Modelling occurrence and status of mat-forming lichens in boreal forests to assess the past and current quality of reindeer winter pastures

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ABSTRACT

Lichens play an essential role in northern ecosystems as important contributors to the water, nutrient and carbon cycles, as well as the main winter food resource for reindeer (*Rangifer tarandus*, also called caribou in North America), the most abundant herbivores in arctic and subarctic regions. Today, climate change and several types of land use are rapidly transforming northern ecosystems and challenging lichen growth. Since lichens are important indicators of ecosystem health and habitat suitability for reindeer, large-scale assessments are needed to estimate their past, present and future status. In our study, we aimed to develop models and equations that can be used by stakeholders to identify the occurrence of lichen-dominated boreal forests and to determine lichen conditions in those forests. Data were collected in Sweden and most input data are publicly available. We focused on mat-forming lichens belonging to the genera *Cladonia* and *Cetraria*, which are dominant species in the reindeer and caribou winter diet. Our models described lichen-dominated forests as being dominated by Scots pine (*Pinus sylvestris*), having low basal area and thin canopy cover, and being located in south- and west-facing areas with low winter temperatures and on gentle slopes. Within those forests, lichen biomass was positively related to tree canopy cover and summer precipitation, while negatively and exponentially related to intensity of use of the area by reindeer. Forest, meteorological, topographic and soil data can be used as input in our models to determine lichen conditions without having to estimate lichen biomass through demanding and expensive fieldwork.

Keywords: ground lichen; lichen growth; lichen volume; reindeer forage; reindeer husbandry; terricolous lichen

1. INTRODUCTION

Climate change and rapid landscape transformation are challenging northern ecosystems around the world. Lichens play an essential role in those ecosystems. They are important contributors to the carbon, water, and nutrient cycles (Cornelissen et al., 2007). Moreover, mat-forming lichens are an essential food resource in winter for an economically and ecologically important herbivore, the reindeer (*Rangifer tarandus*) (Heggberget et al., 2002). Despite their importance, lichens have suffered rapid declines in several parts of the world. The increase and mechanization of forestry activities, coupled in some regions with intense reindeer grazing, have strongly altered the abundance of mat-forming lichens. Examples come from Sweden (Sandström et al., 2006; Sandström et al., 2016), Finland (Kumpula et al., 2000; Uotila et al., 2005; Virtanen et al., 2003), Norway (Evans, 1996; Nygaard and Ødegaard, 1999; Virtanen et al., 2003), Alaska (Collins et al., 2011; Joly et al., 2007a; Joly et al., 2007b), Russia (Rees et al., 2003), some parts of Northern Canada (Rickbeil et al., 2017), and to a lesser extent western Canada (Coxson and Marsh, 2001). On the contrary, forest management and fire have favored the expansion of lichen woodlands in eastern Canada, to the expense of the closed-crown boreal forest (Girard et al., 2008; Payette and Delwaide, 2003). Air pollution was the cause of the declines of forest and mountain heath lichens registered between 1973 and 1999 at the border between Norway and Russia (Aamlid et al., 2000; Tømmervik et al., 2003). Mat-forming lichens are expected to be additionally challenged worldwide by the foreseen expansion of vascular plants into arctic and subarctic regions, as a consequence of climate warming and increased nutrient availability (Cornelissen et al., 2001; Joly et al., 2009; Olthof and Pouliot, 2010).

Lichens are a symbiotic association between a fungus (the mycobiont) and an alga and/or cyanobacterium (the photobiont). *Cladonia arbuscula, C. mitis, C. rangiferina, C. stygia, C. stellaris,* and *Cetraria islandica* are the mat-forming lichen species preferred by reindeer in winter (Andreyev, 1954) and the most abundant in northern ecosystems. All six species have circumpolar arctic and boreal distribution and low growth rates (Sandström et al., 2006; Thomson, 1984). *Cladonia* spp. are characterized by a branched, fruticose growth form and are common on nutrient-poor soils in bogs, tundra, and boreal forests, while *Cetraria* spp. have a leaf-like shape and grow in dry or wet tundra and in old spruce forests (Thomson, 1984). Light exposure, humidity, and air temperature are the key factors determining lichen presence, abundance, and growth (Gaio-Oliveira et al., 2006; Jonsson Čabrajič et al., 2010). Indeed, lichens are poikilohydric organisms that can survive in a metabolically inactive state throughout long dry periods and regain their metabolic and photosynthetic activity only when enough humidity is present. The amount of light that reaches them during this wet period determines their growth rate. In Swedish forests, mat-forming lichens grow primarily in Scots pine (*Pinus sylvestris*) heaths on dry oligotrophic soils (Ahti, 1961). In general, lichen cover decreases in old pine forests on dry sites, probably due to reduced light availability and to increased nutrient availability that promotes the expansion of mosses and shrubs which outcompete lichens (reviewed in Berg et al., 2008). *C. stellaris* and *C. islandica* reach growth peaks at intermediate light exposure and their growth rate is mainly determined by total irradiance they receive when wet, chlorophyll concentration, site openness, and is negatively correlated to air temperature (Čabrajič Jonsson et al., 2010). Čabrajič Jonsson et al. (2010) found that tree basal area (m^2 ha^{-1}) can be used as a proxy for light exposure to determine potential lichen growth. Reindeer grazing can also limit lichen growth (den Herder et al., 2003; Moen and Danell, 2003), keeping mat-forming lichens at a height of few centimeters (Roturier and Roué, 2009). Similarly, reindeer trampling may damage lichens, especially when reoccurring frequently (reviewed in Crittenden, 2000). On the contrary, in some occasions trampling and grazing by reindeer can thin the lichen mats and thus promote recovery of the remaining lichen fragments (Gaio-Oliveira et al., 2006).

Despite the essential role that lichens play in boreal forests, large-scale tools to monitor their status are rare. Some national inventories collect information on lichen horizontal extent, usually quantified in terms of lichen cover. One example is the Swedish National Forest Inventory (NFI, Anonymous, 2015). However, the thickness of the lichen mats, which is strictly correlated to lichen biomass (Moen et al., 2007; Olofsson et al., 2011), is rarely monitored on a large scale. Such monitoring is essential to quantify total lichen biomass and to predict how climate change and human disturbances will affect lichens, ecosystem functioning, and reindeer survival in the future. Reindeer herders, practitioners and conservationists would greatly benefit from tools to estimate the past conditions of mat-forming lichens and to detect current lichen hotspots. The purpose of this study was therefore to develop regression models that can be translated into equations which allow the assessment of lichen conditions when forest, meteorological, topographic and soil characteristics of a certain area are known. We first developed a model describing the occurrence of forests dominated by mat-forming lichens. Secondly, we developed models describing lichen biomass, height (i.e., lichen vertical growth), and cover (i.e., lichen horizontal extension) in those forests in which the ground layer is dominated by mat-forming lichens (fig. 1). We hypothesized those forests to be dominated by Scots pine and characterized by dry soils (Ahti, 1961). We also hypothesized that lichen biomass would be favored by low basal area and thin canopy cover (Berg et al., 2008; Gaio-Oliveira et al., 2006; Jonsson Čabrajič et al., 2010). Lastly, we hypothesized reindeer grazing to negatively affect lichen height (den Herder et al., 2003; Holt et al., 2008; Moen and Danell, 2003), while positively affecting lichen cover (Gaio-Oliveira et al. 2006).

2. METHODS

2.1 Predicting the occurrence of lichen-dominated forests

2.1.1 Input open data

Since the 1920s, each year the NFI has been recording data on the Swedish forests in circular temporary plots (http://www.slu.se/nfi). Since 1953 the plots, with a 10 m radius, have been organized in clusters, distributed over a grid covering the whole country. Each cluster has a squared shape and three to four plots per edge, the length of which can vary between 1 and 2 km (Fridman et al., 2014). The distance between clusters varies between northern and southern Sweden, with clusters in the south being closer to each other than in the north. We selected all forest plots (n = 48267) which were sampled by the NFI between 1983 and 2014, and were located within the reindeer herding husbandry area of northern Sweden, i.e. in the counties of Jämtland, Västerbotten, and Norrbotten. We assigned a unique code to each annual cluster of plots, hereafter referred to as *Cluster*. The NFI classifies each forest plot based on the vegetation group dominating the ground layer, differentiating among dry mosses, wet mosses, and mat-forming lichens. Based on the NFI classification, we divided the plots into two categories: moss-dominated and lichen-dominated. We defined as lichen-dominated those plots classified by the NFI as either “lichen dominant” (>50% lichen cover), “lichen moderate/Sphagnum type” (25-50% lichen cover), or “lichen moderate” (25-50% lichen cover) (Anonymous, 2015). We defined all other plots as moss-dominated. The NFI also records several forest characteristics at each plot, e.g. basal area, tree canopy cover, forest type, forest age, and tree height.

We obtained data on monthly average air temperature and monthly total precipitation from the Swedish Meteorological and Hydrological Institute (SMHI). Data were provided as monthly maps covering the whole country and divided by year (2005-2014). We averaged the monthly temperature data and summed monthly precipitation data by season (winter:

December-February; spring: March-May; summer: June-August; fall: September-November). The temperature map for June 2009 was missing, so we did not develop a temperature map for summer 2009. Similarly, we did not develop temperature and precipitation maps for winter 2005 because maps for December 2004 were not available. A preliminary analysis revealed that meteorological data averaged over a 5-year period (2010-2014) were highly correlated to data averaged over a 10-year period (2005-2014). Therefore, we assumed that data averaged over the 10-year period could confidently represent the spatial variability in climatic conditions among plots in our study area. Similar patterns were suggested by Jonsson Čabrajič et al. (2010). This assumption allowed us to test the importance of meteorological conditions in determining lichen dominance even for those years for which meteorological data were not available in map format (i.e. 1983-2004).

We derived topographic data from DEM maps with 50 m resolution downloaded from the Läntmateriet website (accessed on April 28, 2016: http://www.lantmateriet.se/sv/Kartor-och-geografisk-information/Hojddata/). For those areas where a 50 m resolution map was not available, we used maps with 2 m resolution. In ArcGIS 10.2.1 (ESRI, 2014), we derived slope and aspect maps from the DEMs. We obtained soil data, i.e. a map describing the percentage of sand content and a map of Available Water Capacity (AWC) in the topsoil, from the European Soil Data Centre, http://eusoils.jrc.ec.europa.eu/content/topsoil-physical-properties-europe-based-lucas-topsoil-data (Ballabio et al., 2016). Lastly, we extracted information from the meteorological, topographic and soil maps for each plot.

2.1.2 *Model development*

We developed a quasibinomial mixed-effect regression model in which lichen dominance was the response variable, taking the value 1 for lichen-dominated plots and the value 0 for moss-dominated plots. A quasibinomial model was necessary because the corresponding binomial model suffered of overdispersion. The candidate predictor variables were basal area, tree canopy cover, forest type, forest age, spring, summer and winter precipitation, summer and winter temperature, slope, aspect, sand percentage in the soil (*sand*) and AWC. We did not include spring and fall temperature as candidate predictor variables because they were highly correlated with winter temperature (Pearson's correlation coefficient $r = 0.80$ and 0.88, respectively). Similarly, we excluded fall precipitation from the analysis because it was correlated with winter precipitation ($r = 0.88$). We did not include elevation in the model due to its correlation with summer precipitation and temperature ($r = 0.66$ and $– 0.73$, respectively). We added *Cluster* as a random term in order to take into account the clustered sampling design used by the NFI. We plotted a semivariogram for the within-group residuals, using the *Variogram* function in the nlme package for R (Pinheiro et al., 2018), which suggested that the model residuals were not spatially autocorrelated (Appendix A, fig. A.1, panel A). In the full model, some of the candidate predictor variables were not statistically significant (p-value > 0.05). Therefore, we used the *Anova* function in the car package for R (Fox and Weisberg, 2011) to detect which candidate predictor variables could be removed from the full model (p-value in the likelihood ratio test > 0.05). Models were developed in R 3.3.0 (R Development Core Team, 2017).

2.2 Predicting lichen biomass, height and cover in lichen-dominated forests

2.2.1 Study area

In July and September 2015, we visited 98 sample forest plots distributed in the boreal forest zone within the Swedish reindeer herding husbandry area. Sample plots had been previously inventoried and classified by the NFI as lichen-dominated, but we restricted the selection to plots visited between 2010 and 2014 in order to take advantage of the detailed description of forest characteristics compiled by the NFI. We located all sample plots using the spatial coordinates provided by the NFI, and in most cases the original location was confirmed by a wooden stick left by the NFI to mark the center of the plot. The plots had a 10 m radius, the same as the original NFI plots. We visited areas that are used both by forest reindeer herding districts, which have both winter and summer pastures within the boreal forest, and mountain herding districts, which use the boreal forest only during winter. Two plots were in recent clear-cuts, five were dominated by lodgepole pine (*Pinus contorta*), one by Norway spruce (*Picea abies*), 76 by Scots pine (*Pinus sylvestris*), two were in mixed coniferous forests, and 12 were in mixed forests containing both conifers and deciduous trees, predominantly birches (*Betula* spp.).

2.2.2 Input open data

For each plot visited in 2015, we obtained data on forest type, age, canopy cover and basal area from the NFI dataset. We updated data on forest age to the year of study (i.e. 2015). For recent clear-cuts, we set age, canopy cover and basal area to 0. Since boreal forests have very slow growth rates (Archibold, 1995), data on all other forest characteristics were recent enough to be included in our models as provided by the NFI.

Because mat-forming lichens have very slow growth rates (den Herder et al., 2003; Pegau, 1968; Scotter, 1963; Thomson, 1984), we hypothesized that the meteorological conditions of several previous years would affect current lichen conditions. Since in our study area meteorological data were correlated over a 5- and a 10-year period (see subsection 2.1.1), we decided to consider the average meteorological conditions of each plot over the 5 years preceding the field measurements (i.e., 2010-2014), keeping the data divided by season as described in subsection 2.1.1. For each plot, we extracted information about topography and soil from the same maps described in subsection 2.1.1.

2.2.3 Field measurements

We measured lichen height in all sample plots as the average height of all mat-forming lichen species described in the Introduction, in 20cm-radius circles (hereafter, hits) regularly spaced one meter apart in the direction of the cardinal and half-cardinal points starting from the center of the sample plot, following Uotila et al. (2005) (Appendix A, fig. A.2 – panel A). We used a graduated rod with a plate that rests on the lichen thalli to take the measurements (Olofsson et al., 2011). During the measurement, the rod was held perpendicular to the soil without penetrating into the litter and humus layer. Lichen height was measured with a precision of 0.5 cm. This technique provided 81 measurements of lichen height for each plot. If lichens were not present, we noted lichen height = 0 cm. For each hit, we also recorded which lichen species were present.

We estimated the intensity of use of the area by reindeer by counting reindeer pellet groups in five subplots within each sample plot using the fecal standing crop technique (Appendix A, fig. A.2 – panel B) (McClanahan, 1986). We only counted pellet groups that included at least 50 pellets and which laid for at least half of their extent in the plots (following Skarin, 2007). In mountain herding districts the boreal forest is only used in winter, while in forest herding districts lichen-dominated forests can be used or at least travelled on also during the snow-free season. Therefore, we only counted winter pellets. During winter, reindeer pellets are dryer and appear as separate drops. Summer pellets are wetter and the individual pellets are clumped together, making them easy to distinguish from winter ones.

2.2.4 Model development

Based on the field data collected in 2015, we developed three separate regression models with three proxies of lichen conditions as response variables: lichen biomass (LB), lichen height (LH), and lichen cover (LC). For each sampling plot, we estimated LB by averaging all 81 measurements of lichen height taken in a plot, i.e. including the hits where lichen height = 0 cm. LB is therefore expressed in centimeters. LB is a comprehensive measurement that takes into account both lichen height and cover, thus being a good approximation for food availability for reindeer (Moen et al., 2007). LB is also strictly correlated with lichen volume (Appendix A, fig. A.3). We estimated LH by averaging lichen height over all those hits in which lichens were present (i.e., lichen height > 0 cm). Lastly, we estimated LC as the proportion of hits where lichens were present in each plot.

We started by running a Gaussian mixed-effect linear regression model (GLMM) with LB as response variable, *Cluster* as random term, and all the variables described in Table 1 as candidate predictor variables, plus interaction terms between summer temperature and precipitation and between winter temperature and precipitation, with the purpose of taking into account the effect that extreme meteorological conditions may have on lichen growth (Skuncke, 1969: 29). By visual inspection we determined that the relationship between pellet group counts (*pellets*) and LB followed a decreasing exponential curve, so we included *pellets* in the form of exp(-*pellets*). The GLMM had a lower Akaike Information Criterion (AIC, Burnham and Anderson, 2002) compared to an analogous fixed-term regression model, so we retained the random term. A semivariogram for the within-group residuals, drawn using the *Variogram* function in the nlme package for R (Pinheiro et al., 2018), suggested that the model residuals were not spatially autocorrelated (Appendix A, fig. A.1, panel B). Subsequently, we used the *stepAIC* function in the MASS package for R 3.3.0 (Venables and Ripley, 2002) to run an automatic bidirectional elimination procedure in order to detect the set of predictor variables that provided the best-fit model based on AIC. In addition to the best-fit model, we also developed a reduced model by removing those variables for which the p-value in the likelihood ratio test provided by the Analysis of Variance table produced by the *anova* function in R 3.3.0 (R Development Core Team, 2017) was > 0.05. We developed the reduced model because the purpose of our study was to create relatively simple equations for stakeholders' use. Thus, we believe that a model that performs slightly worse than the best-fit model but contains less predictor variables is more valuable to stakeholders.

Similarly we ran a GLMM with LH as a response variable, and the same random and fixed terms as for the LB model as predictors, with the exception of winter precipitation (*precip_1014w*) which we included as a second-order polynomial because of its parabolic relationship with LH. The semivariogram for the within-group residuals suggested that the model residuals were not spatially autocorrelated (Appendix A, fig. A.1, panel C). Comparing the GLMM with an analogous fixed-term regression model as above, we determined that the random term (*Cluster*) was not needed (Standard Deviation: 0.37), so we proceeded with a fixed-effect linear regression model. Finally, we developed a best-fit and a reduced model following the same procedure as for LB.

Subsequently, we ran a mixed-effect quasibinomial model, i.e. a GLMM with logit function, to link LC to the candidate predictor variables described in Table 1, with the exception of *pellets*, which was included in the form of ln(*pellets*+1) because we determined by visual inspection that its relationship with the logit of LC followed a logarithmic curve. The +1 allows the calculation of the logarithm of values = 0. *Cluster* was the random term. A quasibinomial model was necessary because the corresponding binomial model suffered of overdispersion. The semivariogram for the within-group residuals suggested that the model residuals were not spatially autocorrelated (Appendix A, fig. A.1, panel D). Since AIC cannot be calculated for quasibinomial models, we used the *Anova* function in the car package for R 3.3.0 (Fox and Weisberg, 2011) to detect which predictor variables could be removed from the full model, based on a likelihood-ratio test.

Lastly, we repeated the three procedures above but starting with models which did not contain reindeer pellet counts (*pellets*) as predictor variable, with the purpose of creating equations that could describe past lichen conditions, i.e. when pellet counts are not available.

Table 1. List of all forest, meteorological, biotic, and topographic characteristics included as predictor variables in our models aimed to predict the occurrence of lichen-dominated forests, as well as lichen biomass, height and cover in those forests. All continuous variables are highlighted in italic. See the Methods section for a description of the data sources. The descriptive statistics refer to the two datasets used to model lichen occurrence and lichen conditions (i.e. lichen biomass, height and cover) respectively, and are reported as mean (standard deviation) [minimum; maximum].

Variable	**Description**	**Descriptive statistics (lichen occurrence)**	**Descriptive statistics (lichen conditions)**
basal area	Expressed in m²/ha. For details, see Anonymous (2015).	14.63 (13.08) [0.00; 493.22]	9.18 (8.67) [0.00; 41.89]
age	Average age (in years), estimated as the average age of at least two trees representative for the whole plot. For details, see Anonymous (2015).	66.85 (50.03) [0; 345]	54.92 (47.45) [0; 232]
canopy cover	Tree canopy cover, estimated visually and expressed as a percentage. For details, see Anonymous (2015).	55.97 (20.17) [0; 99]	38.10 (18.42) [0; 72]
pellets	Number of reindeer pellet groups (see section 2.2.3 for details).		1.87 (3.16) [0; 16]

Variable	Description	Descriptive statistics (lichen occurrence)	Descriptive statistics (lichen conditions)
precip_sp	Total spring precipitation (mm) averaged for either the period 2005-2014 or 2010-2014	77.62 (10.76) [0; 186]	72.13 (6.43) [59; 89]
precip_su	Total summer precipitation (mm) averaged for either the period 2005-2014 or 2010-2014	189.41 (27.22) [0; 298]	195.07 (19.79) [126; 245]
precip_w	Total winter precipitation (mm) averaged for either the period 2005-2014 or 2010-2014	101.63 (21.15) [0; 235]	94.91 (20.38) [65; 145]
temp_su	Average summer temperature (ºC), averaged for either the period 2005-2014 or 2010-2014	12.22 (0.97) [0; 14]	12.25 (0.74) [10; 14]
temp_w	Average winter temperature (ºC), averaged for either the period 2005-2014 or 2010-2014	-9.91 (1.87) [-15; 0]	-10.35 (1.72) [-14; -7]
slope	Expressed in degrees and derived from a 50 m Digital Elevation Model (DEM), except for a few plots in Jämtland for which we used a 2 m DEM	4.04 (3.54) [0.00; 37.84]	3.55 (2.92) [0.02; 14.63]
sand	Percentage of sand content in the topsoil	68.88 (10.83) [0.00; 98.81]	70.87 (10.14) [50.81; 94.81]

Variable	Description	Descriptive statistics (lichen occurrence)	Descriptive statistics (lichen conditions)
AWC	Available Water Capacity in the topsoil	0.07 (0.01) [0.00; 0.12]	0.07 (0.01) [0.05; 0.08]
HD	Herding district type: forest or mountain		
forest type	Determined starting from the NFI classification referring to the proportion of each tree species. We assigned a plot to a specific forest type based on the dominant tree species (covering ≥ 70 % of the plot). In some cases, we corrected the NFI classification based on our field observations. We defined forests ≤ 5 years old as clear-cuts. If there was not any dominant tree species (i.e. no species constituted > 70 % of all trees), we defined forest type as “mixed” (including both deciduous trees and conifers) or “mixed conifer” (only including conifers).		
aspect	Derived from the DEM. Then, converted to a categorical		

Variable	Description	Descriptive statistics (lichen occurrence)	Descriptive statistics (lichen conditions)
	variable with 10 categories, divided as follows: Flat: -1 North: 0-22.5 Northeast: 22.5-67.5 East: 67.5-112.5 Southeast: 112.5-157.5 South: 157.5-202.5 Southwest: 202.5-247.5 West: 247.5-292.5 Northwest: 292.5-337.5 North: 337.5-360		

3. RESULTS

3.1 Predicting the occurrence of lichen-dominated forests

Based on data collected in the forests of northern Sweden from 1983 to 2014, we assessed that the odds of a plot being lichen-dominated are higher in Scots pine forests compared to any other forest type, while they are lower on north facing slopes than in any other aspect category (Table 2 and Appendix A, Table A.1). Moreover, the odds of a forest being dominated by lichens are higher if the forest is older and characterized by lower basal area and thinner canopy cover (fig. 2). Finally, areas on gentle slopes with higher summer precipitation and lower winter precipitation and temperature favor lichen occurrence.

Table 2. Quasibinomial mixed-effect regression model predicting the occurrence of lichen-dominated forests. The model was developed based on data from the Swedish National Forest Inventory describing boreal forests. The response variable was a dummy variable distinguishing between lichen-dominated (= 1) and moss-dominated (= 0) forests. For a list of the candidate predictor variables, see subsection 2.1. Random term standard deviation = 1.80. The categories of the "forest type" variable are marked with an asterisk. Scots pine (*Pinus sylvestris*) was the reference category. Lodgepole pine = *Pinus contorta*. Norway spruce = *Picea abies*. The categories of the "aspect" variable are marked with a º. North was the reference category. All continuous variables are highlighted in italic. β = regression coefficient mean estimate, which in a quasibinomial model is the log odd ratio; SE = standard error of the coefficient estimate.

	β	**SE**	**p-value**
intercept	-2.86	0.82	
basal area	-0.0441	0.0055	< 0.0001

	β	**SE**	**p-value**
canopy cover	-0.0345	0.0027	< 0.0001
clear-cut *	-4.64	0.69	< 0.0001
lodgepole pine *	-1.14	0.27	< 0.0001
mixed *	-2.45	0.16	< 0.0001
mixed conifer *	-1.51	0.25	< 0.0001
Norway spruce *	-2.93	0.20	< 0.0001
age	0.0024	0.0009	0.0107
precip_su	0.0119	0.0024	< 0.0001
precip_w	-0.0115	0.0036	0.0012
temp_w	-0.10	0.04	0.0110
slope	-0.06	0.01	< 0.0001
east ^{o}	0.44	0.17	0.0083
northeast ^{o}	0.45	0.16	0.0051
northwest ^{o}	0.73	0.19	0.0001
south ^{o}	0.94	0.16	< 0.0001
southeast ^{o}	0.70	0.18	0.0001
southwest ^{o}	1.00	0.16	< 0.0001
west ^{o}	0.92	0.17	< 0.0001

3.2 Predicting lichen biomass, height and cover in lichen-dominated forests

Lichen biomass (LB) was on average 3.98 (± 2.15) cm (Appendix A, Table A.2) and was positively related to tree canopy cover (fig. 3, panel A) and summer precipitation (fig. 3, panel B), and higher in mountain reindeer herding districts compared to forest herding districts (fig. 3, panel C). The intensity of use of the area by reindeer negatively affected LB, but in an exponential manner. These results are based on the reduced model detailed in Table 3 and in Appendix A, Table A.3, while the best-fit model predicting LB is detailed in Appendix A, Table A.4. For a model without reindeer pellet counts, we refer the reader to Appendix B, Tables B.1 and B.2.

Lichen height (LH) was on average 4.89 (± 2.29) cm (Appendix A, Table A.2) and was higher in forests with denser canopy cover and greater summer precipitation. LH decreased exponentially with an increasing use of the area by reindeer (fig. 4, panel A). Lastly, LH was higher in mountain herding districts compared to forest herding districts, and lower on south- and west-facing slopes compared to north facing slopes. These results are based on a reduced model which is detailed in Appendix A, Tables A.5 and A.6, while the best-fit model is detailed in Appendix A, Table A.7. Those models explained 65 % and 70 % of the variability in LH, respectively. For a model without reindeer pellet counts, we refer the reader to Appendix B, Tables B.3 and B.4.

Lichen cover (LC), estimated as a proportion, was on average 0.82 (± 0.19, Appendix A, Table A.2) and was positively related to use of the area by reindeer (fig. 4, panel B), negatively affected by the sand content in the soil, and highest in Scots pine forests compared to any other forest type, except lodgepole pine (Appendix A, Tables A.8 and A.9). For a model without reindeer pellet counts, we refer the reader to Appendix B, Tables B.5 and B.6.

Table 3. Equations predicting lichen biomass (LB) in boreal forests dominated by mat-forming lichens. The equations were obtained from the reduced regression model described in Appendix A, Table A.3, where the uncertainty in the coefficient estimates is also provided. Predictor variables are described in Table 1 and in subsection 2.2. The regression model included one categorical variable (HD = herding district) and here we report different equations for each category of that variable.

Categorical variable	**Equation**
HD = forest	$LB = -3.92 + 0.02\ \textit{canopy cover} + 0.47\ \exp(-\textit{pellets}) + 0.03\ \textit{precip\_su}$
HD = mountain	$LB = -2.81 + 0.02\ \textit{canopy cover} + 0.47\ \exp(-\textit{pellets}) + 0.03\ \textit{precip\_su}$

4. DISCUSSION

Mat-forming lichens thrive in Scots pine forests, with low basal area and thin canopy cover (Ahti, 1961; Table 2 and fig. 2, this study). The negative effect of a dense canopy cover on lichen growth has been previously demonstrated not only for boreal Scots pine forests in Scandinavia (Bråkenhielm and Persson, 1980; Jonsson Čabrajič et al., 2010; Uotila et al., 2005), but also for pine and spruce forests in North America (Boudreault et al., 2013; Coxson and Marsh, 2001; Foster, 1985). In dense forests, mat-forming lichens do not receive enough light for optimal growth, and the moisture and nutrient levels in the soil are more advantageous for mosses than for lichens (Sulyma and Coxson, 2001). This is the case in old forests which have not been thinned (Bråkenhielm and Persson, 1980) and in young forests, which nowadays in Scandinavia grow much faster and denser than in the past due to silviculture (Axelsson and Östlund, 2001). The agreement between previous studies and our results suggests that our model is robust and describes accurately lichen occurrence in boreal forests.

Once the forest ground layer is dominated by lichens, canopy cover seems to be the only forest characteristic influencing LB, which is higher in forests with denser canopy cover (fig. 3, panel A). This result may seem contradictory with our model describing the occurrence of lichen-dominated forests (Table 2), which suggests that lichens occur in forests with thinner canopy cover (fig. 2, panel B). Čabrajič Jonsson et al. (2010) determined that the dry mass gain of mat-forming lichens peaks at sites with intermediate light exposure levels (corresponding to approximately 40 % canopy openness). A closer look at fig. 3, panel A suggests that LB increases up to 40 % canopy cover. At canopy covers denser than 40 %, variability in LB increases drastically. In forests where LB is high despite canopy cover being dense, lichens are probably tall and sparse, but may be locally abundant. Mat-forming lichens do not usually receive enough light for optimal growth in forests with dense canopy cover

(Boudreault et al., 2013; Bråkenhielm and Persson, 1980; Coxson and Marsh, 2001; Foster, 1985), but the ones that manage to grow in those forests grow taller because they extend vertically in search for light inside the thick moss layer (pers. obs.). Our estimations of LB may be higher in areas with abundant summer precipitation for the same reason (fig. 3, panel B). We therefore advice the end users of the equations produced in this study to keep in mind that high LB values predicted by our equations for forests with dense canopy cover and greater summer precipitation may indicate that the lichen mat is patchy, but could be locally thick.

Reindeer use of the forests negatively affected LH (fig. 4, panel A), but was positively related to LC in winter grazing areas (fig. 4, panel B). Such effects were evident already at low intensity of use of the forests. In winter, lichens constitute the main component of reindeer diet (Heggberget et al., 2002). Thus, reindeer grazing is expected to shorten the lichen mat (den Herder et al., 2003; Holt et al., 2008; Moen and Danell, 2003). However, reindeer feed on lichens by opening craters in the snow in a patchy manner, so their grazing and trampling activities do not affect the lichen mat evenly and by breaking the lichen thalli, reindeer can promote lichen dispersion (Gaio-Oliveira et al. 2006). Moreover, the effects of reindeer grazing are not the same among lichen species. *Cetraria islandica* and *Cladonia stellaris* are the most sensitive to reindeer grazing (Andreyev, 1954; Väre et al., 1996; Väre et al., 1995), while grazing benefits *C. rangiferina* and *C. arbuscula* (Väre et al., 1996). During our 2015 fieldwork, we indeed observed that *C. rangiferina* and *C. arbuscula*/*mitis* dominate the boreal forests of the Swedish reindeer husbandry area, at the expenses of *C. stellaris* and *Cetraria islandica* (Appendix A, fig. A.4). However, the succession dynamics of different lichen species may also be involved in explaining the different abundance of the four species. *C. stellaris* is a late successional species within the lichen community, and if forest disturbance (due to harvesting, scarification, or fire) is frequent enough, late successional lichen communities may have too little time to develop. According to Ahti (1977), *C. arbuscula* and *rangiferina* may be dominant 30-100 years after fire (i.e., they are primary succession species), while *C. stellaris* may not be dominant until 80-120 years after fire.

In this study, we have used long-term and large-scale datasets to describe the optimal habitat for the occurrence and growth of mat-forming lichens. To our knowledge, our study is the first to propose a description of the environmental characteristics that benefit the occurrence of mat-forming lichens based exclusively on publicly available data. Moreover, our LB models are based on a novel method to estimate biomass of mat-forming lichens which can be applied in future studies. Using traditional techniques, one needs to collect lichen samples in the field, take them to a laboratory, dry them and finally weigh them (see e.g. den Herder et al., 2003), which is a cumbersome procedure. With our technique, lichen biomass can instead be quantified directly in the field from measurements of lichen height and cover, or be estimate it directly from forest, meteorological, topographic and soil data using the equations proposed in this study. For a more detailed model predicting lichen growth, we refer the reader to Jonsson Čabrajič et al. (2010).

Due to the recent strong decline in the extent of lichen-dominated forests in northern Sweden (Sandström et al., 2016), we suggest that the equations reported in this study can be useful to a variety of stakeholders, e.g. to detect areas that should receive targeted conservation or management efforts. To calculate the probability of occurrence of lichen-dominated forests, LB, LH, or LC, one has to obtain data on the variables included in the right end side of the equations and make the calculation according to the formula. The equations can be used retrospectively to estimate past conditions of mat-forming lichens in the boreal forest, as well as to map their current distribution or to foresee their future status under different climatic and environmental scenarios.

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6. REFERENCES

Aamlid, D., Vassilieva, N., Aarrestad, P.A., Gytarsky, M.L., Lindmo, S., Karaban, R., Korotkov, V., Rindal, T., Kuzmicheva, V., Venn, K., 2000. The ecological state of the ecosystems in the border areas between Norway and Russia. Boreal Environ Res 5, 257-278.

Ahti, T., 1961. Taxonomic studies on reindeer lichens (*Cladonia*, subgenus *Cladina*). Annales Botanici Societatis 'Vanamo' 32, 1-160.

Ahti, T., 1977. Lichens of the boreal coniferous zone, in: Seaward, M. (Ed.), Lichen ecology. Academic Press, London, UK.

Andreyev, V., 1954. The growth of forage lichens and the methods for their regulation. Geobotanika 9, 11-74.

Anonymous, 2015. Fältinstruktion 2015, riksinventeringen av skog. Swedish University of Agricultural Sciences, Department of Forest Resource Management and Department of Soil and Environment, Sweden.

Archibold, O.W., 1995. The coniferous forests, in: Archibold, O.W. (Ed.), Ecology of world vegetation. Chapman & Hall, Springer Netherlands, pp. 238-279.

Axelsson, A.-L., Östlund, L., 2001. Retrospective gap analysis in a Swedish boreal forest landscape using historical data. Forest Ecol Manag 147, 109-122.

Ballabio, C., Panagos, P., Monatanarella, L., 2016. Mapping topsoil physical properties at European scale using the LUCAS database. Geoderma 261, 110-123.

Berg, A., Östlund, L., Moen, J., Olofsson, J., 2008. A century of logging and forestry in a reindeer herding area in northern Sweden. Forest Ecol Manag 256, 1009-1020.

Boudreault, C., Zouaoui, S., Drapeau, P., Bergeron, Y., Stevenson, S., 2013. Canopy openings created by partial cutting increase growth rates and maintain the cover of three *Cladonia* species in the Canadian boreal forest. Forest Ecol Manag 304, 473-481.

Bråkenhielm, S., Persson, H., 1980. Vegetation dynamics in developing Scots pine stands in central Sweden. Ecol Bull 32, 139-152.

Burnham, K.P., Anderson, D.R., 2002. Model selection and multi-model inference: a practical information-theoretic approach. Springer-Verlag, New York, USA.

Čabrajič Jonsson, A.V., Moen, J., Palmqvist, K., 2010. Predicting growth of mat-forming lichens on a landscape scale – comparing models with different complexities. Ecography 33, 949-960.

Collins, W.B., Dale, B.W., Adams, L.G., McElwain, D.E., Joly, K., 2011. Fire, grazing history, lichen abundance, and winter distribution of caribou in Alaska's taiga. J Wildlife Manage 75, 369-377.

Cornelissen, J.H., Lang, S.I., Soudzilovskaia, N.A., During, H.J., 2007. Comparative cryptogam ecology: a review of bryophyte and lichen traits that drive biogeochemistry. Ann Bot-London 99, 987-1001.

Cornelissen, J.H.C., Callaghan, T.V., Alatalo, J., Michelsen, A., Graglia, E., Hartley, A., Hik, D., Hobbie, S., Press, M., Robinson, C.H., 2001. Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? J Ecol 89, 984-994.

Coxson, D.S., Marsh, J., 2001. Lichen chronosequences (postfire and postharvest) in lodgepole pine (*Pinus contorta*) forests of northern interior British Columbia. Canadian Journal of Botany 79, 1449-1464.

Crittenden, P., 2000. Aspects of the ecology of mat-forming lichens. Rangifer 20, 127-139.

den Herder, M., Kytöviita, M.M., Niemelä, P., 2003. Growth of reindeer lichens and effects of reindeer grazing on ground cover vegetation in a Scots pine forest and a subarctic heathland in Finnish Lapland. Ecography 26, 3-12.

ESRI, 2014. ArcGIS Desktop: Release 10.2.1.

Evans, R., 1996. Some impacts of overgrazing by reindeer in Finnmark, Norway. Rangifer 16, 3-19.

Foster, D.R., 1985. Vegetation development following fire in *Picea mariana* (black spruce)-*Pleurozium* forests of south-eastern Labrador, Canada. The Journal of Ecology 73, 517-534.

Fox, J., Weisberg, S., 2011. An R companion to applied regression. Second Edition. Sage, Thousand Oaks, CA, USA.

Fridman, J., Holm, S., Nilsson, M., Nilsson, P., Ringvall, A.H., Ståhl, G., 2014. Adapting National Forest Inventories to changing requirements–the case of the Swedish National Forest Inventory at the turn of the 20th century. Silva Fennica 48, 1095.

Gaio-Oliveira, G., Moen, J., Danell, Ö., Palmqvist, K., 2006. Effect of simulated reindeer grazing on the re-growth capacity of mat-forming lichens. Basic Appl Ecol 7, 109-121.

Girard, F., Payette, S., Gagnon, R., 2008. Rapid expansion of lichen woodlands within the closed-crown boreal forest zone over the last 50 years caused by stand disturbances in eastern Canada. J Biogeogr 35, 529-537.

Heggberget, T.M., Gaare, E., Ball, J.P., 2002. Reindeer (*Rangifer tarandus*) and climate change: importance of winter forage. Rangifer 22, 13-31.

Holt, E.A., McCune, B., Neitlich, P., 2008. Grazing and fire impacts on macrolichen communities of the Seward Peninsula, Alaska, USA. Bryologist 111, 68-83.

Joly, K., Cole, M.J., Jandt, R.R., 2007a. Diets of overwintering caribou, *Rangifer tarandus*, track decadal changes in Arctic tundra vegetation. Can Field Nat 121, 379-383.

Joly, K., Jandt, R.R., Klein, D.R., 2009. Decrease of lichens in Arctic ecosystems: the role of wildfire, caribou, reindeer, competition and climate in north-western Alaska. Polar Res 28, 433-442.

Joly, K., Jandt, R.R., Meyers, C.R., Cole, M.J., 2007b. Changes in vegetative cover on Western Arctic Herd winter range from 1981 to 2005: potential effects of grazing and climate change. Rangifer 27, 199-207.

Jonsson Čabrajič, A.V., Moen, J., Palmqvist, K., 2010. Predicting growth of mat-forming lichens on a landscape scale – comparing models with different complexities. Ecography 33, 949-960.

Kumpula, J., Colpaert, A., Nieminen, M., 2000. Condition, potential recovery rate, and productivity of lichen (*Cladonia* spp.) ranges in the Finnish reindeer management area. Arctic 53, 152-160.

McClanahan, T., 1986. Quick population survey method using faecal droppings and a steady state assumption. Afr J Ecol 24, 37-39.

Moen, J., Danell, Ö., 2003. Reindeer in the Swedish mountains: an assessment of grazing impacts. Ambio 32, 397-402.

Moen, J., Danell, Ö., Holt, R., 2007. Non-destructive estimation of lichen biomass. Rangifer 27, 41-46.

Nygaard, P.H., Ødegaard, T., 1999. Sixty years of vegetation dynamics in a south boreal coniferous forest in southern Norway. J Veg Sci 10, 5-16.

Olofsson, A., Danell, Ö., Forslund, P., Åhman, B., 2011. Monitoring changes in lichen resources for range management purposes in reindeer husbandry. Ecol Indic 11, 1149-1159.

Olthof, I., Pouliot, D., 2010. Treeline vegetation composition and change in Canada's western Subarctic from AVHRR and canopy reflectance modeling. Remote Sens Environ 114, 805-815.

Payette, S., Delwaide, A., 2003. Shift of conifer boreal forest to lichen–heath parkland caused by successive stand disturbances. Ecosystems 6, 540-550.

Pegau, R.E., 1968. Growth rates of important reindeer forage lichens on the Seward Peninsula, Alaska. Arctic 21, 255-259.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team, 2018. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.4.4. https://CRAN.R-project.org/package=nlme

R Development Core Team, 2017. R: A language and environment for statistical computing. http://www.R-project.org/

Rees, W., Williams, M., Vitebsky, P., 2003. Mapping land cover change in a reindeer herding area of the Russian Arctic using Landsat TM and ETM+ imagery and indigenous knowledge. Remote Sens Environ 85, 441-452.

Rickbeil, G.J., Hermosilla, T., Coops, N.C., White, J.C., Wulder, M.A., 2017. Estimating changes in lichen mat volume through time and related effects on barren ground caribou (*Rangifer tarandus groenlandicus*) movement. PloS one 12, e0172669.

Roturier, S., Roué, M., 2009. Of forest, snow and lichen: Sámi reindeer herders' knowledge of winter pastures in northern Sweden. Forest Ecol Manag 258, 1960-1967.

Sandström, C., Moen, J., Widmark, C., Danell, Ö., 2006. Progressing toward co-management through collaborative learning: forestry and reindeer husbandry in dialogue. Int J Biodiv Sci Managem 2, 326-333.

Sandström, P., Cory, N., Svensson, J., Hedenås, H., Jougda, L., Borchert, N., 2016. On the decline of ground lichen forests in the Swedish boreal landscape: Implications for reindeer husbandry and sustainable forest management. Ambio 45, 415-429.

Scotter, G.W., 1963. Growth rates of *Cladonia alpestris, C. mitis*, and *C. rangiferina* in the Taltson River region, NWT. Canadian Journal of Botany 41, 1199-1202.

Skarin, A., 2007. Habitat use by semi-domesticated reindeer, estimated with pellet-group counts. Rangifer 27, 121-132.

Skuncke, F., 1969. Reindeer ecology and management in Sweden. Biological Papers of the University of Alaska 8, 81.

Sulyma, R., Coxson, D.S., 2001. Microsite displacement of terrestrial lichens by feather moss mats in late seral pine-lichen woodlands of north-central British Columbia. Bryologist 104, 505-516.

Thomson, J.W., 1984. American arctic lichens: the macrolichens. Columbia University Press, New York, USA.

Tømmervik, H., Høgda, K.A., Solheim, I., 2003. Monitoring vegetation changes in Pasvik (Norway) and Pechenga in Kola Peninsula (Russia) using multitemporal Landsat MSS/TM data. Remote Sens Environ 85, 370-388.

Uotila, A., Hotanen, J.-P., Kouki, J., 2005. Succession of understory vegetation in managed and seminatural Scots pine forests in eastern Finland and Russian Karelia. Can J Forest Res 35, 1422-1441.

Venables, W.N., Ripley, B.D., 2002. Modern applied statistics with S. Fourth Edition. Springer Science & Business Media, New York, USA.

Virtanen, R., Eskelinen, A., Gaare, E., 2003. Long-term changes in alpine plant communities in Norway and Finland, in: Nagy, L., Grabherr, G., Körner, C., Thompson, D.B.A. (Eds.), Alpine biodiversity in Europe. Springer-Verlag, Heidelberg, Berlin, Germany, pp. 411-422.

Väre, H., Ohtonen, R., Mikkola, K., 1996. The effect and extent of heavy grazing by reindeer in oligotrophic pine heaths in northeastern Fennoscandia. Ecography 19, 245-253.

Väre, H., Ohtonen, R., Oksanen, J., 1995. Effects of reindeer grazing on understorey vegetation in dry *Pinus sylvestris* forests. J Veg Sci 6, 523-530.

Figure 1. Conceptual representation of the aim and application of the study.

Figure 2. Variability in basal area (y-axis, panel A) and canopy cover (y-axis, panel B) in moss- and lichen-dominated forests (x-axes). For a forest to be classified as being dominated by a certain vegetation group, that group must comprise at least 25 % of the forest ground layer. Data were collected by the Swedish National Forest Inventory in 48267 forest plots, visited from 1983 to 2014. All plots were located in the Swedish reindeer husbandry area. In each boxplot, the median of the data is represented by the bold horizontal bar, the interquartile range is denoted by the horizontal edges of the box, and the dashed vertical lines extend to the range of data. Outliers were removed in order to improve the visibility of the main box. The median and interquartile range of basal area and canopy cover are slightly lower for lichen- compared to moss-dominated forests, which suggests that lichen-dominated forests have usually lower tree density and less dense tree canopy cover compared to moss-dominated forests.

Figure 3. Relationship between lichen biomass (LB) and tree canopy cover (panel A), summer precipitation (*precip_su*, panel B), and type of herding district (HD, panel C) in lichen-dominated forests. A description of how lichen biomass was estimated is available in subsection 2.2. For details on the predictor variables (x-axes) see Table 1.

Figure 4. Relationship between lichen height (LH, y-axis in panel A) and lichen cover (LC, y-axis in panel B) and intensity of use by reindeer of boreal forests dominated by lichens (x-axes), which was estimated based on reindeer pellet counts (*pellets*). A description of how LH, LC, and *pellets* were obtained is available in subsection 2.2.

Appendix A

Modelling occurrence and status of mat-forming lichens in boreal forests to assess the past and current quality of reindeer winter pastures

Alessia Uboni, Alexander Blochel, Danijela Kodnik, and Jon Moen

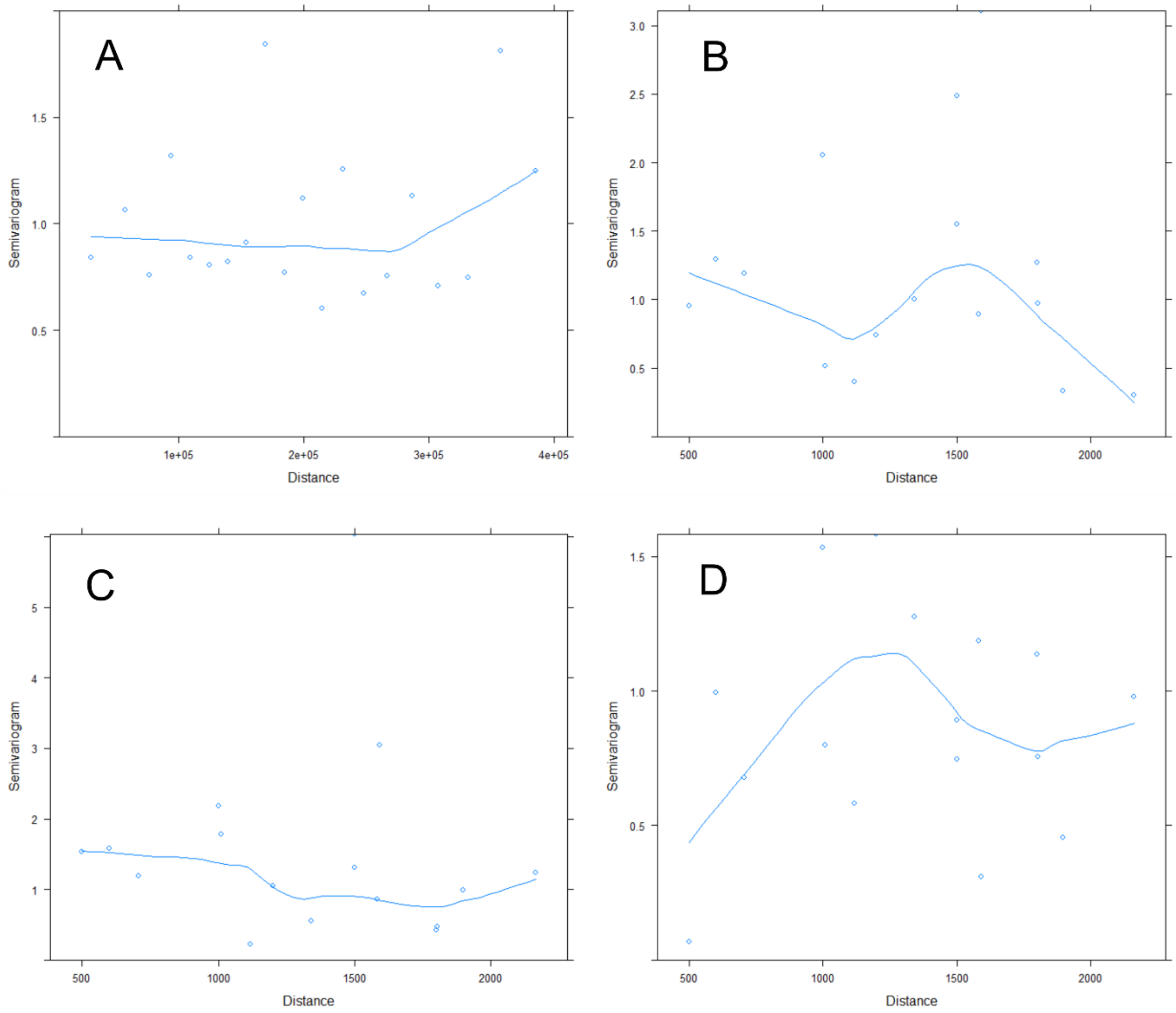

Figure A.1. Semivariogram for the within-group residuals from regression models relating the occurrence of lichen-dominated forests (panel A, quasibinomial mixed-effect model), lichen biomass (panel B, linear mixed-effect model), lichen height (panel C, linear mixed-effect model), and lichen cover (panel D, quasibinomial mixed-effect model) with forest, meteorological, topographic and soil characteristics. For details on the model development see sections 2.1.2 and 2.2.4 in the main manuscript. The x-axes have been limited to distances up to 400000 m.

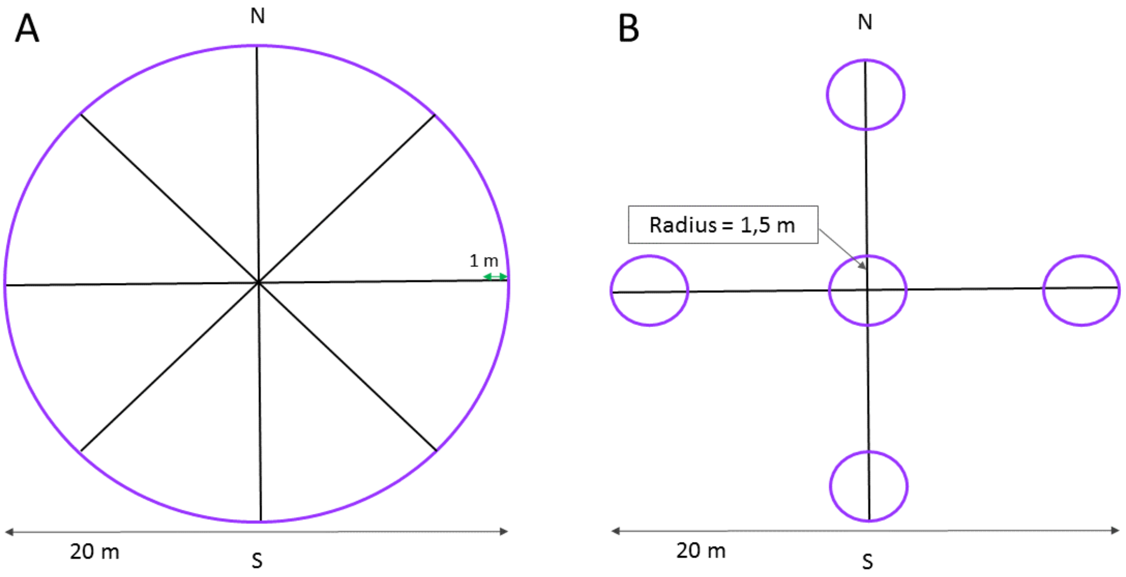

Figure A.2. Data collection design. Panel A represents the protocol followed in 2015 to measure lichen height in Swedish boreal forests dominated by mat-forming lichens. Lichen height was measured in 20cm-radius circles regularly spaced one meter apart along all transects depicted in the figure. Panel B represents the protocol followed to count reindeer pellet groups. Reindeer pellet groups were counted in the 5 subplots depicted in purple in the figure.

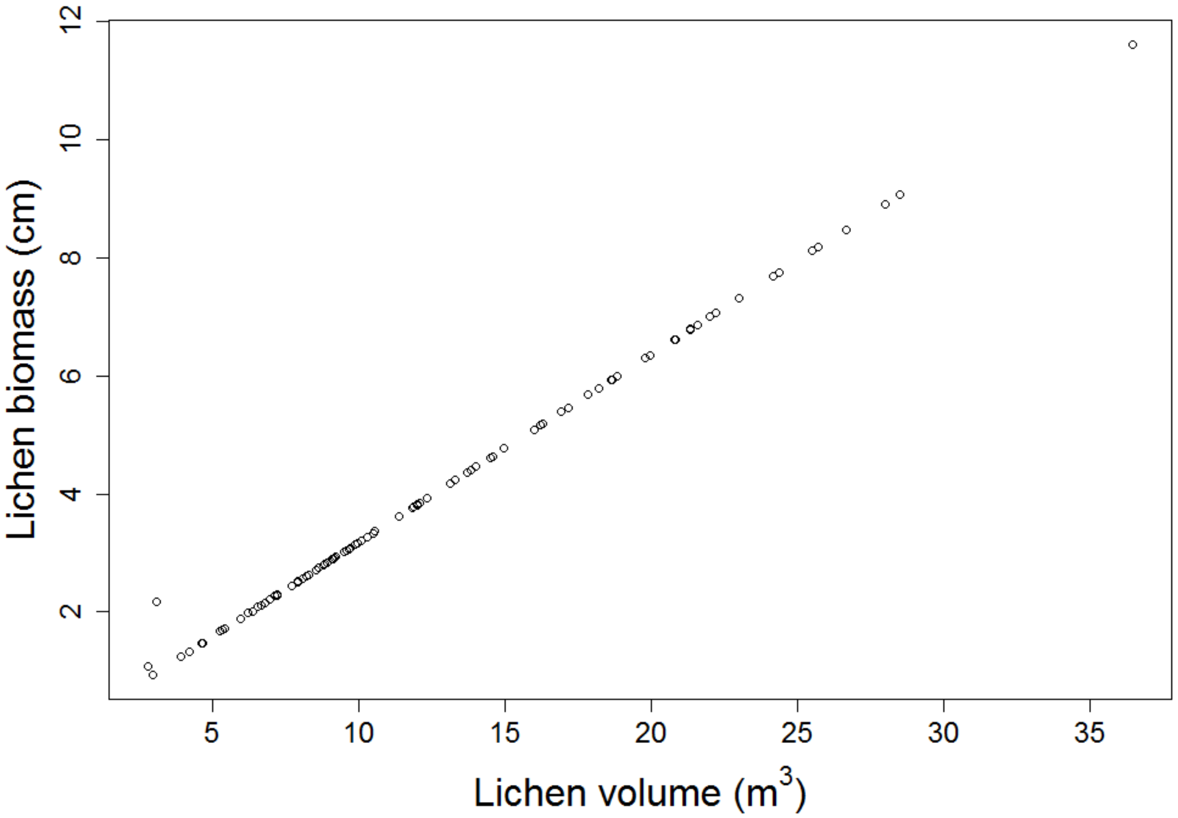

Figure A.3. Correlation between lichen biomass (y-axis) and lichen volume (x-axis) in 98 forest plots distributed within the reindeer herding husbandry area of northern Sweden. Lichen biomass was estimated as the average height of the lichen mat, including all measurements taken in a plot, i.e. also those in which lichen height = 0. Lichen volume was calculated by multiplying average lichen height by lichen cover. In the main manuscript lichen height is referred to as LH and is measured in centimeters, but for this calculation it was converted to meters. Here, lichen cover was estimated by multiplying LC (see main manuscript) by the area of the plot. Thus, here lichen cover is the proportion of the area of the plot, in m^2, covered by mat-forming lichens. Each sample plot had an area of 314.16 m^2. For details about the methods used to collect data on LH and LC, see subsections 2.2.3 and 2.2.4 in the Methods section of the main manuscript. The Pearson correlation coefficient between lichen biomass and lichen volume was 0.99.

Appendix A

Table A.1. Equations predicting the probability (p) of a forest plot being lichen-dominated. The equations were obtained from the regression model described in Table 2. Predictor variables are described in Table 1 and in subsection 2.1 of the main manuscript. The regression model included two categorical variables, aspect (A) and forest type (FT), and here we report different equations for each category of those variables. Scots pine = *Pinus sylvestris*; Lodgepole pine = *Pinus contorta*; Norway spruce = *Picea abies*.

Categorical variable	**Equation**
A = north; FT = Scots pine	$p = \frac{\exp(-2.86 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope)}{\exp(-2.86 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope) + 1}$
A = north; FT = clear-cut	$p = \frac{\exp(-7.50 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope)}{\exp(-7.50 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope) + 1}$
A = north; FT = Lodgepole pine	$p = \frac{\exp(-4.00 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope)}{\exp(-4.00 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope) + 1}$
A = north; FT = mixed	$p = \frac{\exp(-5.30 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope)}{\exp(-5.30 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope) + 1}$
A = north; FT = mixed conifer	$p = \frac{\exp(-4.37 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope)}{\exp(-4.37 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope) + 1}$
A = north; FT = Norway spruce	$p = \frac{\exp(-5.79 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope)}{\exp(-5.79 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope) + 1}$
A = east; FT = Scots pine	$p = \frac{\exp(-2.41 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope)}{\exp(-2.41 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope) + 1}$
A = east; FT = clear-cut	$p = \frac{\exp(-7.06 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope)}{\exp(-7.06 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope) + 1}$
A = east; FT = Lodgepole pine	$p = \frac{\exp(-3.55 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope)}{\exp(-3.55 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope) + 1}$
A = east; FT = mixed	$p = \frac{\exp(-4.86 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope)}{\exp(-4.86 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope) + 1}$

Appendix A

Categorical variable	Equation
A = east; FT = mixed conifer	$p = \frac{\exp(-3.92 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope)}{\exp(-3.92 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope) + 1}$
A = east; FT = Norway spruce	$p = \frac{\exp(-5.35 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope)}{\exp(-5.35 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope) + 1}$
A = northeast; FT = Scots pine	$p = \frac{\exp(-2.41 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope)}{\exp(-2.41 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope) + 1}$
A = northeast; FT = clear-cut	$p = \frac{\exp(-7.05 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope)}{\exp(-7.05 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope) + 1}$
A = northeast; FT = Lodgepole pine	$p = \frac{\exp(-3.55 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope)}{\exp(-3.55 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope) + 1}$
A = northeast; FT = mixed	$p = \frac{\exp(-4.85 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope)}{\exp(-4.85 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope) + 1}$
A = northeast; FT = mixed conifer	$p = \frac{\exp(-3.92 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope)}{\exp(-3.92 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope) + 1}$
A = northeast; FT = Norway spruce	$p = \frac{\exp(-5.34 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope)}{\exp(-5.34 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope) + 1}$
A = northwest; FT = Scots pine	$p = \frac{\exp(-2.13 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope)}{\exp(-2.13 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope) + 1}$
A = northwest; FT = clear-cut	$p = \frac{\exp(-6.77 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope)}{\exp(-6.77 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope) + 1}$
A = northwest; FT = Lodgepole pine	$p = \frac{\exp(-3.27 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope)}{\exp(-3.27 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope) + 1}$
A = northwest; FT = mixed	$p = \frac{\exp(-4.57 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope)}{\exp(-4.57 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope) + 1}$

Appendix A

Categorical variable	**Equation**
A = northwest; FT = mixed conifer	$p = \frac{\exp(-3.64 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope)}{\exp(-3.64 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope) + 1}$
A = northwest; FT = Norway spruce	$p = \frac{\exp(-5.06 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope)}{\exp(-5.06 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope) + 1}$
A = south; FT = Scots pine	$p = \frac{\exp(-1.92 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope)}{\exp(-1.92 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope) + 1}$
A = south; FT = clear-cut	$p = \frac{\exp(-6.56 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope)}{\exp(-6.56 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope) + 1}$
A = south; FT = Lodgepole pine	$p = \frac{\exp(-3.06 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope)}{\exp(-3.06 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope) + 1}$
A = south; FT = mixed	$p = \frac{\exp(-4.36 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope)}{\exp(-4.36 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope) + 1}$
A = south; FT = mixed conifer	$p = \frac{\exp(-3.43 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope)}{\exp(-3.43 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope) + 1}$
A = south; FT = Norway spruce	$p = \frac{\exp(-4.85 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope)}{\exp(-4.85 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope) + 1}$
A = southeast; FT = Scots pine	$p = \frac{\exp(-2.16 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope)}{\exp(-2.16 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope) + 1}$
A = southeast; FT = clear-cut	$p = \frac{\exp(-6.80 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope)}{\exp(-6.80 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope) + 1}$
A = southeast; FT = Lodgepole pine	$p = \frac{\exp(-3.30 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope)}{\exp(-3.30 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\mathrm{precip\_su} - 0.01\,\mathrm{precip\_w} - 0.10\,temp\_w - 0.06\,slope) + 1}$

Appendix A

Categorical variable	**Equation**
A = southeast; FT = mixed	$p = \frac{\exp(-4.61 - 0.04\,\mathit{basal\ area} - 0.03\,\mathit{canopy\ cover} + 0.0024\,\mathit{age} + 0.01\,\text{precip\_su} - 0.01\,\text{precip\_w} - 0.10\,\mathit{temp\_w} - 0.06\,\mathit{slope})}{\exp(-4.61 - 0.04\,\mathit{basal\ area} - 0.03\,\mathit{canopy\ cover} + 0.0024\,\mathit{age} + 0.01\,\text{precip\_su} - 0.01\,\text{precip\_w} - 0.10\,\mathit{temp\_w} - 0.06\,\mathit{slope}) + 1}$
A = southeast; FT = mixed conifer	$p = \frac{\exp(-3.67 - 0.04\,\mathit{basal\ area} - 0.03\,\mathit{canopy\ cover} + 0.0024\,\mathit{age} + 0.01\,\text{precip\_su} - 0.01\,\text{precip\_w} - 0.10\,\mathit{temp\_w} - 0.06\,\mathit{slope})}{\exp(-3.67 - 0.04\,\mathit{basal\ area} - 0.03\,\mathit{canopy\ cover} + 0.0024\,\mathit{age} + 0.01\,\text{precip\_su} - 0.01\,\text{precip\_w} - 0.10\,\mathit{temp\_w} - 0.06\,\mathit{slope}) + 1}$
A = southeast; FT = Norway spruce	$p = \frac{\exp(-5.09 - 0.04\,\mathit{basal\ area} - 0.03\,\mathit{canopy\ cover} + 0.0024\,\mathit{age} + 0.01\,\text{precip\_su} - 0.01\,\text{precip\_w} - 0.10\,\mathit{temp\_w} - 0.06\,\mathit{slope})}{\exp(-5.09 - 0.04\,\mathit{basal\ area} - 0.03\,\mathit{canopy\ cover} + 0.0024\,\mathit{age} + 0.01\,\text{precip\_su} - 0.01\,\text{precip\_w} - 0.10\,\mathit{temp\_w} - 0.06\,\mathit{slope}) + 1}$
A = southwest; FT = Scots pine	$p = \frac{\exp(-1.86 - 0.04\,\mathit{basal\ area} - 0.03\,\mathit{canopy\ cover} + 0.0024\,\mathit{age} + 0.01\,\text{precip\_su} - 0.01\,\text{precip\_w} - 0.10\,\mathit{temp\_w} - 0.06\,\mathit{slope})}{\exp(-1.86 - 0.04\,\mathit{basal\ area} - 0.03\,\mathit{canopy\ cover} + 0.0024\,\mathit{age} + 0.01\,\text{precip\_su} - 0.01\,\text{precip\_w} - 0.10\,\mathit{temp\_w} - 0.06\,\mathit{slope}) + 1}$
A = southwest; FT = clear-cut	$p = \frac{\exp(-6.50 - 0.04\,\mathit{basal\ area} - 0.03\,\mathit{canopy\ cover} + 0.0024\,\mathit{age} + 0.01\,\text{precip\_su} - 0.01\,\text{precip\_w} - 0.10\,\mathit{temp\_w} - 0.06\,\mathit{slope})}{\exp(-6.50 - 0.04\,\mathit{basal\ area} - 0.03\,\mathit{canopy\ cover} + 0.0024\,\mathit{age} + 0.01\,\text{precip\_su} - 0.01\,\text{precip\_w} - 0.10\,\mathit{temp\_w} - 0.06\,\mathit{slope}) + 1}$
A = southwest; FT = Lodgepole pine	$p = \frac{\exp(-3.00 - 0.04\,\mathit{basal\ area} - 0.03\,\mathit{canopy\ cover} + 0.0024\,\mathit{age} + 0.01\,\text{precip\_su} - 0.01\,\text{precip\_w} - 0.10\,\mathit{temp\_w} - 0.06\,\mathit{slope})}{\exp(-3.00 - 0.04\,\mathit{basal\ area} - 0.03\,\mathit{canopy\ cover} + 0.0024\,\mathit{age} + 0.01\,\text{precip\_su} - 0.01\,\text{precip\_w} - 0.10\,\mathit{temp\_w} - 0.06\,\mathit{slope}) + 1}$
A = southwest; FT = mixed	$p = \frac{\exp(-4.30 - 0.04\,\mathit{basal\ area} - 0.03\,\mathit{canopy\ cover} + 0.0024\,\mathit{age} + 0.01\,\text{precip\_su} - 0.01\,\text{precip\_w} - 0.10\,\mathit{temp\_w} - 0.06\,\mathit{slope})}{\exp(-4.30 - 0.04\,\mathit{basal\ area} - 0.03\,\mathit{canopy\ cover} + 0.0024\,\mathit{age} + 0.01\,\text{precip\_su} - 0.01\,\text{precip\_w} - 0.10\,\mathit{temp\_w} - 0.06\,\mathit{slope}) + 1}$
A = southwest; FT = mixed conifer	$p = \frac{\exp(-3.37 - 0.04\,\mathit{basal\ area} - 0.03\,\mathit{canopy\ cover} + 0.0024\,\mathit{age} + 0.01\,\text{precip\_su} - 0.01\,\text{precip\_w} - 0.10\,\mathit{temp\_w} - 0.06\,\mathit{slope})}{\exp(-3.37 - 0.04\,\mathit{basal\ area} - 0.03\,\mathit{canopy\ cover} + 0.0024\,\mathit{age} + 0.01\,\text{precip\_su} - 0.01\,\text{precip\_w} - 0.10\,\mathit{temp\_w} - 0.06\,\mathit{slope}) + 1}$
A = southwest; FT = Norway spruce	$p = \frac{\exp(-4.79 - 0.04\,\mathit{basal\ area} - 0.03\,\mathit{canopy\ cover} + 0.0024\,\mathit{age} + 0.01\,\text{precip\_su} - 0.01\,\text{precip\_w} - 0.10\,\mathit{temp\_w} - 0.06\,\mathit{slope})}{\exp(-4.79 - 0.04\,\mathit{basal\ area} - 0.03\,\mathit{canopy\ cover} + 0.0024\,\mathit{age} + 0.01\,\text{precip\_su} - 0.01\,\text{precip\_w} - 0.10\,\mathit{temp\_w} - 0.06\,\mathit{slope}) + 1}$
A = west; FT = Scots pine	$p = \frac{\exp(-1.94 - 0.04\,\mathit{basal\ area} - 0.03\,\mathit{canopy\ cover} + 0.0024\,\mathit{age} + 0.01\,\text{precip\_su} - 0.01\,\text{precip\_w} - 0.10\,\mathit{temp\_w} - 0.06\,\mathit{slope})}{\exp(-1.94 - 0.04\,\mathit{basal\ area} - 0.03\,\mathit{canopy\ cover} + 0.0024\,\mathit{age} + 0.01\,\text{precip\_su} - 0.01\,\text{precip\_w} - 0.10\,\mathit{temp\_w} - 0.06\,\mathit{slope}) + 1}$
A = west; FT = clear-cut	$p = \frac{\exp(-6.58 - 0.04\,\mathit{basal\ area} - 0.03\,\mathit{canopy\ cover} + 0.0024\,\mathit{age} + 0.01\,\text{precip\_su} - 0.01\,\text{precip\_w} - 0.10\,\mathit{temp\_w} - 0.06\,\mathit{slope})}{\exp(-6.58 - 0.04\,\mathit{basal\ area} - 0.03\,\mathit{canopy\ cover} + 0.0024\,\mathit{age} + 0.01\,\text{precip\_su} - 0.01\,\text{precip\_w} - 0.10\,\mathit{temp\_w} - 0.06\,\mathit{slope}) + 1}$

Appendix A

Categorical variable	Equation
A = west; FT = Lodgepole pine	$p = \frac{\exp(-3.08 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\text{precip\_su} - 0.01\,\text{precip\_w} - 0.10\,temp\_w - 0.06\,slope)}{\exp(-3.08 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\text{precip\_su} - 0.01\,\text{precip\_w} - 0.10\,temp\_w - 0.06\,slope) + 1}$
A = west; FT = mixed	$p = \frac{\exp(-4.39 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\text{precip\_su} - 0.01\,\text{precip\_w} - 0.10\,temp\_w - 0.06\,slope)}{\exp(-4.39 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\text{precip\_su} - 0.01\,\text{precip\_w} - 0.10\,temp\_w - 0.06\,slope) + 1}$
A = west; FT = mixed conifer	$p = \frac{\exp(-3.45 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\text{precip\_su} - 0.01\,\text{precip\_w} - 0.10\,temp\_w - 0.06\,slope)}{\exp(-3.45 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\text{precip\_su} - 0.01\,\text{precip\_w} - 0.10\,temp\_w - 0.06\,slope) + 1}$
A = west; FT = Norway spruce	$p = \frac{\exp(-4.88 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\text{precip\_su} - 0.01\,\text{precip\_w} - 0.10\,temp\_w - 0.06\,slope)}{\exp(-4.88 - 0.04\,basal\ area - 0.03\,canopy\ cover + 0.0024\,age + 0.01\,\text{precip\_su} - 0.01\,\text{precip\_w} - 0.10\,temp\_w - 0.06\,slope) + 1}$

Table A.2. Lichen biomass (LB), lichen height (LH), and lichen cover (LC) values measured in 2015 in 98 plots distributed across the Swedish reindeer husbandry area. For details on how the measurements were performed, see subsections 2.2.3 and 2.2.4 in the Methods section of the main manuscript. SD = standard deviation

Plot ID	**LB**		**LH**		**LC**
	Mean	SD	Mean	SD	
1	5.68	3.59	7.30	2.14	0.78
2	5.46	3.28	6.15	2.80	0.89
3	2.61	2.09	3.85	1.27	0.68
4	1.70	2.82	5.98	1.48	0.28
5	2.02	2.14	3.57	1.59	0.57
6	0.94	1.86	4.22	1.30	0.22
7	2.75	3.48	6.74	1.59	0.41
8	3.27	1.54	3.35	1.47	0.98
9	2.21	2.69	4.48	2.11	0.49
10	2.51	1.28	2.79	1.02	0.90
11	2.79	1.06	2.79	1.06	1.00
12	7.69	3.47	8.42	2.64	0.91
13	6.79	2.03	6.79	2.03	1.00
14	11.60	2.60	11.75	2.26	0.99
15	8.19	3.42	8.61	2.93	0.95
16	6.35	2.49	6.51	2.30	0.98
17	8.48	2.21	8.59	2.01	0.99
18	4.40	3.65	5.93	2.96	0.74
19	1.67	2.22	4.22	1.29	0.40
20	1.08	1.98	3.40	1.37	0.26

Appendix A

Plot ID	LB		LH		LC
	Mean	SD	Mean	SD	
21	1.48	1.96	2.49	2.00	0.59
22	2.28	2.52	4.40	1.69	0.52
23	3.20	1.55	3.55	1.19	0.90
24	2.80	2.07	3.91	1.26	0.72
25	2.29	1.24	2.32	1.22	0.99
26	2.18	0.93	0.98	0.16	1.00
27	2.63	1.60	3.09	1.25	0.85
28	2.44	1.23	2.71	0.98	0.90
29	3.04	1.17	3.04	1.17	1.00
30	2.80	1.52	3.06	1.31	0.91
31	1.72	1.11	2.02	0.92	0.85
32	1.24	1.53	2.51	1.23	0.49
33	3.17	2.09	4.07	1.38	0.78
34	6.30	2.75	6.63	2.40	0.95
35	2.27	2.11	2.55	2.07	0.89
36	4.23	2.32	4.69	1.94	0.90
37	5.19	2.22	5.19	2.22	1.00
38	5.09	3.69	6.34	3.00	0.80
39	2.93	1.98	3.29	1.78	0.89
40	3.84	3.25	5.65	2.28	0.68
41	2.60	3.97	7.81	2.48	0.33
42	1.89	1.90	3.12	1.44	0.60
43	2.52	2.73	4.98	1.55	0.51

Appendix A

Plot ID	LB		LH		LC
	Mean	SD	Mean	SD	
44	5.16	2.00	5.57	1.42	0.93
45	2.89	1.45	3.16	1.20	0.91
46	2.72	2.70	5.00	1.38	0.54
47	3.07	1.74	3.36	1.53	0.91
48	4.46	1.65	4.46	1.65	1.00
49	1.47	0.84	1.47	0.84	1.00
50	1.48	0.73	1.48	0.73	1.00
51	5.93	2.53	6.58	1.66	0.90
52	5.93	1.44	5.93	1.44	1.00
53	3.09	2.53	4.72	1.43	0.65
54	4.36	1.91	4.77	1.42	0.91
55	2.09	1.52	2.09	1.52	1.00
56	2.16	1.47	2.43	1.33	0.89
57	3.07	1.41	3.36	1.09	0.91
58	4.62	2.34	4.99	2.01	0.93
59	4.77	2.04	4.95	1.84	0.96
60	5.39	2.96	6.42	1.94	0.84
61	2.92	2.61	4.38	1.94	0.67
62	5.79	4.00	7.82	2.37	0.74
63	3.93	1.97	3.93	1.97	1.00
64	3.81	1.88	3.81	1.88	1.00
65	3.38	2.65	4.80	1.76	0.70
66	9.07	3.25	9.42	2.77	0.96

Appendix A

Plot ID	**LB**		**LH**		**LC**
	Mean	SD	Mean	SD	
67	7.00	4.34	8.34	3.35	0.84
68	7.75	4.33	9.52	2.45	0.81
69	8.91	3.02	9.14	2.69	0.98
70	8.11	3.62	8.76	2.89	0.93
71	6.78	4.03	8.20	2.82	0.83
72	7.31	3.96	8.35	3.04	0.88
73	7.07	4.79	9.10	3.30	0.78
74	6.62	3.75	7.25	3.29	0.91
75	6.61	5.52	10.30	3.01	0.64
76	2.12	1.50	2.49	1.32	0.85
77	6.86	3.34	7.83	2.25	0.88
78	2.02	1.26	2.34	1.05	0.86
79	2.81	1.16	2.84	1.12	0.99
80	2.57	1.25	2.57	1.25	1.00
81	1.33	0.56	1.33	0.56	1.00
82	1.98	1.12	2.00	1.11	0.99
83	3.77	1.49	3.81	1.44	0.99
84	2.21	1.12	2.21	1.12	1.00
85	2.90	2.02	3.61	1.58	0.80
86	3.33	1.19	3.38	1.14	0.99
87	4.64	2.41	4.88	2.22	0.95
88	4.18	2.65	5.21	1.83	0.80
89	2.83	2.05	3.53	1.66	0.80

Appendix A

Plot ID	**LB**		**LH**		**LC**
	Mean	SD	Mean	SD	
90	3.21	2.34	4.41	1.47	0.73
91	3.02	1.48	3.02	1.48	1.00
92	3.14	2.97	5.53	1.48	0.57
93	2.12	2.71	5.06	1.59	0.42
94	3.62	2.85	4.81	2.24	0.75
95	3.93	2.61	4.42	2.34	0.89
96	5.99	3.43	6.94	2.64	0.86
97	3.82	2.89	4.62	2.52	0.83
98	3.78	2.82	5.10	1.97	0.74
Mean	3.98		4.89		0.82
SD	2.15		2.29		0.19

Table A.3. Reduced mixed-effect regression model predicting lichen biomass in boreal forests dominated by mat-forming lichens. This model was derived from the best-fit model detailed in Table A.4 by removing the non-significant variables as detailed in the Methods section. Mountain is one of the two categories of the variable HD (= herding district), where forest is the reference category. Random term standard deviation = 0.92. β = regression coefficient mean estimate; SE = standard error of the coefficient estimate. This model had an Akaike Information Criterion (AIC, Burnham and Anderson, 2002) = 348.87, which was slightly higher than the AIC of the best-fit model reported in Table A.4 (AIC = 345.96).

Predictor	**β**	**SE**	**p-value**
intercept	-3.92	1.31	
canopy cover	0.02	0.01	0.0087
exp(-*pellets*)	0.47	0.36	0.1937
mountain	1.11	0.38	0.0049
precip_su	0.03	0.01	< 0.0001

Table A.4. Best-fit mixed-effect regression model predicting lichen biomass in boreal forests dominated by mat-forming lichens. This model was developed from a full model including all predictor variables described in Table 1 and in subsection 2.2 of the main manuscript, with *Cluster* as random term (standard deviation = 0.91). Meteorological variables refer to averages calculated over the 5 years preceding the collection of lichen biomass data (i.e. 2010-2014). Mountain is one of the two categories of the variable HD (= herding district), where forest is the reference category. The categories of the “aspect” variable are marked with a º, and north was the reference category. All continuous variables are highlighted in italic. A colon mark (:) indicates an interaction term. β = regression coefficient mean estimate; SE = standard error of the coefficient estimate.

Predictor	β	SE	p-value
intercept	-36.43	24.24	
age	-0.01	0.00	0.1047
canopy cover	0.03	0.01	0.0135
exp(-*pellets*)	0.63	0.40	0.1229
mountain	0.99	0.38	0.0120
precip_su	0.21	0.12	0.0960
temp_su	2.85	1.91	0.1464
east º	0.52	0.60	0.3904
northeast º	0.64	0.57	0.2729
northwest º	1.38	0.86	0.1177
south º	-0.56	0.72	0.4396
southeast º	-0.66	0.61	0.2905
southwest º	-0.23	0.58	0.7008
west º	-0.68	0.76	0.3764
sand	-0.03	0.02	0.1343
precip_su:*temp_su*	-0.02	0.01	0.1353

Table A.5. Reduced linear regression model predicting lichen height in boreal forests dominated by mat-forming lichens. This model was derived from the best-fit model detailed in Table A.7 by removing the non-significant variables as detailed in the Methods section. Mountain is one of the two categories of the variable HD (= herding district), where forest is the reference category. The categories of the “aspect” variable are marked with a ^{o}, and north is the reference category. β = regression coefficient estimate; SE = standard error of the coefficient estimate. This model had an adjusted $R^2 = 0.65$ and an Akaike Information Criterion (AIC, Burnham and Anderson, 2002) = 350.91, which was higher than the AIC of the best-fit model reported in Table A.6 (AIC = 341.61).

Predictor	**β**	**SE**	**p-value**
intercept	-2.78	1.08	
canopy cover	0.02	0.01	0.0122
exp(-*pellets*)	2.08	0.37	<0.0001
mountain	1.52	0.31	<0.0001
precip_su	0.03	0.00	<0.0001
east ^{o}	-0.39	0.62	0.5316
northeast ^{o}	-0.21	0.63	0.7373
northwest ^{o}	-0.97	0.89	0.2793
south ^{o}	-1.87	0.72	0.0107
southeast ^{o}	-1.35	0.68	0.0495
southwest ^{o}	-0.98	0.60	0.1051
west ^{o}	-1.70	0.77	0.0298

Table A.6. Equations predicting lichen height (LH) in boreal forests dominated by mat-forming lichens. The equations were obtained from the reduced regression model described in Table A.5. Predictor variables are described in Table 1 and in the subsection 2.2 of the main manuscript. The regression model included two categorical variables and here we report different equations for each combination of their categories.

Categorical variables	**Model**
HD = forest; aspect = north	$LH = -2.78 + 0.02\ \textit{canopy cover} + 2.08 \exp(-\textit{pellets}) + 0.03\ \textit{precip\_su}$
HD = forest; aspect = east	$LH = -3.17 + 0.02\ \textit{canopy cover} + 2.08 \exp(-\textit{pellets}) + 0.03\ \textit{precip\_su}$
HD = forest; aspect = northeast	$LH = -2.99 + 0.02\ \textit{canopy cover} + 2.08 \exp(-\textit{pellets}) + 0.03\ \textit{precip\_su}$
HD = forest; aspect = northwest	$LH = -3.75 + 0.02\ \textit{canopy cover} + 2.08 \exp(-\textit{pellets}) + 0.03\ \textit{precip\_su}$
HD = forest; aspect = south	$LH = -4.65 + 0.02\ \textit{canopy cover} + 2.08 \exp(-\textit{pellets}) + 0.03\ \textit{precip\_su}$
HD = forest; aspect = southeast	$LH = -4.13 + 0.02\ \textit{canopy cover} + 2.08 \exp(-\textit{pellets}) + 0.03\ \textit{precip\_su}$
HD = forest; aspect = southwest	$LH = -3.76 + 0.02\ \textit{canopy cover} + 2.08 \exp(-\textit{pellets}) + 0.03\ \textit{precip\_su}$
HD = forest; aspect = west	$LH = -4.48 + 0.02\ \textit{canopy cover} + 2.08 \exp(-\textit{pellets}) + 0.03\ \textit{precip\_su}$
HD = mountain; aspect = north	$LH = -1.26 + 0.02\ \textit{canopy cover} + 2.08 \exp(-\textit{pellets}) + 0.03\ \textit{precip\_su}$
HD = mountain; aspect = east	$LH = -1.65 + 0.02\ \textit{canopy cover} + 2.08 \exp(-\textit{pellets}) + 0.03\ \textit{precip\_su}$
HD = mountain; aspect = northeast	$LH = -1.47 + 0.02\ \textit{canopy cover} + 2.08 \exp(-\textit{pellets}) + 0.03\ \textit{precip\_su}$
HD = mountain; aspect = northwest	$LH = -2.23 + 0.02\ \textit{canopy cover} + 2.08 \exp(-\textit{pellets}) + 0.03\ \textit{precip\_su}$
HD = mountain; aspect = south	$LH = -3.13 + 0.02\ \textit{canopy cover} + 2.08 \exp(-\textit{pellets}) + 0.03\ \textit{precip\_su}$

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Categorical variables	**Model**
HD = mountain; aspect = southeast	$LH = -2.60 + 0.02\,\mathit{canopy\ cover} + 2.08\exp(-\mathit{pellets}) + 0.03\,\mathit{precip\_su}$
HD = mountain; aspect = southwest	$LH = -2.24 + 0.02\,\mathit{canopy\ cover} + 2.08\exp(-\mathit{pellets}) + 0.03\,\mathit{precip\_su}$
HD = mountain; aspect = west	$LH = -2.96 + 0.02\,\mathit{canopy\ cover} + 2.08\exp(-\mathit{pellets}) + 0.03\,\mathit{precip\_su}$

Table A.7. Best-fit linear regression model predicting lichen height in boreal forests dominated by mat-forming lichens. This model was developed from a full model including all predictor variables described in Table 1 and in subsection 2.2 of the main manuscript. Meteorological variables refer to averages calculated over the 5 years preceding the collection of lichen height data (i.e. 2010-2014). Mountain is one of the two categories of the variable HD (= herding district), where forest is the reference category. North was the reference category for the “aspect” variable and the other categories are marked with a ^{o}. All continuous variables are highlighted in italic. A colon mark (:) refers to an interaction term. β = regression coefficient estimate; SE = standard error of the coefficient estimate.

Predictor	**β**	**SE**	**p-value**
intercept	-43.89	21.37	
canopy cover	0.01	0.01	0.0939
exp(-*pellets*)	1.56	0.38	0.0001
mountain	1.58	0.40	0.0002
precip_su	0.23	0.10	0.0277
precip_w	-42.30	17.71	0.0193
precip_w^{2}	7.29	1.99	0.0004
temp_su	3.00	1.64	0.0705
temp_w	1.62	0.70	0.0230
east ^{o}	0.04	0.63	0.9479
northeast ^{o}	-0.11	0.60	0.8552
northwest ^{o}	-0.80	0.87	0.3606
south ^{o}	-1.22	0.71	0.0882
southeast ^{o}	-0.97	0.66	0.1444
southwest ^{o}	-0.51	0.59	0.3898
west ^{o}	-1.79	0.78	0.0241
AWC	61.39	28.50	0.0343
temp_su:*precip_su*	-0.02	0.01	0.0446
temp_w:*precip_w*	-0.02	0.01	0.0151

Table A.8. Quasibinomial mixed-effect regression model predicting lichen cover in boreal forests dominated by mat-forming lichens. This model was developed from a full model including all predictor variables described in Table 1 and in subsection 2.2 of the main manuscript. *Cluster* was the random term (standard deviation: 0.74). The categories of the "forest type" variable are marked with an asterisk. Scots pine (*Pinus sylvestris*) was the reference category. Lodgepole pine = *Pinus contorta*. Norway spruce = *Picea abies*. All continuous variables are highlighted in italic. β = regression coefficient mean estimate, which in a quasibinomial model is the log odd ratio; SE = standard error of the coefficient estimate.

Predictor	**β**	**SE**	**p-value**
intercept	4.82	1.02	
clear-cut *	-1.32	0.62	0.0414
lodgepole pine *	-0.15	0.44	0.7345
mixed *	-0.85	0.28	0.0041
mixed conifer *	-1.93	0.73	0.0108
Norway spruce *	-2.03	1.00	0.0468
age	-0.0045	0.0023	0.0520
log(*pellets* + 1)	0.69	0.17	0.0003
sand	-0.04	0.01	0.0023

Table A.9. Equations predicting lichen cover (LC) in boreal forests dominated by mat-forming lichens. The equations were obtained from the reduced regression model described in Table A.8. Predictor variables are described in Table 1 and in subsection 2.2 of the main manuscript. The regression model included one categorical variable, forest type (FT) and here we report different equations for each category of that variable. Scots pine = *Pinus sylvestris*; Lodgepole pine = *Pinus contorta*; Norway spruce = *Picea abies*.

Categorical variable	**Equation**
FT = Scots pine	$\mathrm{LC} = \frac{\exp(4.82 + 0.69\log(pellets + 1) - 0.04\,sand)}{\exp(4.82 + 0.69\log(pellets + 1) - 0.04\,sand) + 1}$
FT = clear-cut	$\mathrm{LC} = \frac{\exp(3.50 + 0.69\log(pellets + 1) - 0.04\,sand)}{\exp(3.50 + 0.69\log(pellets + 1) - 0.04\,sand) + 1}$
FT = Lodgepole pine	$\mathrm{LC} = \frac{\exp(3.35 + 0.69\log(pellets + 1) - 0.04\,sand)}{\exp(3.35 + 0.69\log(pellets + 1) - 0.04\,sand) + 1}$
FT = mixed	$\mathrm{LC} = \frac{\exp(2.50 + 0.69\log(pellets + 1) - 0.04\,sand)}{\exp(2.50 + 0.69\log(pellets + 1) - 0.04\,sand) + 1}$
FT = mixed conifer	$\mathrm{LC} = \frac{\exp(0.57 + 0.69\log(pellets + 1) - 0.04\,sand)}{\exp(0.57 + 0.69\log(pellets + 1) - 0.04\,sand) + 1}$
FT = Norway spruce	$\mathrm{LC} = \frac{\exp(-1.46 + 0.69\log(pellets + 1) - 0.04\,sand)}{\exp(-1.46 + 0.69\log(pellets + 1) - 0.04\,sand) + 1}$

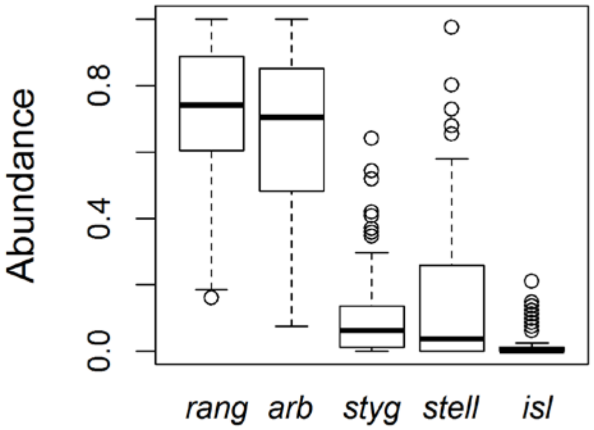

Figure A.4. Distribution of the abundance (y axis) of each of five mat-forming lichen species (x axis) in lichen-dominated boreal forests of northern Sweden. Data were collected in 2015 in 98 forest plots located in the counties of Jämland, Västerbotten and Norrbotten, Sweden. Forest plots are the sample unit. Species abundance is reported as the proportion of hits in a plot containing a certain species (see section 2.2 in the main manuscript for details on data collection). In each boxplot the median is represented by a bold horizontal bar, the interquartile range corresponds to the horizontal edges of the box, the dashed vertical lines extend to the range of data, and the circles outside the box indicate outliers. rang = *Cladonia rangiferina*; arb = *Cladonia arbuscula/mitis*; styg = *Cladonia stygia*; stell = *Cladonia stellaris*; isl = *Cetraria islandica*. *C. arbuscula* and *C. mitis* were pooled because they are impossible to distinguish visually. The median and interquartile range of the abundance of *C. rangiferina* and *C. arbuscula* are much higher than for the other species, which suggests that those two species are the most abundant in the lichen-dominated boreal forests of northern Sweden.

References

Burnham, K.P., Anderson, D.R., 2002. Model selection and multi-model inference: a practical information-theoretic approach. Springer-Verlag, New York, USA.