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1 **Modelling occurrence and status of mat-forming lichens in boreal forests to**

2 **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

62 winter (Andreyev, 1954) and the most abundant in northern ecosystems. All six species have

63 circumpolar arctic and boreal distribution and low growth rates (Sandström et al., 2006;

64 Thomson, 1984). *Cladonia* spp. are characterized by a branched, fruticose growth form and

65 are common on nutrient-poor soils in bogs, tundra, and boreal forests, while *Cetraria* spp.

66 have a leaf-like shape and grow in dry or wet tundra and in old spruce forests (Thomson,

67 1984). Light exposure, humidity, and air temperature are the key factors determining lichen

68 presence, abundance, and growth (Gaio-Oliveira et al., 2006; Jonsson Čabrajič et al., 2010).

69 Indeed, lichens are poikilohydric organisms that can survive in a metabolically inactive state

70 throughout long dry periods and regain their metabolic and photosynthetic activity only when

71 enough humidity is present. The amount of light that reaches them during this wet period

72 determines their growth rate. In Swedish forests, mat-forming lichens grow primarily in Scots

73 pine (*Pinus sylvestris*) heaths on dry oligotrophic soils (Ahti, 1961). In general, lichen cover

74 decreases in old pine forests on dry sites, probably due to reduced light availability and to

75 increased nutrient availability that promotes the expansion of mosses and shrubs which

76 outcompete lichens (reviewed in Berg et al., 2008). *C. stellaris* and *C. islandica* reach growth

77 peaks at intermediate light exposure and their growth rate is mainly determined by total

78 irradiance they receive when wet, chlorophyll concentration, site openness, and is negatively

79 correlated to air temperature (Čabrajič Jonsson et al., 2010). Čabrajič Jonsson et al. (2010)

80 found that tree basal area (m^2 ha^{-1}) can be used as a proxy for light exposure to determine

81 potential lichen growth. Reindeer grazing can also limit lichen growth (den Herder et al.,

82 2003; Moen and Danell, 2003), keeping mat-forming lichens at a height of few centimeters

83 (Roturier and Roué, 2009). Similarly, reindeer trampling may damage lichens, especially

84 when reoccurring frequently (reviewed in Crittenden, 2000). On the contrary, in some

85 occasions trampling and grazing by reindeer can thin the lichen mats and thus promote

86 recovery of the remaining lichen fragments (Gaio-Oliveira et al., 2006).

87   Despite the essential role that lichens play in boreal forests, large-scale tools to monitor

88   their status are rare. Some national inventories collect information on lichen horizontal

89   extent, usually quantified in terms of lichen cover. One example is the Swedish National

90   Forest Inventory (NFI, Anonymous, 2015). However, the thickness of the lichen mats, which

91   is strictly correlated to lichen biomass (Moen et al., 2007; Olofsson et al., 2011), is rarely

92   monitored on a large scale. Such monitoring is essential to quantify total lichen biomass and

93   to predict how climate change and human disturbances will affect lichens, ecosystem

94   functioning, and reindeer survival in the future. Reindeer herders, practitioners and

95   conservationists would greatly benefit from tools to estimate the past conditions of mat-

96   forming lichens and to detect current lichen hotspots. The purpose of this study was therefore

97   to develop regression models that can be translated into equations which allow the

98   assessment of lichen conditions when forest, meteorological, topographic and soil

99   characteristics of a certain area are known. We first developed a model describing the

100   occurrence of forests dominated by mat-forming lichens. Secondly, we developed models

101   describing lichen biomass, height (i.e., lichen vertical growth), and cover (i.e., lichen

102   horizontal extension) in those forests in which the ground layer is dominated by mat-forming

103   lichens (fig. 1). We hypothesized those forests to be dominated by Scots pine and

104   characterized by dry soils (Ahti, 1961). We also hypothesized that lichen biomass would be

105   favored by low basal area and thin canopy cover (Berg et al., 2008; Gaio-Oliveira et al.,

106   2006; Jonsson Čabrajič et al., 2010). Lastly, we hypothesized reindeer grazing to negatively

107   affect lichen height (den Herder et al., 2003; Holt et al., 2008; Moen and Danell, 2003), while

108   positively affecting lichen cover (Gaio-Oliveira et al. 2006).

109

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:

135   December-February; spring: March-May; summer: June-August; fall: September-November).

136   The temperature map for June 2009 was missing, so we did not develop a temperature map

137   for summer 2009. Similarly, we did not develop temperature and precipitation maps for

138   winter 2005 because maps for December 2004 were not available. A preliminary analysis

139   revealed that meteorological data averaged over a 5-year period (2010-2014) were highly

140   correlated to data averaged over a 10-year period (2005-2014). Therefore, we assumed that

141   data averaged over the 10-year period could confidently represent the spatial variability in

142   climatic conditions among plots in our study area. Similar patterns were suggested by

143   Jonsson Čabrajič et al. (2010). This assumption allowed us to test the importance of

144   meteorological conditions in determining lichen dominance even for those years for which

145   meteorological data were not available in map format (i.e. 1983-2004).

146   We derived topographic data from DEM maps with 50 m resolution downloaded from the

147   Läntmateriet website (accessed on April 28, 2016: http://www.lantmateriet.se/sv/Kartor-och-

148   geografisk-information/Hojddata/). For those areas where a 50 m resolution map was not

149   available, we used maps with 2 m resolution. In ArcGIS 10.2.1 (ESRI, 2014), we derived

150   slope and aspect maps from the DEMs. We obtained soil data, i.e. a map describing the

151   percentage of sand content and a map of Available Water Capacity (AWC) in the topsoil,

152   from the European Soil Data Centre, http://eusoils.jrc.ec.europa.eu/content/topsoil-physical-

153   properties-europe-based-lucas-topsoil-data (Ballabio et al., 2016). Lastly, we extracted

154   information from the meteorological, topographic and soil maps for each plot.

155

156   *2.1.2 Model development*

157   We developed a quasibinomial mixed-effect regression model in which lichen dominance

158   was the response variable, taking the value 1 for lichen-dominated plots and the value 0 for

159   moss-dominated plots. A quasibinomial model was necessary because the corresponding

160   binomial model suffered of overdispersion. The candidate predictor variables were basal area,

161   tree canopy cover, forest type, forest age, spring, summer and winter precipitation, summer

162   and winter temperature, slope, aspect, sand percentage in the soil (*sand*) and AWC. We did

163   not include spring and fall temperature as candidate predictor variables because they were

164   highly correlated with winter temperature (Pearson's correlation coefficient $r = 0.80$ and 0.88,

165   respectively). Similarly, we excluded fall precipitation from the analysis because it was

166   correlated with winter precipitation ($r = 0.88$). We did not include elevation in the model due

167   to its correlation with summer precipitation and temperature ($r = 0.66$ and -0.73,

168   respectively). We added *Cluster* as a random term in order to take into account the clustered

169   sampling design used by the NFI. We plotted a semivariogram for the within-group residuals,

170   using the *Variogram* function in the nlme package for R (Pinheiro et al., 2018), which

171   suggested that the model residuals were not spatially autocorrelated (Appendix A, fig. A.1,

172   panel A). In the full model, some of the candidate predictor variables were not statistically

173   significant (p-value > 0.05). Therefore, we used the *Anova* function in the car package for R

174   (Fox and Weisberg, 2011) to detect which candidate predictor variables could be removed

175   from the full model (p-value in the likelihood ratio test > 0.05). Models were developed in R

176   3.3.0 (R Development Core Team, 2017).

177

178   **2.2 Predicting lichen biomass, height and cover in lichen-dominated forests**

179   *2.2.1   Study area*

180   In July and September 2015, we visited 98 sample forest plots distributed in the boreal

181   forest zone within the Swedish reindeer herding husbandry area. Sample plots had been

182   previously inventoried and classified by the NFI as lichen-dominated, but we restricted the

183   selection to plots visited between 2010 and 2014 in order to take advantage of the detailed

184   description of forest characteristics compiled by the NFI. We located all sample plots using

185 the spatial coordinates provided by the NFI, and in most cases the original location was

186 confirmed by a wooden stick left by the NFI to mark the center of the plot. The plots had a

187 10 m radius, the same as the original NFI plots. We visited areas that are used both by forest

188 reindeer herding districts, which have both winter and summer pastures within the boreal

189 forest, and mountain herding districts, which use the boreal forest only during winter. Two

190 plots were in recent clear-cuts, five were dominated by lodgepole pine (*Pinus contorta*), one

191 by Norway spruce (*Picea abies*), 76 by Scots pine (*Pinus sylvestris*), two were in mixed

192 coniferous forests, and 12 were in mixed forests containing both conifers and deciduous trees,

193 predominantly birches (*Betula* spp.).

194

195   *2.2.2 Input open data*

196   For each plot visited in 2015, we obtained data on forest type, age, canopy cover and basal

197 area from the NFI dataset. We updated data on forest age to the year of study (i.e. 2015). For

198 recent clear-cuts, we set age, canopy cover and basal area to 0. Since boreal forests have very

199 slow growth rates (Archibold, 1995), data on all other forest characteristics were recent

200 enough to be included in our models as provided by the NFI.

201   Because mat-forming lichens have very slow growth rates (den Herder et al., 2003; Pegau,

202 1968; Scotter, 1963; Thomson, 1984), we hypothesized that the meteorological conditions of

203 several previous years would affect current lichen conditions. Since in our study area

204 meteorological data were correlated over a 5- and a 10-year period (see subsection 2.1.1), we

205 decided to consider the average meteorological conditions of each plot over the 5 years

206 preceding the field measurements (i.e., 2010-2014), keeping the data divided by season as

207 described in subsection 2.1.1. For each plot, we extracted information about topography and

208 soil from the same maps described in subsection 2.1.1.

209

210   *2.2.3 Field measurements*

211   We measured lichen height in all sample plots as the average height of all mat-forming

212   lichen species described in the Introduction, in 20cm-radius circles (hereafter, hits) regularly

213   spaced one meter apart in the direction of the cardinal and half-cardinal points starting from

214   the center of the sample plot, following Uotila et al. (2005) (Appendix A, fig. A.2 – panel A).

215   We used a graduated rod with a plate that rests on the lichen thalli to take the measurements

216   (Olofsson et al., 2011). During the measurement, the rod was held perpendicular to the soil

217   without penetrating into the litter and humus layer. Lichen height was measured with a

218   precision of 0.5 cm. This technique provided 81 measurements of lichen height for each plot.

219   If lichens were not present, we noted lichen height = 0 cm. For each hit, we also recorded

220   which lichen species were present.

221   We estimated the intensity of use of the area by reindeer by counting reindeer pellet

222   groups in five subplots within each sample plot using the fecal standing crop technique

223   (Appendix A, fig. A.2 – panel B) (McClanahan, 1986). We only counted pellet groups that

224   included at least 50 pellets and which laid for at least half of their extent in the plots

225   (following Skarin, 2007). In mountain herding districts the boreal forest is only used in

226   winter, while in forest herding districts lichen-dominated forests can be used or at least

227   travelled on also during the snow-free season. Therefore, we only counted winter pellets.

228   During winter, reindeer pellets are dryer and appear as separate drops. Summer pellets are

229   wetter and the individual pellets are clumped together, making them easy to distinguish from

230   winter ones.

231

232   *2.2.4 Model development*

233   Based on the field data collected in 2015, we developed three separate regression models

234   with three proxies of lichen conditions as response variables: lichen biomass (LB), lichen

235 height (LH), and lichen cover (LC). For each sampling plot, we estimated LB by averaging

236 all 81 measurements of lichen height taken in a plot, i.e. including the hits where lichen

237 height = 0 cm. LB is therefore expressed in centimeters. LB is a comprehensive measurement

238 that takes into account both lichen height and cover, thus being a good approximation for

239 food availability for reindeer (Moen et al., 2007). LB is also strictly correlated with lichen

240 volume (Appendix A, fig. A.3). We estimated LH by averaging lichen height over all those

241 hits in which lichens were present (i.e., lichen height > 0 cm). Lastly, we estimated LC as the

242 proportion of hits where lichens were present in each plot.

243   We started by running a Gaussian mixed-effect linear regression model (GLMM) with LB

244 as response variable, *Cluster* as random term, and all the variables described in Table 1 as

245 candidate predictor variables, plus interaction terms between summer temperature and

246 precipitation and between winter temperature and precipitation, with the purpose of taking

247 into account the effect that extreme meteorological conditions may have on lichen growth

248 (Skuncke, 1969: 29). By visual inspection we determined that the relationship between pellet

249 group counts (*pellets*) and LB followed a decreasing exponential curve, so we included

250 *pellets* in the form of exp(-*pellets*). The GLMM had a lower Akaike Information Criterion

251 (AIC, Burnham and Anderson, 2002) compared to an analogous fixed-term regression model,

252 so we retained the random term. A semivariogram for the within-group residuals, drawn

253 using the *Variogram* function in the nlme package for R (Pinheiro et al., 2018), suggested

254 that the model residuals were not spatially autocorrelated (Appendix A, fig. A.1, panel B).

255 Subsequently, we used the *stepAIC* function in the MASS package for R 3.3.0 (Venables and

256 Ripley, 2002) to run an automatic bidirectional elimination procedure in order to detect the

257 set of predictor variables that provided the best-fit model based on AIC. In addition to the

258 best-fit model, we also developed a reduced model by removing those variables for which the

259 p-value in the likelihood ratio test provided by the Analysis of Variance table produced by

260   the *anova* function in R 3.3.0 (R Development Core Team, 2017) was > 0.05. We developed

261   the reduced model because the purpose of our study was to create relatively simple equations

262   for stakeholders' use. Thus, we believe that a model that performs slightly worse than the

263   best-fit model but contains less predictor variables is more valuable to stakeholders.

264   Similarly we ran a GLMM with LH as a response variable, and the same random and fixed

265   terms as for the LB model as predictors, with the exception of winter precipitation

266   (*precip_1014w*) which we included as a second-order polynomial because of its parabolic

267   relationship with LH. The semivariogram for the within-group residuals suggested that the

268   model residuals were not spatially autocorrelated (Appendix A, fig. A.1, panel C).

269   Comparing the GLMM with an analogous fixed-term regression model as above, we

270   determined that the random term (*Cluster*) was not needed (Standard Deviation: 0.37), so we

271   proceeded with a fixed-effect linear regression model. Finally, we developed a best-fit and a

272   reduced model following the same procedure as for LB.

273   Subsequently, we ran a mixed-effect quasibinomial model, i.e. a GLMM with logit

274   function, to link LC to the candidate predictor variables described in Table 1, with the

275   exception of *pellets*, which was included in the form of ln(*pellets*+1) because we determined

276   by visual inspection that its relationship with the logit of LC followed a logarithmic curve.

277   The +1 allows the calculation of the logarithm of values = 0. *Cluster* was the random term. A

278   quasibinomial model was necessary because the corresponding binomial model suffered of

279   overdispersion. The semivariogram for the within-group residuals suggested that the model

280   residuals were not spatially autocorrelated (Appendix A, fig. A.1, panel D). Since AIC cannot

281   be calculated for quasibinomial models, we used the *Anova* function in the car package for R

282   3.3.0 (Fox and Weisberg, 2011) to detect which predictor variables could be removed from

283   the full model, based on a likelihood-ratio test.

12

284   Lastly, we repeated the three procedures above but starting with models which did not

285   contain reindeer pellet counts (*pellets*) as predictor variable, with the purpose of creating

286   equations that could describe past lichen conditions, i.e. when pellet counts are not available.

287

288   **Table 1.** List of all forest, meteorological, biotic, and topographic characteristics included as predictor variables in our models aimed to

289   predict the occurrence of lichen-dominated forests, as well as lichen biomass, height and cover in those forests. All continuous variables are

290   highlighted in italic. See the Methods section for a description of the data sources. The descriptive statistics refer to the two datasets used to

291   model lichen occurrence and lichen conditions (i.e. lichen biomass, height and cover) respectively, and are reported as mean (standard deviation)

292   [minimum; maximum].

293

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		

294

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 °. 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 °	0.44	0.17	0.0083
northeast °	0.45	0.16	0.0051
northwest °	0.73	0.19	0.0001
south °	0.94	0.16	< 0.0001
southeast °	0.70	0.18	0.0001
southwest °	1.00	0.16	< 0.0001
west °	0.92	0.17	< 0.0001

316

317 **3.2 Predicting lichen biomass, height and cover in lichen-dominated forests**

318   Lichen biomass (LB) was on average 3.98 (± 2.15) cm (Appendix A, Table A.2) and was

319 positively related to tree canopy cover (fig. 3, panel A) and summer precipitation (fig. 3,

320 panel B), and higher in mountain reindeer herding districts compared to forest herding

321 districts (fig. 3, panel C). The intensity of use of the area by reindeer negatively affected LB,

322   but in an exponential manner. These results are based on the reduced model detailed in Table

323   3 and in Appendix A, Table A.3, while the best-fit model predicting LB is detailed in

324   Appendix A, Table A.4. For a model without reindeer pellet counts, we refer the reader to

325   Appendix B, Tables B.1 and B.2.

326   Lichen height (LH) was on average 4.89 (± 2.29) cm (Appendix A, Table A.2) and was

327   higher in forests with denser canopy cover and greater summer precipitation. LH decreased

328   exponentially with an increasing use of the area by reindeer (fig. 4, panel A). Lastly, LH was

329   higher in mountain herding districts compared to forest herding districts, and lower on south-

330   and west-facing slopes compared to north facing slopes. These results are based on a reduced

331   model which is detailed in Appendix A, Tables A.5 and A.6, while the best-fit model is

332   detailed in Appendix A, Table A.7. Those models explained 65 % and 70 % of the variability

333   in LH, respectively. For a model without reindeer pellet counts, we refer the reader to

334   Appendix B, Tables B.3 and B.4.

335   Lichen cover (LC), estimated as a proportion, was on average 0.82 (± 0.19, Appendix A,

336   Table A.2) and was positively related to use of the area by reindeer (fig. 4, panel B),

337   negatively affected by the sand content in the soil, and highest in Scots pine forests compared

338   to any other forest type, except lodgepole pine (Appendix A, Tables A.8 and A.9). For a

339   model without reindeer pellet counts, we refer the reader to Appendix B, Tables B.5 and B.6.

340

341   **Table 3**. Equations predicting lichen biomass (LB) in boreal forests dominated by mat-forming lichens. The equations were obtained from the

342   reduced regression model described in Appendix A, Table A.3, where the uncertainty in the coefficient estimates is also provided. Predictor

343   variables are described in Table 1 and in subsection 2.2. The regression model included one categorical variable (HD = herding district) and here

344   we report different equations for each category of that variable.

345

Categorical variable	Equation
HD = forest	LB = -3.92 + 0.02 *canopy cover* + 0.47 exp(-*pellets*) + 0.03 *precip_su*
HD = mountain	LB = -2.81 + 0.02 *canopy cover* + 0.47 exp(-*pellets*) + 0.03 *precip_su*

346

347

4. DISCUSSION

349   Mat-forming lichens thrive in Scots pine forests, with low basal area and thin canopy

350   cover (Ahti, 1961; Table 2 and fig. 2, this study). The negative effect of a dense canopy cover

351   on lichen growth has been previously demonstrated not only for boreal Scots pine forests in

352   Scandinavia (Bråkenhielm and Persson, 1980; Jonsson Čabrajič et al., 2010; Uotila et al.,

353   2005), but also for pine and spruce forests in North America (Boudreault et al., 2013; Coxson

354   and Marsh, 2001; Foster, 1985). In dense forests, mat-forming lichens do not receive enough

355   light for optimal growth, and the moisture and nutrient levels in the soil are more

356   advantageous for mosses than for lichens (Sulyma and Coxson, 2001). This is the case in old

357   forests which have not been thinned (Bråkenhielm and Persson, 1980) and in young forests,

358   which nowadays in Scandinavia grow much faster and denser than in the past due to

359   silviculture (Axelsson and Östlund, 2001). The agreement between previous studies and our

360   results suggests that our model is robust and describes accurately lichen occurrence in boreal

361   forests.

362   Once the forest ground layer is dominated by lichens, canopy cover seems to be the only

363   forest characteristic influencing LB, which is higher in forests with denser canopy cover (fig.

364   3, panel A). This result may seem contradictory with our model describing the occurrence of

365   lichen-dominated forests (Table 2), which suggests that lichens occur in forests with thinner

366   canopy cover (fig. 2, panel B). Čabrajič Jonsson et al. (2010) determined that the dry mass

367   gain of mat-forming lichens peaks at sites with intermediate light exposure levels

368   (corresponding to approximately 40 % canopy openness). A closer look at fig. 3, panel A

369   suggests that LB increases up to 40 % canopy cover. At canopy covers denser than 40 %,

370   variability in LB increases drastically. In forests where LB is high despite canopy cover being

371   dense, lichens are probably tall and sparse, but may be locally abundant. Mat-forming lichens

372   do not usually receive enough light for optimal growth in forests with dense canopy cover

373 (Boudreault et al., 2013; Bråkenhielm and Persson, 1980; Coxson and Marsh, 2001; Foster,

374 1985), but the ones that manage to grow in those forests grow taller because they extend

375 vertically in search for light inside the thick moss layer (pers. obs.). Our estimations of LB

376 may be higher in areas with abundant summer precipitation for the same reason (fig. 3, panel

377 B). We therefore advice the end users of the equations produced in this study to keep in mind

378 that high LB values predicted by our equations for forests with dense canopy cover and

379 greater summer precipitation may indicate that the lichen mat is patchy, but could be locally

380 thick.

381   Reindeer use of the forests negatively affected LH (fig. 4, panel A), but was positively

382 related to LC in winter grazing areas (fig. 4, panel B). Such effects were evident already at

383 low intensity of use of the forests. In winter, lichens constitute the main component of

384 reindeer diet (Heggberget et al., 2002). Thus, reindeer grazing is expected to shorten the

385 lichen mat (den Herder et al., 2003; Holt et al., 2008; Moen and Danell, 2003). However,

386 reindeer feed on lichens by opening craters in the snow in a patchy manner, so their grazing

387 and trampling activities do not affect the lichen mat evenly and by breaking the lichen thalli,

388 reindeer can promote lichen dispersion (Gaio-Oliveira et al. 2006). Moreover, the effects of

389 reindeer grazing are not the same among lichen species. *Cetraria islandica* and *Cladonia*

390 *stellaris* are the most sensitive to reindeer grazing (Andreyev, 1954; Väre et al., 1996; Väre et

391 al., 1995), while grazing benefits *C. rangiferina* and *C. arbuscula* (Väre et al., 1996). During

392 our 2015 fieldwork, we indeed observed that *C. rangiferina* and *C. arbuscula/mitis* dominate

393 the boreal forests of the Swedish reindeer husbandry area, at the expenses of *C. stellaris* and

394 *Cetraria islandica* (Appendix A, fig. A.4). However, the succession dynamics of different

395 lichen species may also be involved in explaining the different abundance of the four species.

396 *C. stellaris* is a late successional species within the lichen community, and if forest

397 disturbance (due to harvesting, scarification, or fire) is frequent enough, late successional

398   lichen communities may have too little time to develop. According to Ahti (1977), *C.*

399   *arbuscula* and *rangiferina* may be dominant 30-100 years after fire (i.e., they are primary

400   succession species), while *C. stellaris* may not be dominant until 80-120 years after fire.

401   In this study, we have used long-term and large-scale datasets to describe the optimal

402   habitat for the occurrence and growth of mat-forming lichens. To our knowledge, our study is

403   the first to propose a description of the environmental characteristics that benefit the

404   occurrence of mat-forming lichens based exclusively on publicly available data. Moreover,

405   our LB models are based on a novel method to estimate biomass of mat-forming lichens

406   which can be applied in future studies. Using traditional techniques, one needs to collect

407   lichen samples in the field, take them to a laboratory, dry them and finally weigh them (see

408   e.g. den Herder et al., 2003), which is a cumbersome procedure. With our technique, lichen

409   biomass can instead be quantified directly in the field from measurements of lichen height

410   and cover, or be estimate it directly from forest, meteorological, topographic and soil data

411   using the equations proposed in this study. For a more detailed model predicting lichen

412   growth, we refer the reader to Jonsson Čabrajič et al. (2010).

413   Due to the recent strong decline in the extent of lichen-dominated forests in northern

414   Sweden (Sandström et al., 2016), we suggest that the equations reported in this study can be

415   useful to a variety of stakeholders, e.g. to detect areas that should receive targeted

416   conservation or management efforts. To calculate the probability of occurrence of lichen-

417   dominated forests, LB, LH, or LC, one has to obtain data on the variables included in the

418   right end side of the equations and make the calculation according to the formula. The

419   equations can be used retrospectively to estimate past conditions of mat-forming lichens in

420   the boreal forest, as well as to map their current distribution or to foresee their future status

421   under different climatic and environmental scenarios.

422

433

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576

577

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

579

580   **Figure 2**. Variability in basal area (y-axis, panel A) and canopy cover (y-axis, panel B) in

581   moss- and lichen-dominated forests (x-axes). For a forest to be classified as being dominated

582   by a certain vegetation group, that group must comprise at least 25 % of the forest ground

583   layer. Data were collected by the Swedish National Forest Inventory in 48267 forest plots,

584   visited from 1983 to 2014. All plots were located in the Swedish reindeer husbandry area. In

585   each boxplot, the median of the data is represented by the bold horizontal bar, the

586   interquartile range is denoted by the horizontal edges of the box, and the dashed vertical lines

587   extend to the range of data. Outliers were removed in order to improve the visibility of the

588   main box. The median and interquartile range of basal area and canopy cover are slightly

589   lower for lichen- compared to moss-dominated forests, which suggests that lichen-dominated

590   forests have usually lower tree density and less dense tree canopy cover compared to moss-

591   dominated forests.

592

593   **Figure 3**. Relationship between lichen biomass (LB) and tree canopy cover (panel A),

594   summer precipitation (*precip_su*, panel B), and type of herding district (HD, panel C) in

595   lichen-dominated forests. A description of how lichen biomass was estimated is available in

596   subsection 2.2. For details on the predictor variables (x-axes) see Table 1.

597

598   **Figure 4**. Relationship between lichen height (LH, y-axis in panel A) and lichen cover

599   (LC, y-axis in panel B) and intensity of use by reindeer of boreal forests dominated by

600   lichens (x-axes), which was estimated based on reindeer pellet counts (*pellets*). A description

601   of how LH, LC, and *pellets* were obtained is available in subsection 2.2.

1 **Modelling occurrence and status of mat-forming lichens in boreal forests to**

2 **assess the past and current quality of reindeer winter pastures**

3 Alessia Uboni, Alexander Blochel, Danijela Kodnik, and Jon Moen
4
5
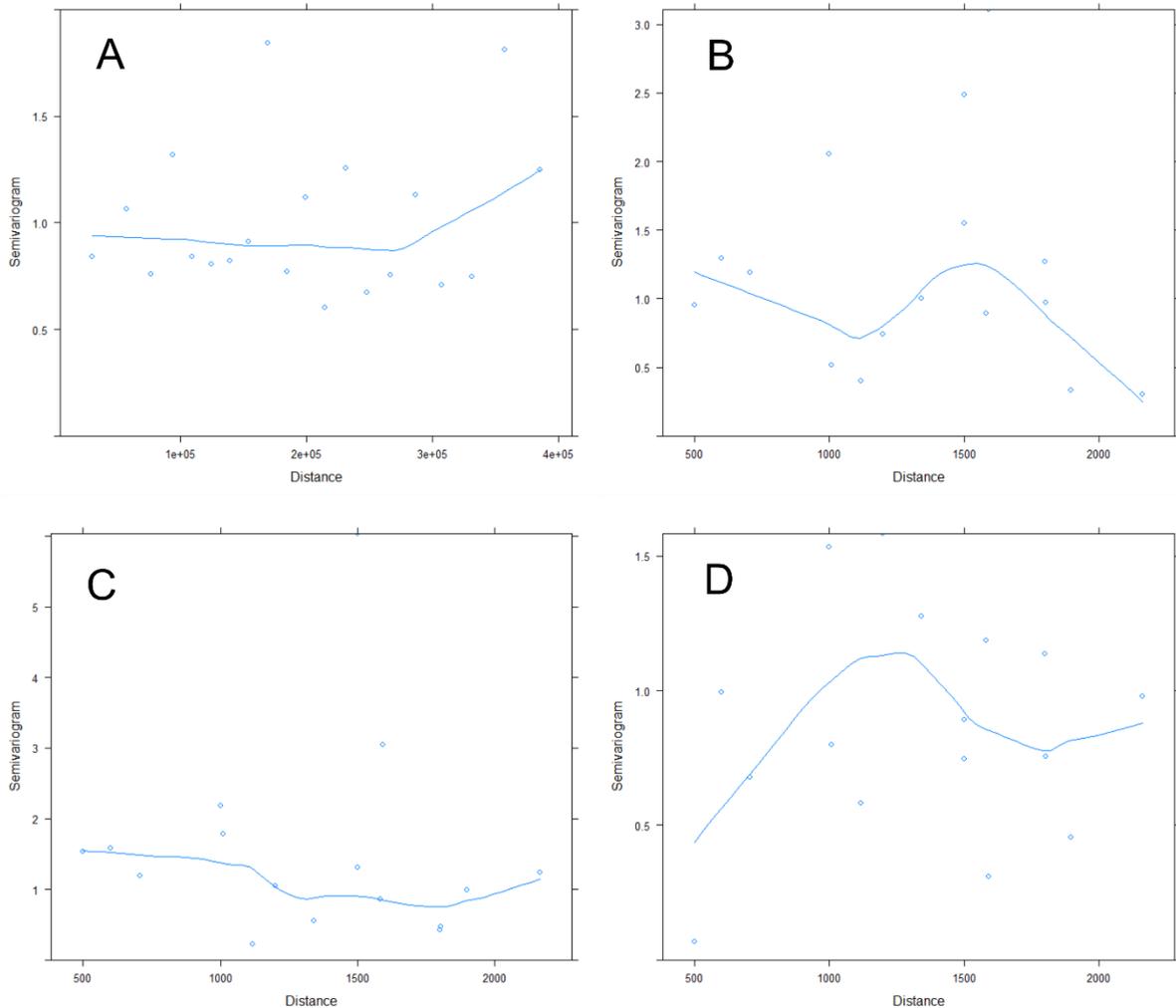
6
7 **Figure A.1**. Semivariogram for the within-group residuals from regression models relating
8 the occurrence of lichen-dominated forests (panel A, quasibinomial mixed-effect model),
9 lichen biomass (panel B, linear mixed-effect model), lichen height (panel C, linear mixed-
10 effect model), and lichen cover (panel D, quasibinomial mixed-effect model) with forest,
11 meteorological, topographic and soil characteristics. For details on the model development
12 see sections 2.1.2 and 2.2.4 in the main manuscript. The x-axes have been limited to distances
13 up to 400000 m.
14

15

A

N

1 m

20 m

S

B

N

Radius = 1,5 m

20 m

S
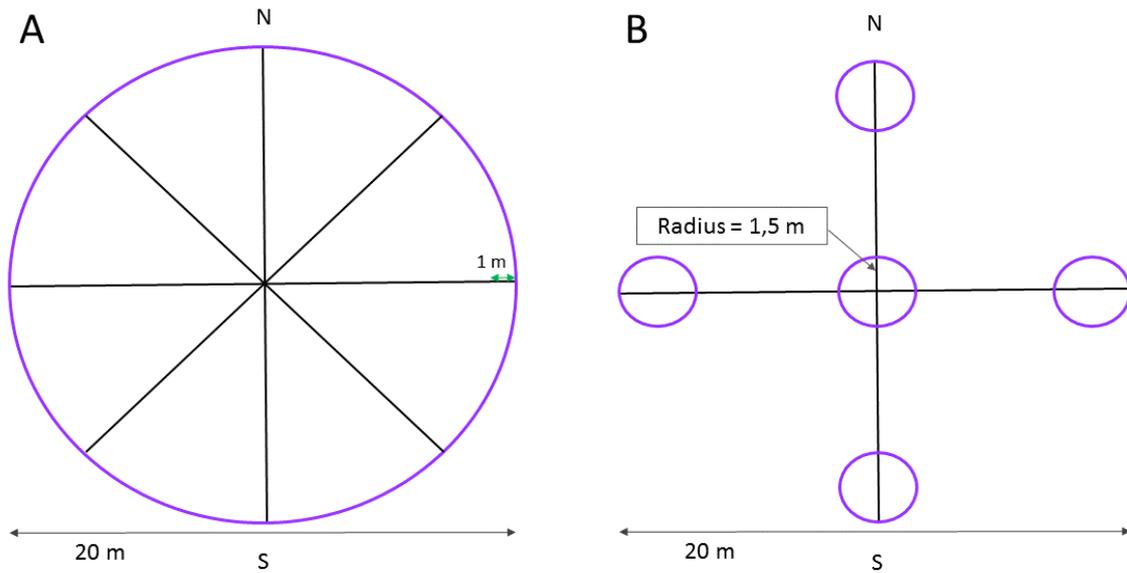
16
17 **Figure A.2**. Data collection design. Panel A represents the protocol followed in 2015 to
18 measure lichen height in Swedish boreal forests dominated by mat-forming lichens. Lichen
19 height was measured in 20cm-radius circles regularly spaced one meter apart along all
20 transects depicted in the figure. Panel B represents the protocol followed to count reindeer
21 pellet groups. Reindeer pellet groups were counted in the 5 subplots depicted in purple in the
22 figure.
23
24

25
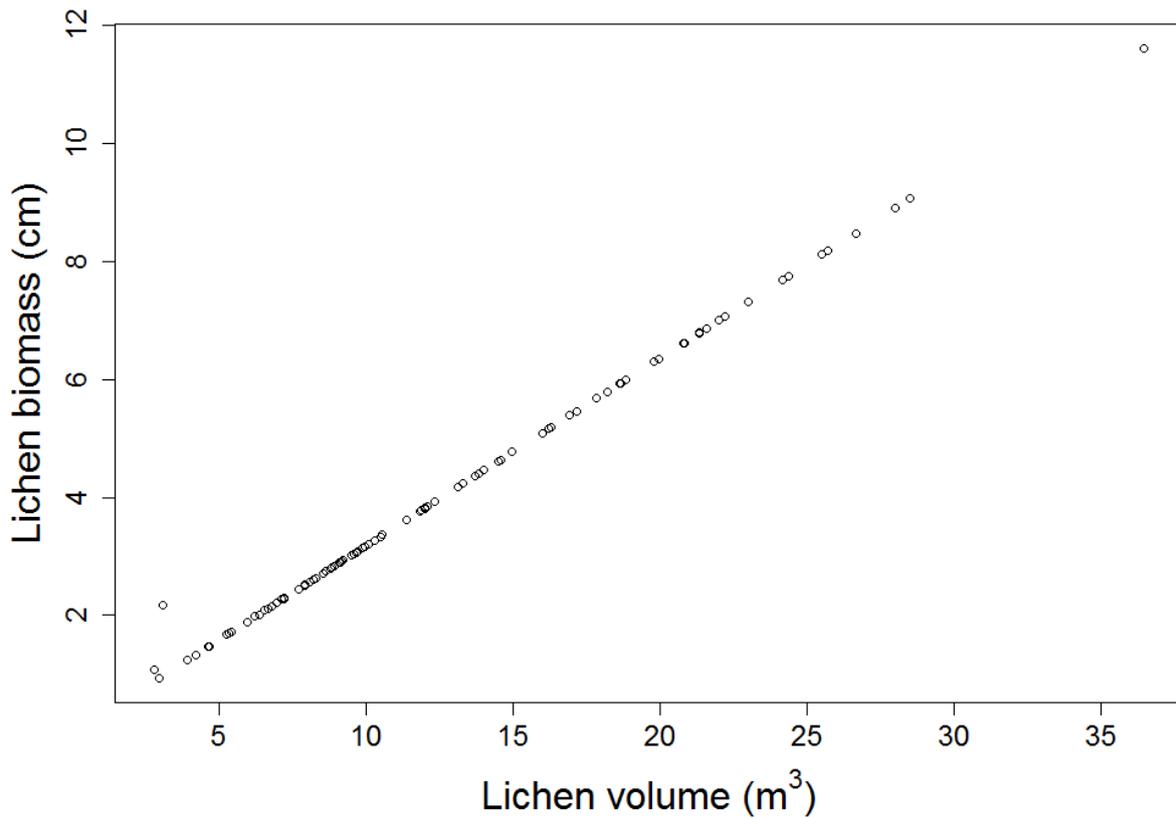
26
27 **Figure A.3**. Correlation between lichen biomass (y-axis) and lichen volume (x-axis) in 98
28 forest plots distributed within the reindeer herding husbandry area of northern Sweden.
29 Lichen biomass was estimated as the average height of the lichen mat, including all
30 measurements taken in a plot, i.e. also those in which lichen height = 0. Lichen volume was
31 calculated by multiplying average lichen height by lichen cover. In the main manuscript
32 lichen height is referred to as LH and is measured in centimeters, but for this calculation it
33 was converted to meters. Here, lichen cover was estimated by multiplying LC (see main
34 manuscript) by the area of the plot. Thus, here lichen cover is the proportion of the area of the
35 plot, in m², covered by mat-forming lichens. Each sample plot had an area of 314.16 m². For
36 details about the methods used to collect data on LH and LC, see subsections 2.2.3 and 2.2.4
37 in the Methods section of the main manuscript. The Pearson correlation coefficient between
38 lichen biomass and lichen volume was 0.99.
39

Appendix A

40 **Table A.1**. Equations predicting the probability (p) of a forest plot being lichen-dominated. The equations were obtained from the regression model described
41 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,
42 aspect (A) and forest type (FT), and here we report different equations for each category of those variables. Scots pine = *Pinus sylvestris*; Lodgepole pine =
43 *Pinus contorta*; Norway spruce = *Picea abies*.
44

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

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

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

Appendix A

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

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

45
46

47 **Table A.2**. Lichen biomass (LB), lichen height (LH), and lichen cover (LC) values measured
48 in 2015 in 98 plots distributed across the Swedish reindeer husbandry area. For details on
49 how the measurements were performed, see subsections 2.2.3 and 2.2.4 in the Methods
50 section of the main manuscript. SD = standard deviation
51

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

52

53

54   **Table A.3**. Reduced mixed-effect regression model predicting lichen biomass in boreal
55   forests dominated by mat-forming lichens. This model was derived from the best-fit model
56   detailed in Table A.4 by removing the non-significant variables as detailed in the Methods
57   section. Mountain is one of the two categories of the variable HD (= herding district), where
58   forest is the reference category. Random term standard deviation = 0.92. β = regression
59   coefficient mean estimate; SE = standard error of the coefficient estimate. This model had an
60   Akaike Information Criterion (AIC, Burnham and Anderson, 2002) = 348.87, which was
61   slightly higher than the AIC of the best-fit model reported in Table A.4 (AIC = 345.96).
62

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

63

64 **Table A.4**. Best-fit mixed-effect regression model predicting lichen biomass in boreal forests
65 dominated by mat-forming lichens. This model was developed from a full model including all
66 predictor variables described in Table 1 and in subsection 2.2 of the main manuscript, with
67 *Cluster* as random term (standard deviation = 0.91). Meteorological variables refer to
68 averages calculated over the 5 years preceding the collection of lichen biomass data (i.e.
69 2010-2014). Mountain is one of the two categories of the variable HD (= herding district),
70 where forest is the reference category. The categories of the "aspect" variable are marked
71 with a °, and north was the reference category. All continuous variables are highlighted in
72 italic. A colon mark (:) indicates an interaction term. β = regression coefficient mean
73 estimate; SE = standard error of the coefficient estimate.
74

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 °	0.52	0.60	0.3904
northeast °	0.64	0.57	0.2729
northwest °	1.38	0.86	0.1177
south °	-0.56	0.72	0.4396
southeast °	-0.66	0.61	0.2905
southwest °	-0.23	0.58	0.7008
west °	-0.68	0.76	0.3764
sand	-0.03	0.02	0.1343
precip_su:temp_su	-0.02	0.01	0.1353

75
76

77 **Table A.5**. Reduced linear regression model predicting lichen height in boreal forests
78 dominated by mat-forming lichens. This model was derived from the best-fit model detailed
79 in Table A.7 by removing the non-significant variables as detailed in the Methods section.
80 Mountain is one of the two categories of the variable HD (= herding district), where forest is
81 the reference category. The categories of the "aspect" variable are marked with a º, and north
82 is the reference category. β = regression coefficient estimate; SE = standard error of the
83 coefficient estimate. This model had an adjusted R^2 = 0.65 and an Akaike Information
84 Criterion (AIC, Burnham and Anderson, 2002) = 350.91, which was higher than the AIC of
85 the best-fit model reported in Table A.6 (AIC = 341.61).
86

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

87
88

89 **Table A.6**. Equations predicting lichen height (LH) in boreal forests dominated by mat-forming lichens. The equations were obtained from the
90 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.
91 The regression model included two categorical variables and here we report different equations for each combination of their categories.
92

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

Appendix A

Categorical variables	Model
HD = mountain; aspect = southeast	LH = -2.60 + 0.02 *canopy cover* + 2.08 exp(-*pellets*) + 0.03 *precip_su*
HD = mountain; aspect = southwest	LH = -2.24 + 0.02 *canopy cover* + 2.08 exp(-*pellets*) + 0.03 *precip_su*
HD = mountain; aspect = west	LH = -2.96 + 0.02 *canopy cover* + 2.08 exp(-*pellets*) + 0.03 *precip_su*

93
94

95 **Table A.7**. Best-fit linear regression model predicting lichen height in boreal forests
96 dominated by mat-forming lichens. This model was developed from a full model including all
97 predictor variables described in Table 1 and in subsection 2.2 of the main manuscript.
98 Meteorological variables refer to averages calculated over the 5 years preceding the
99 collection of lichen height data (i.e. 2010-2014). Mountain is one of the two categories of the
100 variable HD (= herding district), where forest is the reference category. North was the
101 reference category for the "aspect" variable and the other categories are marked with a °. All
102 continuous variables are highlighted in italic. A colon mark (:) refers to an interaction term. β
103 = regression coefficient estimate; SE = standard error of the coefficient estimate.
104

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_w²	7.29	1.99	0.0004
temp_su	3.00	1.64	0.0705
temp_w	1.62	0.70	0.0230
east °	0.04	0.63	0.9479
northeast °	-0.11	0.60	0.8552
northwest °	-0.80	0.87	0.3606
south °	-1.22	0.71	0.0882
southeast °	-0.97	0.66	0.1444
southwest °	-0.51	0.59	0.3898
west °	-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

105 **Table A.8**. Quasibinomial mixed-effect regression model predicting lichen cover in boreal
106 forests dominated by mat-forming lichens. This model was developed from a full model
107 including all predictor variables described in Table 1 and in subsection 2.2 of the main
108 manuscript. *Cluster* was the random term (standard deviation: 0.74). The categories of the
109 "forest type" variable are marked with an asterisk. Scots pine (*Pinus sylvestris*) was the
110 reference category. Lodgepole pine = *Pinus contorta*. Norway spruce = *Picea abies*. All
111 continuous variables are highlighted in italic. β = regression coefficient mean estimate, which
112 in a quasibinomial model is the log odd ratio; SE = standard error of the coefficient estimate.
113

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

114
115

116 **Table A.9**. Equations predicting lichen cover (LC) in boreal forests dominated by mat-forming lichens. The equations were obtained from the
117 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
118 regression model included one categorical variable, forest type (FT) and here we report different equations for each category of that variable.
119 Scots pine = *Pinus sylvestris*; Lodgepole pine = *Pinus contorta*; Norway spruce = *Picea abies*.
120

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

121
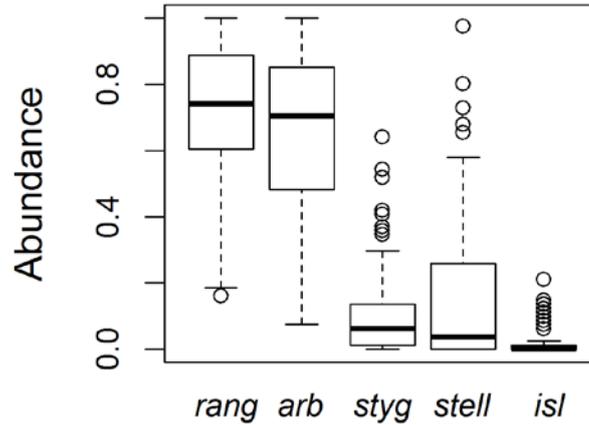
Figure A.4. Distribution of the abundance (y axis) of each of five mat-forming lichen species (x axis) in lichen-dominated boreal forests of northern Sweden. Data were collected in 2015 in 98 forest plots located in the counties of Jämland, Västerbotten and Norrbotten, Sweden. Forest plots are the sample 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

139

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142

1 **Modelling occurrence and status of mat-forming lichens in boreal forests to**

2 **assess the past and current quality of reindeer winter pastures**

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

4
5
6
7

8 **Table B.1**. Reduced mixed-effect regression model predicting lichen biomass in boreal
9 forests dominated by mat-forming lichens. Compared to the model detailed in Appendix A,
10 Table A.3, this model did not include reindeer pellet count as a predictor variable. Mountain
11 is one of the two categories of the variable HD (= herding district), where forest is the
12 reference category. Random term standard deviation = 0.97. β = regression coefficient mean
13 estimate; SE = standard error of the coefficient estimate.
14

Predictor	β	SE	p-value
intercept	-3.90	1.34	
canopy cover	0.02	0.01	0.0054
mountain	1.24	0.37	0.0015
precip_su	0.03	0.01	< 0.0001

15
16

17   **Table B.2**. Equations predicting lichen biomass in boreal forests dominated by mat-forming lichens. The equations were obtained from the
18   reduced regression model described in Table B.1. Predictor variables are described in Table 1 and in subsection 2.2 of the main manuscript. The
19   regression model included one categorical variable (HD = herding district) and here we report different equations for each category of that
20   variable.
21

Categorical variable	Equation
HD = forest	LB = -3.90 + 0.02 *canopy cover* + 0.03 *precip_su*
HD = mountain	LB = -2.66 + 0.02 *canopy cover* + 0.03 *precip_su*

22

23 **Table B.3**. Reduced linear regression model predicting lichen height in boreal forests
24 dominated by mat-forming lichens. Compared to the model detailed in Appendix A, Table
25 A.5, this model did not include reindeer pellet count as a predictor variable. Mountain is one
26 of the two categories of the variable HD (= herding district), where forest is the reference
27 category. The categories of the "aspect" variable are marked with a °, and north is the
28 reference category. A colon mark (:) refers to an interaction term. β = regression coefficient
29 estimate; SE = standard error of the coefficient estimate. This model had an adjusted R^2 =
30 0.61.
31

Predictor	β	SE	p-value
intercept	-3.12	1.96	
canopy cover	0.03	0.01	0.0017
mountain	1.55	0.44	0.0007
precip_su	0.03	0.01	<0.0001
precip_w	-36.68	18.44	0.0500
precip_w²	9.07	2.17	0.0001
temp_w	1.58	0.71	0.0281
east °	0.27	0.67	0.6919
northeast °	0.24	0.67	0.7202
northwest °	-0.26	0.97	0.7925
south °	-0.60	0.74	0.4201
southeast °	-0.88	0.72	0.2293
southwest °	-0.23	0.63	0.7179
west °	-2.55	0.85	0.0036
precip_w : *temp_w*	-0.02	0.01	0.0365

32
33

34 **Table B.4**. Equations predicting lichen height (LH) in boreal forests dominated by mat-forming lichens. The equations were obtained from the
35 reduced regression model described in Table B.3. Predictor variables are described in Table 1 and in the subsection 2.2 of the main manuscript.
36 The regression model included two categorical variables and here we report different equations for each combination of their categories. A colon
37 mark (:) refers to an interaction term (i.e. one must multiply the two variables).
38

Categorical variables	Model
HD = forest; aspect = north	LH = -3.12 + 0.03 *canopy cover* + 0.03 *precip_su* - 36.68 *precip_w* + 9.07 *precip_w²* + 1.58 *temp_w* - 0.02 *precip_w:temp_w*
HD = forest; aspect = east	LH = -2.85 + 0.03 *canopy cover* + 0.03 *precip_su* - 36.68 *precip_w* + 9.07 *precip_w²* + 1.58 *temp_w* - 0.02 *precip_w:temp_w*
HD = forest; aspect = northeast	LH = -2.88 + 0.03 *canopy cover* + 0.03 *precip_su* - 36.68 *precip_w* + 9.07 *precip_w²* + 1.58 *temp_w* - 0.02 *precip_w:temp_w*
HD = forest; aspect = northwest	LH = -3.38 + 0.03 *canopy cover* + 0.03 *precip_su* - 36.68 *precip_w* + 9.07 *precip_w²* + 1.58 *temp_w* - 0.02 *precip_w:temp_w*
HD = forest; aspect = south	LH = -3.72 + 0.03 *canopy cover* + 0.03 *precip_su* - 36.68 *precip_w* + 9.07 *precip_w²* + 1.58 *temp_w* - 0.02 *precip_w:temp_w*
HD = forest; aspect = southeast	LH = -4.00 + 0.03 *canopy cover* + 0.03 *precip_su* - 36.68 *precip_w* + 9.07 *precip_w²* + 1.58 *temp_w* - 0.02 *precip_w:temp_w*
HD = forest; aspect = southwest	LH = -3.35 + 0.03 *canopy cover* + 0.03 *precip_su* - 36.68 *precip_w* + 9.07 *precip_w²* + 1.58 *temp_w* - 0.02 *precip_w:temp_w*
HD = forest; aspect = west	LH = -5.67 + 0.03 *canopy cover* + 0.03 *precip_su* - 36.68 *precip_w* + 9.07 *precip_w²* + 1.58 *temp_w* - 0.02 *precip_w:temp_w*
HD = mountain; aspect = north	LH = -1.57 + 0.03 *canopy cover* + 0.03 *precip_su* - 36.68 *precip_w* + 9.07 *precip_w²* + 1.58 *temp_w* - 0.02 *precip_w:temp_w*
HD = mountain; aspect = east	LH = -1.30 + 0.03 *canopy cover* + 0.03 *precip_su* - 36.68 *precip_w* + 9.07 *precip_w²* + 1.58 *temp_w* - 0.02 *precip_w:temp_w*
HD = mountain; aspect = northeast	LH = -1.33 + 0.03 *canopy cover* + 0.03 *precip_su* - 36.68 *precip_w* + 9.07 *precip_w²* + 1.58 *temp_w* - 0.02 *precip_w:temp_w*
HD = mountain; aspect = northwest	LH = -1.83 + 0.03 *canopy cover* + 0.03 *precip_su* - 36.68 *precip_w* + 9.07 *precip_w²* + 1.58 *temp_w* - 0.02 *precip_w:temp_w*
HD = mountain; aspect = south	LH = -2.17 + 0.03 *canopy cover* + 0.03 *precip_su* - 36.68 *precip_w* + 9.07 *precip_w²* + 1.58 *temp_w* - 0.02 *precip_w:temp_w*

Categorical variables	Model
HD = mountain; aspect = southeast	LH = -2.45 + 0.03 *canopy cover* + 0.03 *precip_su* - 36.68 *precip_w* + 9.07 *precip_w²* + 1.58 *temp_w* - 0.02 *precip_w:temp_w*
HD = mountain; aspect = southwest	LH = -1.80 + 0.03 *canopy cover* + 0.03 *precip_su* - 36.68 *precip_w* + 9.07 *precip_w²* + 1.58 *temp_w* - 0.02 *precip_w:temp_w*
HD = mountain; aspect = west	LH = -4.12 + 0.03 *canopy cover* + 0.03 *precip_su* - 36.68 *precip_w* + 9.07 *precip_w²* + 1.58 *temp_w* - 0.02 *precip_w:temp_w*

39
40

41 **Table B.5**. Quasibinomial mixed-effect regression model predicting lichen cover in boreal
42 forests dominated by mat-forming lichens. Compared to the model detailed in Appendix A,
43 Table A.8, this model did not include reindeer pellet count as a predictor variable. *Cluster*
44 was the random term (standard deviation: 0.78). Mountain is one of the two categories of the
45 variable HD (= herding district), where forest is the reference category. The categories of the
46 "forest type" variable are marked with an asterisk. Scots pine (*Pinus sylvestris*) was the
47 reference category. Lodgepole pine = *Pinus contorta*. Norway spruce = *Picea abies*. All
48 continuous variables are highlighted in italic. β = regression coefficient mean estimate, which
49 in a quasibinomial model is the log odd ratio; SE = standard error of the coefficient estimate.
50

Predictor	β	SE	p-value
intercept	6.53	1.02	
clear-cut *	-1.39	0.65	0.0395
lodgepole pine *	-0.50	0.45	0.2734
mixed *	-1.01	0.29	0.0011
mixed conifer *	-1.62	0.78	0.0414
Norway spruce *	-1.23	1.04	0.2456
age	-0.0046	0.0023	0.0489
mountain	-0.89	0.31	0.0066
sand	-0.05	0.01	0.0003

51
52

53 **Table B.6**. Equations predicting lichen cover (LC) in boreal forests dominated by mat-forming lichens. The equations were obtained from the
54 reduced regression model described in Table B.5. Predictor variables are described in Table 1 and in subsection 2.2 of the main manuscript. The
55 regression model included two categorical variables, herding district type (HD) and forest type (FT). Here, we report different equations for each
56 category of those variables. Scots pine = *Pinus sylvestris*; Lodgepole pine = *Pinus contorta*; Norway spruce = *Picea abies*.
57

Categorical variable	Equation
HD = forest; FT = Scots pine	$LC = \dfrac{\exp(6.53 - 0.0046\ age\ -\ 0.05\ sand)}{\exp(6.53 - 0.0046\ age\ -\ 0.05\ sand) + 1}$
HD = forest; FT = clear-cut	$LC = \dfrac{\exp(5.14 - 0.0046\ age\ -\ 0.05\ sand)}{\exp(5.14 - 0.0046\ age\ -\ 0.05\ sand) + 1}$
HD = forest; FT = lodgepole pine	$LC = \dfrac{\exp(6.04 - 0.0046\ age\ -\ 0.05\ sand)}{\exp(6.04 - 0.0046\ age\ -\ 0.05\ sand) + 1}$
HD = forest; FT = mixed	$LC = \dfrac{\exp(5.53 - 0.0046\ age\ -\ 0.05\ sand)}{\exp(5.53 - 0.0046\ age\ -\ 0.05\ sand) + 1}$
HD = forest; FT = mixed conifer	$LC = \dfrac{\exp(4.91 - 0.0046\ age\ -\ 0.05\ sand)}{\exp(4.91 - 0.0046\ age\ -\ 0.05\ sand) + 1}$
HD = forest; FT = Norway spruce	$LC = \dfrac{\exp(5.31 - 0.0046\ age\ -\ 0.05\ sand)}{\exp(5.31 - 0.0046\ age\ -\ 0.05\ sand) + 1}$
HD = mountain; FT = Scots pine	$LC = \dfrac{\exp(5.65 - 0.0046\ age\ -\ 0.05\ sand)}{\exp(5.65 - 0.0046\ age\ -\ 0.05\ sand) + 1}$

Appendix B

Categorical variable	Equation
HD = mountain; FT = clear-cut	$LC = \dfrac{\exp(4.26 - 0.0046\, age - 0.05\, sand)}{\exp(4.26 - 0.0046\, age - 0.05\, sand) + 1}$
HD = mountain; FT = lodgepole pine	$LC = \dfrac{\exp(5.15 - 0.0046\, age - 0.05\, sand)}{\exp(5.15 - 0.0046\, age - 0.05\, sand) + 1}$
HD = mountain; FT = mixed	$LC = \dfrac{\exp(4.64 - 0.0046\, age - 0.05\, sand)}{\exp(4.64 - 0.0046\, age - 0.05\, sand) + 1}$
HD = mountain; FT = mixed conifer	$LC = \dfrac{\exp(4.03 - 0.0046\, age - 0.05\, sand)}{\exp(4.03 - 0.0046\, age - 0.05\, sand) + 1}$
HD = mountain; FT = Norway spruce	$LC = \dfrac{\exp(4.42 - 0.0046\, age - 0.05\, sand)}{\exp(4.42 - 0.0046\, age - 0.05\, sand) + 1}$

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