *Journal of Geophysical Research: Biogeosciences* **121**: 841–854.

Gelman A, Su Y-S. **2007**. arm: Data Analysis Using Regression and Multilevel/Hierarchical Models. R package version 1.10-1. *URL https://CRAN.R-project.org/package=arm*.

Gorelick N, Hancher M, Dixon M, Ilyushchenko S, Thau D, Moore R. **2017**. Google Earth Engine: Planetary-scale geospatial analysis for everyone. *Remote Sensing of Environment* **202**: 18–27.

Gough L. **2006**. Neighbor effects on germination, survival, and growth in two arctic tundra plant communities. *Ecography* **29**: 44–56.

de Groot WJ, Wein RW. **2004**. Effects of fire severity and season of burn on Betula glandulosa growth dynamics. *International Journal of Wildland Fire* **13**: 287–295.

Hallinger M, Manthey M, Wilmking M. **2010**. Establishing a missing link: warm summers and winter snow cover promote shrub expansion into alpine tundra in Scandinavia. *New Phytologist* **186**: 890–899.

Heinken T. **1999**. Dispersal patterns of terricolous lichens by thallus fragments. *The Lichenologist* **31**: 603–612.

Higuera PE, Brubaker LB, Anderson PM, Brown TA, Kennedy AT, Hu FS. **2008**. Frequent fires in ancient shrub tundra: Implications of paleorecords for arctic environmental change. *PLoS ONE* **3**: 1–7.

Higuera PE, Brubaker LB, Anderson PM, Hu FS, Brown TA. **2009**. Vegetation mediated the impacts of postglacial climate change on fire regimes in the south-central Brooks Range, Alaska. *Ecological Monographs* **79**: 201–219.

Higuera PE, Chipman ML, Barnes JL, Urban MA, Hu FS. **2011**. Variability of tundra fire regimes in Arctic Alaska: Millennial-scale patterns and ecological implications. *Ecological Applications* **21**: 3211–3226.

Hobbie SE, Nadelhoffer KJ, Högberg P. **2002**. A synthesis: the role of nutrients as constraints on carbon balances in boreal and arctic regions. *Plant and Soil* **242**: 163–170.

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Hu FS, Higuera PE, Duffy P, Chipman ML, Rocha A V., Young AM, Kelly R, Dietze MC. **2015**. Arctic tundra fires: Natural variability and responses to climate change. *Frontiers in Ecology and the Environment* **13**: 369–377.

Hudson JMG, Henry GHR, Cornwell WK. **2011**. Taller and larger: Shifts in Arctic tundra leaf traits after 16 years of experimental warming. *Global Change Biology* **17**: 1013–1021.

Hylander K, Johnson S. **2010**. In situ survival of forest bryophytes in small-scale refugia after an intense forest fire. *Journal of Vegetation Science* **21**: 1099–1109.

IUSS Working Group WRB. **2015**. *World Reference Base for Soil Resources 2014, update 2015 International soil classification system for naming soils and creating legends for soil maps. World Soil Resources Reports No. 106.* Rome: FAO.

Jandt R, Joly K, Meyers CR, Racine C. **2008**. Slow Recovery of Lichen on Burned Caribou Winter Range in Alaska Tundra: Potential Influences of Climate Warming and Other Disturbance Factors. *Arctic, Antarctic, and Alpine Research* **40**: 89–95.

Jiang Y, Rastetter EB, Shaver GR, Rocha A V., Zhuang Q, Kwiatkowski BL. **2017**. Modeling long-term changes in tundra carbon balance following wildfire, climate change, and potential nutrient addition: *Ecological Applications* **27**: 105–117.

Jiang Y, Rocha A V, O'Donnell JA, Drysdale JA, Rastetter EB, Shaver GR, Zhuang Q. **2015**. Contrasting soil thermal responses to fire in Alaskan tundra and boreal forest. *Journal of Geophysical Research: Earth Surface* **120**: 363–378.

Johansson M, Callaghan T V, Bosiö J, Åkerman HJ, Jackowicz-Korczynski M, Christensen TR. **2013**. Rapid responses of permafrost and vegetation to experimentally increased snow cover in sub-arctic Sweden. *Environmental Research Letters* **8**: 35025.

Joly K, Jandt RR, Klein DR. **2009**. Decrease of lichens in Arctic ecosystems: The role of wildfire, caribou, reindeer, competition and climate in north-western Alaska. *Polar Research* **28**: 433–442.

Jones BM, Breen AL, Gaglioti B V, Mann DH, Rocha A V, Grosse G, Arp CD, Kunz ML, Walker DA. **2013**. Identification of unrecognized tundra fire events on the north slope of Alaska. *Journal of Geophysical Research: Biogeosciences* **118**: 1334–1344.

Jones BM, Grosse G, Arp CD, Miller E, Liu L, Hayes DJ, Larsen CF. **2015**. Recent Arctic tundra fire initiates widespread thermokarst development. *Scientific Reports* **5**: 1–13.

Kazakov K. **2019**. *Spravochno-informatsionnyy portal 'Pogoda i klimat' [Reference information portal 'Weather and Climate']*. [WWW document] URL

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http://www.pogodaiklimat.ru/msummary.php?m=all&y=all&id=23256. [accessed 2 May 2019].

Keeley JE, Pausas JG, Rundel PW, Bond WJ, Bradstock RA. **2011**. Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science* **16**: 406–411.

Korner-Nievergelt F, Roth T, Felten S Von, Guelat J, Almasi B, Korner-Nievergelt P. **2015**. *Bayesian Data Analysis in Ecology using Linear Models with R, BUGS and Stan*. London: Elsevier.

Kornienko SG. **2018**. Cartography of pyrogenic violations of the vegetation cover on the Tazovsky Peninsula with satellite data. *Actual problems of oil and gas* **1**: 1–11.

Kummerow J, Mills JN, Ellis BA, Hastings SJ, Kummerow A. **1987**. Downslope fertilizer movement in arctic tussock tundra. *Ecography* **10**: 312–319.

Lambert JDH, Maycock PF. **1968**. The ecology of terricolous lichens of the northern conifer–hardwood forests of central Eastern Canada. *Canadian Journal of Botany* **46**: 1043–1078.

Landhausser SM, Wein RW. **1993**. Postfire Vegetation Recovery and Tree Establishment at the Arctic Treeline: Climate-Change-Vegetation-Response Hypotheses. *Journal of Ecology* **81**: 665–672.

Lantz TC, Gergel SE, Henry GHR. **2010**. Response of green alder (Alnus viridis subsp. fruticosa) patch dynamics and plant community composition to fire and regional temperature in north-western Canada. *Journal of Biogeography* **37**: 1597–1610.

Lantz TC, Marsh P, Kokelj S V. **2013**. Recent shrub proliferation in the Mackenzie Delta uplands and microclimatic implications. *Ecosystems* **16**: 47–59.

Lawrence DM, Swenson SC. **2011**. Permafrost response to increasing Arctic shrub abundance depends on the relative influence of shrubs on local soil cooling versus large-scale climate warming. *Environmental Research Letters* **6**: 45504.

Lefcheck JS. **2016**. piecewiseSEM: Piecewise structural equation modeling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution* **7**: 573–579.

Lefcheck JS, Byrnes J, Grace J. **2016**. Package 'piecewiseSEM'. *R package version* **1**.

Li B, Heijmans MMPD, Berendse F, Blok D, Maximov T, Sass-Klaassen U. **2016**. The role of summer precipitation and summer temperature in establishment and growth of dwarf shrub Betula nana in northeast Siberian tundra. *Polar Biology* **39**: 1245–1255.

Liljedahl A, Hinzman L, Busey R, Yoshikawa K. **2007**. Physical short-term changes after a tussock tundra fire, Seward Peninsula, Alaska. *Journal of Geophysical Research: Earth Surface*

bioRxiv preprint doi: https://doi.org/10.1101/756163; this version posted September 5, 2019. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

112.

Loranty MM, Natali SM, Berner LT, Goetz SJ, Holmes RM, Davydov SP, Zimov NS, Zimov SA. **2014**. Siberian tundra ecosystem vegetation and carbon stocks four decades after wildfire. *Journal of Geophysical Research: Biogeosciences* **119**: 2144–2154.

Masrur A, Petrov AN, DeGroote J. **2018**. Circumpolar spatio-temporal patterns and contributing climatic factors of wildfire activity in the Arctic tundra from 2001–2015. *Environmental Research Letters* **13**: 14019.

McLaren JR, Buckeridge KM, van de Weg MJ, Shaver GR, Schimel JP, Gough L. **2017**. Shrub encroachment in Arctic tundra: Betula nana effects on above-and belowground litter decomposition. *Ecology* **98**: 1361–1376.

Michaelides R, Schaefer K, Zebker H, Parsekian A, Liu L, Chen J, Natali SM, Ludwig S, Schaefer S. **2018**. Inference of the impact of wildfire on permafrost and active layer thickness in a discontinuous permafrost region using the remotely sensed active layer thickness (ReSALT) algorithm. *Environmental Research Letters*.

Mollicone D, Eva HD, Achard F. **2006**. Ecology: Human role in Russian wild fires. *Nature* **440**: 436.

Moritz MA, Parisien M-A, Batllori E, Krawchuk MA, Van Dorn J, Ganz DJ, Hayhoe K. **2012**. Climate change and disruptions to global fire activity. *Ecosphere* **3**: 1–22.

Myers-Smith IH, Forbes BC, Wilmking M, Hallinger M, Lantz T, Blok D, Tape KD, Maclas-Fauria M, Sass-Klaassen U, Lévesque E, *et al.* 2011. Shrub expansion in tundra ecosystems: Dynamics, impacts and research priorities. *Environmental Research Letters* **6**.

Myers-Smith IH, Hallinger M, Blok D, Sass-Klaassen U, Rayback SA, Weijers S, Trant AJ, Tape KD, Naito AT, Wipf S, *et al.* 2015. Methods for measuring arctic and alpine shrub growth: A review. *Earth-Science Reviews* **140**: 1–13.

Myers-Smith IH, Hik DS. **2013**. Shrub canopies influence soil temperatures but not nutrient dynamics: an experimental test of tundra snow–shrub interactions. *Ecology and Evolution* **3**: 3683–3700.

Myers-Smith IH, Thomas HJD, Bjorkman AD. **2019**. Plant traits inform predictions of tundra responses to global change. *New Phytologist* **221**: 1742–1748.

Naito AT, Cairns DM. **2011**. Patterns and processes of global shrub expansion. *Progress in Physical Geography* **35**: 423–442.

Narita K, Harada K, Saito K, Sawada Y, Fukuda M, Tsuyuzaki S. **2015**. Vegetation and

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Permafrost Thaw Depth 10 Years after a Tundra Fire in 2002, Seward Peninsula, Alaska. *Arctic, Antarctic, and Alpine Research* **47**: 547–559.

Nielsen SS, Arx G von, Damgaard CF, Abermann J, Buchwal A, Büntgen U, Treier UA, Barfod AS, Normand S. **2017**. Xylem anatomical trait variability provides insight on the climate-growth relationship of Betula nana in western Greenland. *Arctic, Antarctic, and Alpine Research* **49**: 359–371.

Pachauri RK, Allen MR, Barros VR, Broome J, Cramer W, Christ R, Church JA, Clarke L, Dahe Q, Dasgupta P. **2014**. *Climate change 2014: synthesis report. Contribution of Working Groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change*. IPCC.

Pechony O, Shindell DT. **2010**. Driving forces of global wildfires over the past millennium and the forthcoming century. *Proceedings of the National Academy of Sciences* **107**: 19167–19170.

Perez-Harguindeguy N, Diaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, Bret-Harte MS, Cornwell WK, Craine JM, Gurvich DE. **2016**. Corrigendum to: new handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of botany* **64**: 715–716.

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team. **2018**. *nlme: Linear and Nonlinear Mixed Effects Models_. R package version 3.1-137*. URL https://CRAN.R-project.org/package=nlme.

Racine CH. **1981**. Tundra Fire Effects on Soils and Three Plant Communities along a Hill-Slope Gradient in the Seward Peninsula , Alaska. *Arctic* **34**: 71–84.

Racine CH, Jandt R, Meyers C, Dennis J, Peninsula S, Racine C, Jandt R, Meyers C, Dennis J. **2004**. Tundra Fire and Vegetation Change along a Hillslope on the Seward Peninsula , Tundra Fire and Vegetation Change along a Hillslope on the. **36**: 1–10.

Racine CH, Johnson LA, Viereck LA. **1987**. Patterns of vegetation recovery after tundra fires in northwestern Alaska, USA. *Arctic and Alpine Research* **19**: 461–469.

R Core Team. **2019**. *R: A language and environment for statistical computing. R Foundation for Statistical Computing*. Vienna: URL https://www.R-project.org/.

Rhemtulla JM, Mladenoff DJ. **2007**. Why history matters in landscape ecology. *Landscape Ecology* **22**: 1–3.

Rocha A V., Loranty MM, Higuera PE, MacK MC, Hu FS, Jones BM, Breen AL, Rastetter EB,

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Goetz SJ, Shaver GR. **2012**. The footprint of Alaskan tundra fires during the past half-century: Implications for surface properties and radiative forcing. *Environmental Research Letters* **7**.

Ross-Davis AL, Frego KA. **2004**. Propagule sources of forest floor bryophytes: spatiotemporal compositional patterns. *Bryologist*: 88–97.

Rustad L, Campbell J, Marion G, Norby R, Mitchell M, Hartley A, Cornelissen J, Gurevitch J. **2001**. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia* **126**: 543–562.

Ryömä R, Laaka-Lindberg S. **2005**. Bryophyte recolonization on burnt soil and logs. *Scandinavian Journal of Forest Research* **20**: 5–16.

Shaver GR, Bret-Harte MS, Jones MH, Johnstone J, Gough L, Laundre J, Chapin FS. **2001**. Species composition interacts with fertilizer to control long-term change in tundra productivity. *Ecology* **82**: 3163–3181.

Turetsky MR, Bond-Lamberty B, Euskirchen E, Talbot J, Frolking S, McGuire AD, Tuittila E. **2012**. The resilience and functional role of moss in boreal and arctic ecosystems. *New Phytologist* **196**: 49–67.

Turner MG. **2010**. Disturbance and landscape dynamics in a changing world. *Ecology* **91**: 2833–2849.

Viereck LA, Schandelmeier LA. **1980**. *Effects of fire in Alaska and adjacent Canada: a literature review*. US Department of the Interior, Bureau of Land Management, Alaska State Office.

Vilchek GE, Bykova OY. **1992**. The origin of regional ecological problems within the northern Tyumen Oblast, Russia. *Arctic and Alpine Research* **24**: 99–107.

Walker MD, Wahren CH, Hollister RD, Henry GHR, Ahlquist LE, Alatalo JM, Bret-Harte MS, Calef MP, Callaghan T V., Carroll AB, *et al.* 2006. From The Cover: Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences* **103**: 1342–1346.

Watts J. **2019**. *Arctic wildfires spew soot and smoke cloud bigger than EU: Plume from unprecedented blazes forecast to reach Alaska as fires rage for third month.* The Guardian, URL https://www.theguardian.com/world/2019/aug/12/arctic-wildfires-smoke-cloud. [accessed 12 August 2019].

Webb ET. **1998**. Survival, persistence, and regeneration of the reindeer lichens, Cladina stellaris, C. rangiferina, and C. mitis following clearcut logging and forest fire in northwestern

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Ontario. *Rangifer* **18**: 41–47.

Wein RW, Bliss LC. **1973**. Changes in arctic Eriophorum tussock communities following fire. *Ecology* **54**: 845–852.

Wickham H. **2009**. *ggplot2: Elegant Graphics for Data Analysis*. Dordrecht: Springer.

Wilke CO. **2019**. *cowplot: Streamlined Plot Theme and Plot Annotations for 'ggplot2'. R package version 0.9.4.* URL https://CRAN.R-project.org/package=cowplot.

Young AM, Higuera PE, Duffy PA, Hu FS. **2016**. Climatic thresholds shape northern high-latitude fire regimes and imply vulnerability to future climate change. *Ecography* **39**: 1–12.

Yu Q, Epstein HE, Engstrom R, Shiklomanov N, Strelestskiy D. **2015**. Land cover and land use changes in the oil and gas regions of Northwestern Siberia under changing climatic conditions. *Environmental Research Letters* **10**: 124020.

Yurkovskaya TK. **2011**. Vegetation map [Karta rastitel'nosti]. In: Shoba SA, Alyabina IO, Urusevskaya IS, Chernova O V., eds. National Atlas of Soils of the Russian Federation [Natsional'nyy atlas pochv Rossiyskoy Federatsii]. Moscow: Moscow State University, 46–48.

Zhang Y, Wolfe SA, Morse PD, Olthof I, Fraser RH. **2015**. Spatiotemporal impacts of wildfire and climate warming on permafrost across a subarctic region, Canada. *Journal of Geophysical Research: Earth Surface* **120**: 2338–2356.

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Tables:

Table 1: Mean values of change in soil temperature (12 cm depth) and active layer depth after fire, estimated by linear mixed effects model, between years since fire in the different groups. Means, 2.5%, 97.5% quantiles of the posterior distributions are given. Effects of change are shown in bold, if there is a high probability of the estimate to be different from 0 (P(*estimate*>0)>0.95, P(*estimate*>0)<0.05).

Variable	Years since fire	Mean	2.50%	97.50%	P(*estimate*>0)
Soil temperature $R^2 = 0.53$	**12**	**4.49**	**6.29**	**8.08**	**1**
	28	**1.92**	**6.27**	**10.65**	**1**
	>44	-4.09	0.28	4.41	0.62
Active layer depth $R^2 = 0.55$	**12**	**-44.51**	**-32.88**	**-21.48**	**0**
	28	**-59.51**	**-32.00**	**-4.72**	**0**
	>44	-21.19	6.60	34.37	0.88

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Table 2: Mean values of relative cover and height change after fire, estimated by linear mixed effects models, between years since fire in the different groups. Means, 2.5%, 97.5% quantiles of the posterior distributions are given. Effects of change are shown in bold, if there is a high probability of the estimate to be different from 0 (P(*estimate*>0)>0.95 or P(*estimate*>0)<0.05).

Group	Years since fire	Cover				Height			
		R^2 = 0.80				R^2_{marg} = 0.19, R^2_{cond} = 0.23			
		Mean	2.50%	97.50%	P	Mean	2.50%	97.50%	P
lichens	12	**-42.21**	**-49.85**	**-34.76**	**0**	**-7.85**	**-14.44**	**-0.91**	**0.01**
	28	**-74.35**	**-82.43**	**-66.66**	**0**	**-8.00**	**-14.69**	**-1.47**	**0.01**
	>44	**-42.00**	**-49.76**	**-34.34**	**0**	-3.45	-10.06	3.53	0.17
bryophytes	12	**8.30**	**0.31**	**16.10**	**0.98**	-0.40	-7.50	6.47	0.45
	28	**10.87**	**3.03**	**18.76**	**1**	-0.65	-7.95	6.74	0.45
	>44	**11.93**	**3.75**	**19.35**	**1**	0.70	-6.05	7.44	0.58
grasses	12	**6.15**	**-1.86**	**14.08**	**0.95**	**-6.50**	**-12.94**	**0.38**	**0.03**
	28	2.66	-5.45	10.48	0.73	-5.50	-12.33	1.56	0.06
	>44	0.27	-7.11	8.10	0.51	-4.00	-10.27	3.00	0.13
herbs	12	3.83	-3.89	12.01	0.82	0.10	-6.66	6.78	0.51
	28	2.57	-5.37	10.28	0.75	2.17	-4.90	9.04	0.74
	>44	0.78	-6.81	8.64	0.58	-5.00	-11.73	1.39	0.08
dwarf shrubs	12	1.40	-6.35	9.63	0.62	-2.30	-9.12	4.14	0.24
	28	**9.70**	**2.28**	**17.90**	**0.99**	-3.40	-10.29	3.33	0.15
	>44	**9.30**	**1.10**	**16.71**	**0.99**	0.00	-7.09	7.09	0.49
shrubs	12	-5.00	-12.87	2.98	0.11	1.50	-5.47	8.67	0.67
	28	**15.30**	**7.67**	**22.97**	**1.00**	**9.60**	**2.72**	**16.11**	**1.00**
	>44	**21.30**	**13.68**	**28.84**	**1.00**	**11.00**	**4.45**	**17.96**	**1.00**

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Table 3: Mean values of change in traits after fire, estimated by linear mixed effects model, between years since fire in the different groups. Means, 2.5%, 97.5% quantiles of the posterior distributions are given. Effects of change are shown in bold, if there is a high probability of the estimate to be different from 0 (P(*estimate*>0)>0.95).

Trait	Species	Years since fire	Mean	2.50%	97.50%	P(*estimate*>0)
Mean aboveground cover $R^2_{marg} = 0.11$, $R^2_{cond} = 0.28$	*V. uliginosum*	12	8.76	-11.76	29.07	0.81
		28	**23.82**	**4.89**	**42.77**	**0.99**
		>44	11.95	-7.85	30.99	0.89
	B. nana	12	13.84	-5.89	33.47	0.91
		28	**20.34**	**1.91**	**39.39**	**0.99**
		>44	**38.50**	**19.37**	**58.18**	**1.00**
Height $R^2_{marg} = 0.14$, $R^2_{cond} = 0.44$	*V. uliginosum*	12	-0.55	-11.08	9.86	0.48
		28	0.10	-10.46	11.01	0.50
		>44	-4.10	-15.05	6.90	0.23
	B. nana	12	5.10	-5.62	16.35	0.84
		28	2.32	-8.43	12.68	0.61
		>44	**17.20**	**6.68**	**28.11**	**1.00**
Blade length $R^2 = 0.04$	*V. uliginosum*	12	-0.04	-0.30	0.23	0.39
		28	0.18	-0.08	0.45	0.90
		>44	0.22	-0.04	0.50	0.94
	B. nana	12	0.11	-0.17	0.38	0.76
		28	0.10	-0.17	0.37	0.51
		>44	**0.22**	**-0.07**	**0.48**	**0.95**
Leaf thickness $R^2_{marg} = 0.08$, $R^2_{cond} = 0.09$	*V. uliginosum*	12	0.02	-0.02	0.05	0.82
		28	-0.01	-0.05	0.03	0.29
		>44	-0.02	-0.06	0.02	0.12
	B. nana	12	0.02	-0.02	0.06	0.84
		28	0.02	-0.02	0.05	0.84
		>44	-0.01	-0.04	0.03	0.39
SLA $R^2 = 0.08$	*V. uliginosum*	12	2.82	-21.63	26.99	0.60
		28	2.29	-21.35	24.44	0.60
		>44	-0.55	-22.75	21.89	0.49
	B. nana	12	-6.83	-29.08	16.98	0.28
		28	3.05	-25.15	30.26	0.59
		>44	**23.63**	**0.85**	**45.40**	**0.99**
LDMC $R^2_{marg} = 0.09$, $R^2_{cond} = 0.52$	*V. uliginosum*	12	-3.26	-96.68	85.05	0.47
		28	-23.09	-106.37	61.21	0.30
		>44	**73.54**	**-12.77**	**160.53**	**0.95**
	B. nana	12	43.61	-50.07	139.63	0.83
		28	40.18	-61.68	139.16	0.79
		>44	-39.83	-127.13	47.23	0.18

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Table 4: Mean slopes of the posterior distribution of relative cover change after fire in regard to time, estimated by linear mixed effects model for different groups. Scenario 1 includes the continuous variable time with raw data related to 12, 28 and 44 years since fire. Scenario 2 includes raw data related to 12, 28 and 100 years since fire. Values are in bold if relative cover change increases strongly with years since fire (P(*slope*>0)>0.95).

	Cover				Height			
Group	Scenario 1 R^2_{marg} = 0.19, R^2_{cond} = 0.22		Scenario 2 R^2_{marg} = 0.18, R^2_{cond} = 0.22		Scenario 1 R^2_{marg} = 0.19, R^2_{cond} = 0.22		Scenario 2 R^2_{marg} = 0.18, R^2_{cond} = 0.22	
	Mean	P	Mean	P	Mean	P	Mean	P
lichens	0.01	0.50	**0.14**	**0.98**	0.14	0.81	0.05	0.85
bryophytes	0.11	0.73	0.03	0.68	0.02	0.59	0.01	0.60
grasses	-0.18	0.16	-0.06	0.19	0.07	0.68	0.02	0.69
herbs	-0.10	0.30	-0.03	0.31	-0.16	0.14	-0.07	0.09
dwarf shrubs	0.25	0.89	0.06	0.80	0.07	0.69	0.029	0.75
shrubs	**0.82**	**1**	**0.23**	**1**	**0.29**	**0.98**	0.22	0.94

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Table 5: Mean slopes of change within traits of the dwarf shrub species *V. uliginosum* and the shrub species *B. nana* after fire in regard to time, estimated by linear mixed effects model for different groups. Scenario 1 includes the continuous variable time with raw data related to 12, 28 and 44 years since fire. Scenario 2 includes raw data related to 12, 28 and 100 years since fire. Values are in bold if relative cover change increases strongly (P(*slope*>0)>0.95).

Trait	Species	Scenario 1			Scenario 2		
		Mean Slope	P(ß>0)	R^2	Mean Slope	P(ß>0)	R^2
Mean cover	*V. uliginosum*	0.09	0.58	$_{marg}$=0.05	-0.03	0.42	$_{marg}$=0.06
	B. nana	**0.80**	**0.97**	$_{cond}$=0.24	**0.28**	**0.98**	$_{cond}$=0.24
Height	*V. uliginosum*	-0.08	0.36	$_{marg}$=0.12	-0.04	0.31	$_{marg}$=0.14
	B. nana	0.38	0.92	$_{cond}$=0.39	**0.16**	**0.97**	$_{cond}$=0.43
Blade length	*V. uliginosum*	$6.81*10^{-3}$	0.88	=0.03	$1.83*10^{-3}$	0.80	=0.03
	B. nana	$3.76*10^{-3}$	0.73		$1.84*10^{-3}$	0.80	
Leaf thickness	*V. uliginosum*	$-1.13*10^{-3}$	0.09	=0.07	$-3.27*10^{-4}$	0.13	$_{marg}$=0.06
	B. nana	$-8.13*10^{-4}$	0.16		$-2.49*10^{-4}$	0.19	$_{cond}$=0.08
SLA	*V. uliginosum*	-0.12	0.44	$_{marg}$=0.06	-0.04	0.42	=0.07
	B. nana	**0.96**	**0.98**	$_{cond}$=0.45	**0.33**	**0.97**	
LDMC	*V. uliginosum*	2.51	0.89	$_{marg}$=0.06	**1.04**	**0.94**	$_{marg}$=0.08
	B. nana	-2.66	0.10	$_{cond}$=0.45	0.98	0.07	$_{cond}$=0.51