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Broad-scale distribution of epiphytic hair lichens correlates more with climate and nitrogen deposition than with forest structure


Abstract: Hair lichens are strongly influenced by forest structure at local scales, but their broad-scale distributions are less understood. We compared the occurrence and length of Alectoria sarmentosa (Ach.) Ach., Bryoria spp., and Usnea spp. in the lower canopy of > 5000 Picea abies (L.) Karst. trees within the National Forest Inventory across all productive forest in Sweden. We used logistic regression to analyse how climate, nitrogen deposition, and forest variables influence lichen occurrence. Distributions overlapped, but the distribution of Bryoria was more northern and that of Usnea was more southern, with Alectoria’s distribution being intermediate. Lichen length increased towards northern regions, indicating better conditions for biomass accumulation. Logistic regression models had the highest pseudo R² value for Bryoria, followed by Alectoria. Temperature and nitrogen deposition had higher explanatory power than precipitation and forest variables. Multiple logistic regressions suggest that lichen genera respond differently to increases in several variables. Warming decreased the odds for Bryoria occurrence at all temperatures. Corresponding odds for Alectoria and Usnea decreased in warmer climates, but in colder climates, they increased. Nitrogen addition decreased the odds for Alectoria and Usnea occurrence under high deposition, but under low deposition, the odds increased. Our analyses suggest major shifts in the broad-scale distribution of hair lichens with changes in climate, nitrogen deposition, and forest management.

Key words: climate change, epiphytic lichens, forest structure, nitrogen deposition, temperature.

Introduction

Filamentous “hair” lichens in the genera Alectoria, Bryoria, and Usnea often dominate forest canopies throughout the boreal zone, as well as some temperate forests. Globally, Alectoria and Bryoria mainly occur in cool and cold climates, whereas Usnea occurs worldwide (Brodo and Hawksworth 1977; Thell and Moberg 2011). Hair lichens have important functions in forests. They participate in nutrient and water cycling, provide habitat and food for animals, and constitute a significant part of the winter diet for caribou and reindeer (subspecies of Rangifer tarandus (Linnaeus, 1758); Hauck 2011; Stanton et al. 2014; Esseen and Coxson 2015). Hair lichens are useful indicators of forest ecosystem integrity and have strongly declined in areas with atmospheric pollution (Kuusinen et al. 1990; Bruteig 1993) and intensive forestry (Esseen et al. 1996). Hair lichens such as Alectoria sarmentosa (Ach.) Ach., Bryoria nadvornikiana (Gyeln.) Brodo & D. Hawksw., and Usnea longissima Ach. are now red-listed in Fennoscandia (Kålás et al. 2010; Rassi et al. 2010; ArtDatabanken 2015).

Lichen abundance results from a balance between positive and negative factors that differ among species. Positive factors include availability of specific substrata (Ellis 2012), a suitable combination of water, light, and temperature, and a balanced availability.
of nutrients (Palmqvist et al. 2008). Negative factors include environmental stressors (e.g., pollution, suboptimal microclimate) and disturbances (e.g., fire, wind, herbivory, forestry; Hauck 2011). For example, the essential nutrient nitrogen enhances lichen growth in low to moderate doses, whereas high doses of nitrogen are detrimental (Geiser et al. 2010; Johansson et al. 2012). Environmental variability and dispersal limitation operating at tree, stand, and landscape scales also influence epiphytic lichens (Ellis 2012). Key factors at a tree scale include tree species, canopy height, branch size, tree age, and nutrient availability (Esseen et al. 1996; Ellis 2012). Important stand factors include horizontal and vertical distributions of the canopy, stand age, and microclimate (Coxson and Coyle 2003; Sillett and Antoine 2004).

Anthropogenic airborne sulphur and nitrogen strongly negatively affected forest ecosystems in Europe and North America (Bobbink et al. 2010; Hauck 2011). The SO2 emissions were highly detrimental to epiphytic lichens in western Europe but have been reduced since the 1970s (Vestreng et al. 2007). Therefore, many lichens have recovered locally, but emissions of nitrogen are still high or increasing with a negative impact on lichens inhabiting oligotrophic environments such as Bryoria and Usnea (van Herk et al. 2003; Hultengren et al. 2004). Hair lichens are particularly sensitive to pollution and climate change, as their large surface area to mass ratios filter moisture and elements from the air (e.g., Knops et al. 1996; Stanton et al. 2014). In Sweden, nitrogen deposition shows a steep south–north gradient and exceeds 10 kg N·ha−1·year−1 in southern regions (Pihl Karlsson et al. 2011). This is above or close to the critical load (threshold between harmless and harmful nitrogen deposition) for many lichens (Bobbink and Hettelingh 2011; Pardo et al. 2011; Johansson et al. 2012).

The regional distribution of hair lichens has received considerable interest (e.g., Brodo and Hawksworth 1977; Thell and Moberg 2011), but there are still knowledge gaps. Ahlner (1948) mapped the distribution of several hair lichens in Fennoscandia before the start of large-scale clearcutting in the 1950s. Hair lichen maps based on large-scale surveys are available for Finland (Kuusinen et al. 1990; Poikolainen et al. 1998) and Norway (Bruteig 1993). However, few have applied statistically rigorous methods to analyse how environmental factors affect the regional distribution of hair lichens (e.g., Bruteig 1993; van Herk et al. 2003; Berryman and McCune 2006; Shrestha et al. 2012). Recently, Boudreault et al. (2015) analysed forest characteristics influencing hair lichen distribution in ecosystems dominated by Picea mariana (Mill.) Britton, Sterns & Poggenb. across a large west–east gradient in Quebec, Canada. These studies help to explain mechanisms behind broad-scale distribution of hair lichens. However, we need more detailed data and better models to understand how climate, nitrogen deposition, and forestry interact and influence the distribution of different hair lichens.

Our study analyses factors correlating with the large-scale distribution of the hair lichen genera Alectoria, Bryoria, and Usnea in the lower canopy of Picea abies (L.) Karst. in Sweden, from temperate to boreal and subalpine forests. We base our analyses on data from the National Forest Inventory (NFI) that provides a large probability sample. The aims of our study are to (i) compare the distribution of the three genera in NFI plots across five regions differing in climate and in human impact; (ii) compare the thallus length (indicating growth conditions) among these regions; and (iii) use logistic regressions for quantification of links between the occurrence of hair lichens and macroclimate, nitrogen deposition, and forest structure.

Materials and methods

Study area

The study area is in Sweden (55°N–69°N) with a length of 1500 km and a width up to 400 km (Fig. 1). The productive forests (site productivity ≥ 1 m3·ha−1·year−1) cover 23 million ha; in addition, there are 5 million ha of unproductive forest and 2 million ha of other wooded land (Anon 2014). There are strong south–north gradients in climate, forest composition, land use, and element deposition. The climate ranges from humid warm temperate climate in the south to a humid snow climate with a cold summer in most of the country, with polar tundra in northwestern mountains. The temperate (nemoral) zone forms a narrow belt in the south and southwest. It not only has coniferous forest (P. abies), but also comprises substantial amounts of broad-leaved trees, particularly Betula spp. and Fagus sylvatica L., as well as Acer spp., Fraxinus excelsior L., Quercus spp., and Tilia cordata Mill. Most of southern Sweden is in the hemiboreal zone, which is a transition zone between the temperate and the boreal zones, where temperate deciduous trees together with P. abies dominate on nutrient-rich soils, whereas Pinus sylvestris L. dominates nutrient-poor soils. The boreal zone, dominated by P. abies, P. sylvestris, and Betula spp., covers most of Sweden. Industrial forestry (mainly even-aged forest management) is the dominant land use, whereas agriculture occurs mainly in the southern and central regions. The mean volume on productive forest land in Sweden is 135 m3·ha−1 and is dominated by P. abies (42%), F. sylvestris (39%), and Betula spp. (12%,
Anon 2014). The onset of forest exploitation started in the late 1700s in the southernmost parts, with a northward expanding timber frontier during the 1800s and 1900s (Östlund et al. 1997). Since the 1950s, forest management has largely been based on even-aged forestry, i.e., clear-cut harvesting followed by artificial planting of conifers (Östlund et al. 1997). Rotation periods range from 50 years in the south to 120 years in the north (Fries et al. 2015), resulting in a highly fragmented landscape, particularly in southern and central regions (Esseen et al. 2016). Only along the Scandinavian mountain range is the current forestry less intense.

Study species
Alectoria is here represented by only A. sarmentosa, a large, pendent species widely distributed across Eurasia and North America (Ahler 1948; Brodo and Hawksworth 1977; McMullin et al. 2016). Alectoria sarmentosa is strongly associated with old-growth P. abies forests in Fennoscandia (Esseen et al. 1996). Bryoria and Usnea are species-rich and taxonomically difficult genera containing both pendent and shrubby species (Thell and Moberg 2011). The most widespread Bryoria in Sweden are B. capillaris (Ach.) Brodo & D. Hawksw. and B. fuscocarinata (Gyeln.) Brodo & D. Hawksw., followed by B. fremontii (Tuck.) Brodo & D. Hawksw. and B. furcellata (Fr.) Brodo & D. Hawksw., both preferring drier forests and also reflecting canopy cover and thus light availability. Stand age (time for lichen development) is weighed by basal area for stands taller than 7 m. Site quality index for P. abies, an index of potential forest production capacity (m³·ha⁻¹·year⁻¹), was estimated from forest and site characteristics.

We obtained climate data with monthly averages for the last full reference period 1961–1990 in a 4 km × 4 km grid from the Swedish Meteorological and Hydrological Institute (SMHI). We extracted mean annual temperature and mean total annual precipitation for each NFI plot using ArcGis version 10.3. An index of continentality was calculated as the difference in mean temperature between July and January. Continentality correlates with less rain and higher diurnal temperature amplitude during summer, implying more frequent dew formation (Gauslaa 2014). Much precipitation in northern areas falls as snow in seasons not supporting high lichen growth rates. Instead of using total annual precipitation with low explanatory power, we calculated a “rain index”, which was the total precipitation in months with mean temperature ≥ 0 °C during which lichens can grow. Finally, we extracted data on annual deposition of inorganic nitrogen (dry plus wet depositions). We obtained nitrogen data (NOₓ + NH₄) in a 20 km × 20 km grid from SMHI using the Match model (available from http://www.smhi.se/klimatdata/miljo/atmosfarskemi). We calculated mean annual nitrogen deposition for 1998–2002 in each grid cell and then extracted data for each NFI plot.

Data analysis
The total data consisted of 5586 plots (but we excluded 105 plots; see below), each with lichen data from one P. abies tree. We calculated percent lichen occurrence, mean length, and standard error (SE) for each region. A general linear model was used to test whether thallus length differed by region. Length was log transformed to obtain approximately normal distributions, and the Tukey–Kramer posthoc test was used to evaluate differences among regions. We calculated means and SE for explanatory variables by regions, as well as their intercorrelations across all regions.

We used logistic regression ( Hosmer et al. 2013) to predict occurrence of the three genera using climate, nitrogen deposition, and forest variables. To simplify model construction, we excluded plots classified as unstocked (basal area < 3 m²·ha⁻¹, n = 16), thicket (mean height < 1.3 m, n = 13), and young stands (mean height ≥ 1.3 m and < 10 cm DBH of dominant trees, n = 75). These plots mainly had residual trees from the previous stand (before logging), and the observed lichen data are not strongly linked to current forest structure. We also excluded one plot with no data for basal area, thus resulting in 5481 plots. To account for the possibility of nonlinear relationships, fractional polynomials of first and second degree were applied (Sauerbrei and Royston 1999). We fitted separate and multiple fractional polynomial logistic regression models (Appendix A) with the library mfp in R version 3.1.0 (R Core Team 2014). Continentality was removed from the multiple model for Usnea to avoid multicollinearity. We used odds ratios to help interpret the derived logistic regression models. The odds ratio is widely used as a measure of association, as it approximates how much more likely or unlikely (in terms of
odds) it is for the outcome (lichen) to be present among those subjects (\(P. \text{abies}\)) with a one-unit increment in an explanatory variable, i.e., \(x + 1\) versus \(x\) (Hosmer et al. 2013). That is, the odds ratio is the relative change in the odds of occurrence when increasing the explanatory variable while holding other explanatory variables fixed. Several analogues to the linear regression \(R^2\) have been proposed for logistic regression, but McFadden’s pseudo \(R^2\) (recommended by Menard (2000)) is used throughout this study. It is computed as follows:

\[
1 - \frac{\text{maximized log likelihood for the model containing only the intercept}}{\text{maximized log likelihood for the fitted model}}
\]

which, like linear regression \(R^2\), is on a [0,1] scale.

Results

Distribution and length

\(Bryoria\) was most common (44.6% of the trees), followed by \(Usnea\) (37.5%) and \(Alectoria\) (16.7%). \(Alectoria\) was exclusive on 1.0%, \(Bryoria\) was exclusive on 11.3% and \(Usnea\) was exclusive on 9.7%, while all genera co-occurred on 7.7% of the trees. The distributions overlapped broadly, but \(Bryoria\) had a mostly northern distribution and \(Usnea\)’s distribution was mostly southern, with \(Alectoria\) being intermediate (Fig. 2). \(Bryoria\) and \(Alectoria\) in particular had low frequency along the southwest coast, and all hair lichens were absent from the very south. \(Alectoria\) had its highest frequency in northern and central regions and was extremely rare in southern regions (Fig. 3A). \(Bryoria\) gradually increased towards northern regions, whereas \(Usnea\) peaked in region 3.

The thalli were longest in \(Alectoria\) (19.0 ± 0.4 cm, overall mean ± SE) followed by \(Bryoria\) (13.0 ± 0.2 cm) and \(Usnea\) (8.4 ± 0.1 cm). All genera had longer thalli in northern than in southern regions (Fig. 3B). Four, eight, and six of the 10 pairwise comparisons be-
between regions were significant in Alectoria, Bryoria, and Usnea, respectively (Supplementary material, Table S1').

**Explanatory variables**

All explanatory variables except forest age and continentality decreased from south to north (Table 1). Site quality and nitrogen deposition showed the steepest gradients, followed by precipitation. Southern regions had fewer live branches in lower canopy than northern regions: 61% of P. abies had a crown limit < 5 m in region 5 compared with 92% in region 1. Intercorrelations between all variables were significant due to the large sample size (Supplementary material, Table S21).

Figure 4 shows hair lichen occurrence in relation to the combination of mean annual temperature and mean annual precipitation (1961–1990). Black dots show plots with lichen occurrence, and blue dots show plots with P. abies present but without lichens. Figure provided in colour online.

**Table 1.** Means (±1 standard error) of explanatory variables in the five regions and range across all regions.

<table>
<thead>
<tr>
<th>Variable (abbreviation), unit</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of plots</td>
<td>332</td>
<td>1210</td>
<td>1019</td>
<td>2120</td>
<td>800</td>
<td>5481</td>
</tr>
<tr>
<td>DBHa, cm</td>
<td>23.7±0.4</td>
<td>24.6±0.2</td>
<td>25.1±0.2</td>
<td>27.6±0.2</td>
<td>28.1±0.3</td>
<td>15.0−74.0</td>
</tr>
<tr>
<td>Crown limit (CLa), m</td>
<td>2.4±0.1</td>
<td>3.4±0.1</td>
<td>4.3±0.1</td>
<td>4.0±0.1</td>
<td>4.7±0.1</td>
<td>0−19</td>
</tr>
<tr>
<td>Stand heightb, m</td>
<td>14.7±0.2</td>
<td>17.0±0.1</td>
<td>19.0±0.1</td>
<td>20.1±0.1</td>
<td>19.6±0.2</td>
<td>5.5−36.0</td>
</tr>
<tr>
<td>Stand age (AGE), years</td>
<td>122.3±9.2</td>
<td>106.9±10.1</td>
<td>83.1±10.1</td>
<td>68.4±10.1</td>
<td>59.1±10.1</td>
<td>15−315</td>
</tr>
<tr>
<td>Basal area (BA), m²·ha−¹</td>
<td>18.6±0.4</td>
<td>25.0±0.3</td>
<td>27.3±0.3</td>
<td>27.4±0.2</td>
<td>28.9±0.3</td>
<td>3−75</td>
</tr>
<tr>
<td>Site quality (SQ), m³·ha−¹·year−¹</td>
<td>2.4±0.0</td>
<td>3.5±0.0</td>
<td>6.4±0.1</td>
<td>9.4±0.0</td>
<td>10.9±0.1</td>
<td>1.2−217</td>
</tr>
<tr>
<td>Temperature (TEMP), °C</td>
<td>–0.41±0.04</td>
<td>1.35±0.03</td>
<td>3.51±0.04</td>
<td>5.69±0.01</td>
<td>6.62±0.01</td>
<td>–2.68−7.54</td>
</tr>
<tr>
<td>Continentality (CONT), °C</td>
<td>26.09±0.08</td>
<td>24.39±0.06</td>
<td>22.20±0.03</td>
<td>19.20±0.02</td>
<td>17.58±0.01</td>
<td>16.18−29.26</td>
</tr>
<tr>
<td>Precipitationb, mm·year−¹</td>
<td>649±3.8</td>
<td>657±2.2</td>
<td>734±2.1</td>
<td>714±2.4</td>
<td>851±5.4</td>
<td>491−1214</td>
</tr>
<tr>
<td>Rain index (RAIN), mm·year−¹</td>
<td>381±2.3</td>
<td>411±1.3</td>
<td>493±1.5</td>
<td>526±1.8</td>
<td>674±3.9</td>
<td>275−940</td>
</tr>
<tr>
<td>Nitrogen deposition (NDEP), kg·ha−¹·year−¹</td>
<td>3.55±0.02</td>
<td>4.17±0.02</td>
<td>6.44±0.03</td>
<td>9.78±0.05</td>
<td>14.09±0.08</td>
<td>2.64−18.24</td>
</tr>
</tbody>
</table>

For sample trees.

bStand height and precipitation were not included in the logistic regression models.

**Table 2.** Pseudo $R^2$ values for separate variables (after transformation; see Supplementary material, Table S3') in logistic regression models predicting the occurrence of Alectoria, Bryoria, and Usnea in the lower canopy of P. abies (N = 5481).

<table>
<thead>
<tr>
<th>Explanatory variable</th>
<th>Alectoria</th>
<th>Bryoria</th>
<th>Usnea</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature, °C</td>
<td>0.312</td>
<td>0.419</td>
<td>0.171</td>
</tr>
<tr>
<td>Nitrogen deposition, kg·ha−¹·year−¹</td>
<td>0.290</td>
<td>0.405</td>
<td>0.174</td>
</tr>
<tr>
<td>Continentality, °C</td>
<td>0.254</td>
<td>0.392</td>
<td>0.167</td>
</tr>
<tr>
<td>Site quality</td>
<td>0.265</td>
<td>0.366</td>
<td>0.139</td>
</tr>
<tr>
<td>Rain index, mm·year−¹</td>
<td>0.139</td>
<td>0.254</td>
<td>0.077</td>
</tr>
<tr>
<td>Stand age, years</td>
<td>0.149</td>
<td>0.156</td>
<td>0.077</td>
</tr>
<tr>
<td>Basal area, m²·ha−¹</td>
<td>0.019</td>
<td>0.033</td>
<td>0.005</td>
</tr>
<tr>
<td>Crown limit, m</td>
<td>0.022</td>
<td>0.026</td>
<td>0.021</td>
</tr>
<tr>
<td>DBH, cm</td>
<td>0.001</td>
<td>0.007</td>
<td>0.003</td>
</tr>
</tbody>
</table>

Note: All models are statistically significant ($P < 0.001$). Variables are sorted by $R^2$ for Bryoria. DBH, diameter at breast height (1.3 m).

**Logistic regression models for separate variables**

Most models were nonlinear and all variables had highly significant slope coefficients (Supplementary material, Table S3') with highest pseudo $R^2$ value for Bryoria, followed by Alectoria and Usnea (Table 2). The sequence of variables was similar for all genera.

1Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2016-0113.

Fig. 4. Occurrence of Alectoria, Bryoria, and Usnea in the lower canopy of P. abies in relation to mean annual temperature and mean annual precipitation (1961–1990). Black dots show plots with lichen occurrence, and blue dots show plots with P. abies present but without lichens. Figure provided in colour online.
when ranked by $R^2$ values. Temperature, nitrogen, continentality, and site quality had higher $R^2$ value than the rain index. Stand age had the highest $R^2$ value of the forest variables, whereas basal area, crown limit, and DBH had low explanatory power (in terms of pseudo $R^2$ values). 

The odds ratios (Fig. 6) show how odds for lichen occurrence change when increasing one variable in the models. The odds increase significantly when the lower confidence bound is higher than 1.0 and decrease when the upper confidence bound is lower than 1.0. The odds ratio curves for increasing temperature with 1 °C differed among genera. 

**Discussion**

Compared with former studies on regional distribution of hair lichens, our study is based on the largest sample so far. Monitor-
ing programs such as NFI s have large potential to analyse factors affecting broad-scale distributions of forest organisms. Although based on simple measures of presence and absence and a crude abundance estimate (thallus length), the large number of sample plots enables highly valuable information on factors potentially affecting broad-scale distributions of forest organisms. Although confounding natural and anthropogenic factors complicate the separation and identification of mechanisms controlling the distribution of hair lichens in the study area. However, although forestry is intense throughout Sweden, air pollution is low in northern regions (Pihl Karlsson et al. 2011). This suggests that climate and forest structure are main drivers for hair lichens in northern regions. The more open, low forests and drier continental climate likely cause the high frequency of *Bryoria* in the two northernmost regions (cf. Gauslaa 2014). Among lichens, *Bryoria* growing in the lower canopy has one of the lowest capacities to store internal water (Esseen et al. 2015) but rapidly takes up water from humid air and dewfall. Dewfall is an important water source for *Bryoria* in open, continental forests with large diurnal temperature amplitude (Gauslaa 2014). *Bryoria* also has dark absorbing pigments (melanins) that efficiently screen and protect the underlying algae from excess light (Farber et al. 2014). These pigments allow *Bryoria* to grow in lower canopies of open forests, as well as in exposed upper canopies. Their high absorbance causes snowmelt, supplying *Bryoria* with water and allowing photosynthesis during winter (Coxson and Coyle 2003). By contrast, *Alectoria* and *Usnea* have the bright reflecting pigment usnic acid and are more susceptible to high light in the desiccated state than *Bryoria* (Farber et al. 2014). This mechanism may contribute to the lower frequency of *Alectoria* and *Usnea* in northern regions that generally have a drier climate and smaller areas of shady and moist *P. abies* dominated forests. *Alectoria* is associated with humid forests in Fennoscandia (Ahlner 1948) and North America (McCune and Geiser 2009; Boudreault et al. 2015). This also applies to many pendulous *Usnea* species.

The northward decrease of *Usnea* was correlated with lower temperatures (Figs. 4 and 5), suggesting that *Usnea* is sensitive to cold climates. However, low temperatures per se may not limit *Usnea*, as boreal lichens are tolerant to freezing (Haukk 2011). Instead, we hypothesize that the low amount of rain limits *Usnea* in northern regions (Figs. 4 and 5), where more than one-third of the precipitation falls as snow. *Usnea dasypoga*, the most common *Usnea* in northern Sweden, has a lower internal water storage capacity than *Alectoria* (Esseen et al. 2015). Compared with *Alectoria*, *U. dasypoga* needs more frequent hydration to maintain high growth, which may explain why *Usnea* becomes more restricted to humid sites in northern regions such as riparian forests and gullies. In Norway, *Usnea* is abundant in rainy coastal areas with high rainfall, whereas *Bryoria* is scarce (Bruteig 1993), as this genus is sensitive to excess hydration (Goward 1998).

The factors affecting hair lichens in southern regions are less known. Air pollution still reduces hair lichens in southern and southwestern Sweden, despite the strong reduction in SO2 pollution since the 1970s. Only minor recovery in lichen communities has occurred, likely because nitrogen deposition is still high (van Herk et al. 2003; Hultengren et al. 2004; Grandin 2011). Nitrogen deposition in southern Sweden (9.8 and 14.1 kg N·ha-1·year-1 in regions 4 and 5, respectively) exceeds critical loads for acidophytic lichens. Our odds ratio curves from multiple logistic models (Fig. 6) suggest that the critical load is 3.9 kg N·ha-1·year-1 for *Alectoria* and 5.7 kg N·ha-1·year-1 for *Usnea*. Nitrogen was not included in the multiple model for *Bryoria*, but the separate model (Fig. 5) indicates a somewhat lower critical load than for *Alectoria* and *Usnea*. Our critical loads are in the same range as for other nitrogen-sensitive species (Geiser et al. 2010; Bobbink and Hettelingh 2011; Pardo et al. 2011). In a whole-tree experiment in an oligotrophic boreal forest, Johansson et al. (2010, 2012) found that *Alectoria* and *Bryoria* increased at 6 kg N·ha-1·year-1 and remained stable or decreased at 12.5 kg N·ha-1·year-1 after 4 years. These levels are higher than our critical loads, but nitrogen loads that are neutral or positive
in a short-term perspective could be negative over longer periods. McCune and Geiser (2009) classified most hair lichens as oligotrophs in nutrient-poor sites, but some were mesotrophs. They reported a peak detection frequency of 2.4 kg N·ha⁻¹·year⁻¹ for *A. sarmentosa*, 2.0 kg N·ha⁻¹·year⁻¹ (mean) for 12 *Bryoria* species, and 2.3 kg N·ha⁻¹·year⁻¹ (mean) for 12 *Usnea* species in the Pacific Northwest, USA. However, *U. subfloridana* was eutrophic, with a peak detection at 6.1 kg N·ha⁻¹·year⁻¹ (McCune and Geiser 2009). In fact, *U. subfloridana* probably contributed to our higher critical load for *Usnea*. It is one of the most widespread *Usnea* species in southern regions (Halonen et al. 1999; Thell and Moberg 2011), likely favoured by nitrogen on conifers with acidic bark.

The lower importance of forest variables in our models follows partly from sampling confined to large trees and by excluding early-successional stands. However, the higher crown limit in southern regions (mean, 4.0–4.7 m; Table 1) suggests that the scarcity of live branches in the lower canopy contributed to the low occurrence of hair lichens in these regions. Moreover, the high basal area in southern regions suggests that low light limits hair lichens, particularly *Bryoria* in productive forests such as dense *P. abies* plantations. *Bryoria* has a higher light compensation point than *Alectoria* (Coxson and Coyle 2003). Overall, hair lichens in southern regions are negatively impacted by changes in land use, including clearcutting, planting of conifers, and denser forests. *Bryoria* and *Usnea* are also more common on deciduous trees than on *P. abies* along the western coast (S. Hultengren, personal communication).

Our results reinforce the fundamental importance of high forest age for the accumulation of hair lichens (Esseen et al. 1996; Horstkotte et al. 2011; Boudreault et al. 2015). Timber harvesting has negative impact on hair lichens throughout Sweden because rotation cycles are too short (50–120 years) for high biomass to accumulate (Dettki and Esseen 2003). *Alectoria* depended most on high forest age and prefers slow-growing forests considerably older than the current rotation cycles. Less efficient dispersal in *Alectoria* than in *Bryoria* (Esseen et al. 1996) is a likely cause.

**Factors affecting length**

Hair lichens have considerable growth potential and can grow several centimetres per year (Stevenson and Coxson 2003; Jansson et al. 2009). The maximum length of *Alectoria* across Sweden (19 cm) was half the length in northern, old-growth *P. abies* forests (41 cm, Esseen 2006). *Alectoria* can be 0.5–1 m long in optimal sites (Esseen and Renhorn 1998), thus the larger dimensions in *Alectoria* than in *Bryoria* are not surprising. The small size of *Usnea* (8.4 cm) across Sweden and of *Alectoria* and *Bryoria* in southern Sweden (regions 4 and 5) is remarkable. Short *Bryoria* and *Usnea* thalli on *P. sylvestris* in southern Norway result from air pollution (Bruteig 1993). *Usnea dasypogca* could be 30–50 cm long or even longer. Thereby, conditions for *Usnea* are hardly optimal in large parts of Sweden. However, we do not know how many observations are shrubby species such as *U. subfloridana*. Our length data cannot be converted to
lichen biomass in the lower canopy. However, Esseen (2006) showed that a 2-fold increase in maximum length corresponded to a 5-fold biomass increase in Alectoria. Hence, regional differences in biomass are likely significantly larger than indicated by our length data.

**Model performance**

Many factors influence model performance, including accuracy of lichen observations, forest data, gridded climate, and nitrogen data, as well as variable selection and transformations used in model construction. We have no data on observer accuracy, but lichen identification was likely less problematic in this study focusing on genera and not individual species. However, small thalli are difficult to detect and possibly overlooked in the inventory.Using genera and not individual species. However, small thalli are difficult to detect and possibly overlooked in the inventory. Curingongeneraandnotindividualspecies. However, small thalli are difficult to detect and possibly overlooked in the inventory..subtractingfrommodels may have been influenced by variable

R. in drier microclimates, to long, pendulous species such as U. dasypoga and U. longissima in humid forests (Thell and Moberg 2011). The variability in habitat preferences is partly explained by greater variability in water storage capacity in Usnea than in Bryoria (Gauslaa 2014; Esseen et al. 2015; P.-A. Esseen, unpublished data). Future studies should address factors affecting regional distribution of individual Bryoria and Usnea species (Shrestha et al. 2012) and include higher canopy positions.

Our models could probably be improved by including light availability and landscape context variables (not available in the NFI) such as proximity to old forests functioning as a propagule source (Dettki et al. 2000). Distance to forest edge could also be of interest, as hair lichens are sensitive to edge microclimates (Esseen and Renhorn 1998). Sweden’s forests, particularly the southern and central regions, are highly fragmented by forestry and agriculture with a large extent of abrupt forest edges (Esseen et al. 2016) that may strongly influence hair lichens.

**Implications**

If our models truly reflect species requirements, they suggest major range shifts in the distribution of hair lichens following changes in climate, nitrogen deposition, and forest structure. Climate scenarios for Sweden predict a 2–6°C increase in mean annual temperature and a 10%–40% increase in precipitation by the end of the century, with the largest changes in northern regions (Sjökvist et al. 2015). In fact, the changes in the estimated odds of occurrence were surprisingly large following relatively moderate increases in some of the variables such as a temperature increase of 1°C (Fig. 6). Our models suggest that a warmer climate would always be negative for Bryoria. By contrast, warming might be positive for Alectoria and particularly for Usnea in colder climates but negative in warmer climates. Such effects also depend on whether predicted altered precipitation patterns during warmer winters would affect lichens negatively (cf. Bjerke 2011). Results also suggest that a wetter climate facilitates Usnea (Figs. 4 and 5), whereas Bryoria would decrease (Fig. 6). If nitrogen deposition increased, the occurrence of Alectoria and Usnea, probably also of Bryoria, would decline in most of Sweden but not necessarily in northern regions with low deposition. Extending the rotation periods would increase hair lichen occurrence (Figs. 5 and 6), whereas shorter rotation periods would have a very negative effect (Dettki and Esseen 2003), particularly for Alectoria. If several factors change simultaneously, we could expect synergistic responses that could dramatically disrupt ecological functions of hair lichens in forests. This may have cascading negative effects on other organisms such as reindeer, canopy-living invertebrates, and passerine birds (Pettersson et al. 1995) and adversely impact water and nutrient cycling (e.g., Knops et al. 1996; Stanton et al. 2014).

**Conclusions**

Hair lichens are key components in forest canopies but face multiple environmental hazards threatening their function in forest ecosystems. Our models may help to interpret and (or) predict current and future changes in regional distribution of hair lichens. Such knowledge is critical for choosing adequate measures to mitigate impacts of climate change, element deposition, and forestry on hair lichens. The correlations between hair lichen occurrence and explanatory variables presented here suggest mechanistic hypotheses for future experimental testing. We conclude that broad-scale distribution of hair lichens in the lower canopy of P. abies is stronger coupled to macroclimate and nitrogen deposition than to forest structure in Sweden with strong south–north environmental gradients. The three hair lichen genera show broad similarities in response to environmental variables but differ in important aspects such as the shape of relationships with temperature, rain, nitrogen deposition, and stand age. The multiple logistic regression models suggest major range shifts in the regional distribution of the three hair lichen genera following future changes in climate, nitrogen deposition, and forest management. Our study also shows that odds ratios is a useful tool for interpreting complex logistic regression models of lichen occurrence. More studies are needed from other parts of Eurasia and North America to test our hypotheses at global scales.

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line model \(g(x) = \beta_0 + \beta_1 x\), where \(g(x) = \ln(\pi(x)/(1 - \pi(x)))\) denotes the logit and \(\pi(x)\) is the probability of occurrence given \(x\), is the natural starting point, but nonlinear relationships need to be investigated for possible improvements of fit. In the first-degree fractional polynomial algorithm, the best power transformation \(x^p\) is found, with the power \(p\) selected from a small predefined set, \(\mathcal{P} = \{-2, -1, -0.5, 0, 0.5, 1, 2, 3\}\), where \(x^0\) denotes \(\ln x\). For example, for \(p = -1\), the logit is \(g(x) = \beta_0 + \beta_1 / x\). In the second-degree fractional polynomial algorithm, the logits are of the form \(g(x) = \beta_0 + \beta_1 x^p + \beta_2 x^q\), for the limiting case where \(p = q\). \(g(x) = \beta_0 + \beta_1 x^p + \beta_2 x^q \ln x\), where \(p\) and \(q\) are selected from the set \(\mathcal{P}\). An explanatory variable is shifted and rescaled before being power transformed if nonpositive values are encountered or if the range of the variable is large. When there are several explanatory variables, backward elimination is combined with the search of the best fractional polynomial transformation for each explanatory variable. At each step of a “backfitting” algorithm, the method finds a fractional polynomial transformation for each explanatory variable while keeping the current functional forms of the other explanatory variables fixed (Benner 2005). The algorithm ends when the functional forms of the explanatory variables do not change anymore. In cases where the “best” fractional polynomial model is better than the linear model, it is common that there is another fractional polynomial model that is also better and whose deviance is trivially larger than the selected “best” model. If that other model makes more sense from a subject-matter perspective and is more easily explained than the “best” model, one should not hesitate to use the other model, see, for example, Hosmer et al. (2013, p. 98) for a similar reasoning. Finally, various residual plots were used for assessing goodness of fit (Hosmer et al. 2013). We used the library mfp in R (Benner 2005) for fitting multiple fractional polynomial models.

References