What is good for birds is not always good for lichens: Interactions between forest structure and species richness in managed boreal forests

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ABSTRACT

Forestry in the boreal region increasingly replaces natural disturbances in shaping biodiversity. Large-scale removal of small diameter trees (thinning), is ubiquitous in northern European forestry, yet an understanding of how it relates to biodiversity across taxa is lacking. To address this, we examined how two forest structural elements, commonly impacted by forest thinning (i.e. vegetation density in the understory and overstory), are correlated with the species richness of forest-dwelling birds and epiphytic lichens. These taxa were chosen because they likely have opposing habitat demands: epiphytic lichens potentially benefitting from more light in open forests, and birds benefitting from structurally complex forests for foraging, nesting and cover. We used remote sensing tools, already applied in forestry planning, to see if management recommendations could be found that balance the needs of both taxonomic groups within the same forests. Our results show that richness in epiphytic lichens and forest-dwelling birds is not correlated and that a high species richness (~15 birds & ~40 epiphytic lichens) in both taxa is only predicted in the same stand under a specific vertical distribution and density of the forest's vegetation: this occurs when the vegetation above 3 m is open (to promote epiphytic lichen richness) and below 3 m is dense (to promote bird richness). Dense vegetation up to 7 m above ground has a diverging effect on forest birds (positive) and epiphytic lichens (negative). A larger stem diameter further increases species richness in both taxa. Our study provides results that are directly implementable in forestry planning over large areas with the help of remote sensing tools (LiDAR).

1. Introduction

There is increasing evidence that modern forestry leads to diminished biodiversity in boreal forests (Burton et al., 2010), which has resulted in political targets that combine economic and ecological sustainability within the forestry sector (CBD, 2010). Forest management in this region often replaces natural disturbances and succession as the drivers of structural complexity (Brumelis et al., 2011) and with that biodiversity (Stein et al., 2014). Therefore, forest managers that aim at combining biomass extraction with conserving biodiversity, need to know how the promotion or removal of various forest structural elements affect biodiversity across different taxonomic groups (Sabatini et al., 2016). Here, research has provided clear suggestions for the retention level of green trees (e.g. Sterkenburg et al., 2019; Ylisirniö and Hallikainen, 2018) and key structural elements for biodiversity such as coarse woody debris (e.g. Rudolphi et al., 2014) and deciduous trees (e.g. Lundström et al., 2013). This research, however, is almost exclusively focused on the final felling stage of the forestry cycle.

Management intervention prior to final felling is likely to be at least as consequential for boreal forest biodiversity, especially since management intervention during this period affects a much larger forest area, at least in Fennoscandia (Swedish Forest Agency, 2017). Despite this, research here is largely missing (but see Muir et al., 2006; Root et al., 2010; Widenfalk and Weslien, 2009). One such management intervention is forest thinning, which in Sweden affects approximately 60% of the productive forest land (Swedish National Forest Inventory (NFI), 2019), is likely to have a significant impact on biodiversity because it strongly affects the variety and amount of forest structural elements, such as tree species composition, understory shrubs, dead wood and the ground vegetation (Holm, 2015).

Forest thinning further turns previously dense forests into forests with an open vegetation in the understory (thinning from below, e.g. removal of smaller than average merchantable trees) and/or with an open vegetation in the overstory (thinning from above, i.e. harvesting the largest trees; Verschuyl et al., 2011). For sessile and photosynthetically active organisms like vascular plants (Hedwall et al.,

2013) and lichens (Gauslaa and Solhaug, 1996), forest thinning may improve growth conditions through increased light penetration to lower levels of the forest (Neitlich and McCune, 2003). In contrast, for mobile organisms such as mammals, arthropods and birds, a reduction in the density and spread of the vertical distribution of the forest's vegetation may have negative consequences (Tews et al., 2004). Few studies have investigated these relationships for boreal forests or similar habitats in alpine regions, and those that have, focused on structurally rich natural forest habitats or only on one species group (McMullin et al., 2010; Muir et al., 2006; Müller et al., 2010). Because managed forests often consist of a relatively low structural diversity in general (Linder and Östlund, 1998), using results from complex forest systems to inform biodiversity-conservation forest management in simple systems might be inappropriate. In structurally poor forests, small changes in the vegetation density may result in relatively stronger responses in biodiversity than in complex systems, and mechanistic relationships might be more easily exposed (Hilborn and Stearns, 1982). While some studies have investigated the effect of vegetation density on mobile and sessile species groups in simple forest systems (Lindberg et al., 2015; Neitlich and McCune, 2003), there is no information comparing taxa with differing habitat requirements from the same location. This is essential for drawing solid conclusions about the effect of forest thinning on biodiversity across several organism groups and will decrease the risk of taking a positive conservation decision for one taxon while unknowingly diminishing the diversity of another.

We approach this question by examining the relationships between the vegetation density in the understory (defined as all plant/tree biomass below a certain height) and overstory (defined as all plant/tree biomass above a certain height), to the species richness (hereafter richness) of sessile (i.e. epiphytic lichens) and mobile taxa (i.e. forest-dwelling birds; excluding birds with large home-ranges such as birds of prey or ravens, hereafter birds) in intensively managed boreal forests of central Sweden (Fig. S.1). We compare the taxon-specific relationships, as well as the relationship between forest structure and the summed expected richness of all species across both taxa to determine whether biodiversity can be maintained through a single management approach, or requires a combination of approaches across multiple forest stands. In order to make our results relevant for forestry thinning management, we used forest vegetation measures that: (i) are known to be affected by forest thinning, (ii) have been previously identified as important for biodiversity across different organism groups, and (iii) are measurable with remote sensing tools. Thus in this study we focus on the tree stem diameter and the density and vertical distribution of the forest's vegetation (understory/overstory density), which is most effectively measured with light detection and ranging (LiDAR; Lindberg et al., 2012); information that is available to forest managers nationwide.

Epiphytic lichens are photosynthetically active (Palmqvist, 2000) and their richness is therefore expected to be higher in forests with open under and overstory with higher light penetration. In contrast, forest-dwelling birds are expected to profit from a dense understory since it provides predator protection when feeding on the ground (Hakkarainen et al., 2004) as well as more suitable nesting opportunities (Eggers and Low, 2014). However, it is less clear whether a dense overstory would benefit forest bird species, as the reduced light penetration will make the microclimate colder during breeding and consequently lead to lower food abundance during this time (especially insects; Hedwall et al., 2013; Williams, 1961). While this might suggest that we can already predict the impacts of forest thinning management on biodiversity, the story is more complicated because of the additional effect that thinning has on the stem diameters among retained trees (thinning from below promotes larger stem diameters; Mäkinen and Isomäki, 2004). A larger stem diameter can lead to a higher abundance of microstructures (e.g. crevices) while not necessarily increasing macrostructures (e.g. forest vegetation density; Barbier et al., 2008). This may improve growth conditions for epiphytic lichens (Thor et al., 2010; Ylisirniö and Hallikainen, 2018) and reproductive success for birds as

tree bark crevices are important for insect abundance (MacFarlane and Luo, 2009). We therefore hypothesise that: (1) a dense overstory will have a negative effect on the richness of epiphytic lichens but no clear effect on birds, (2) a dense understory will be positive for birds but not for epiphytic lichens and that the strength of the taxa's response differs, (3) that the average tree stem diameter has a positive impact on the richness of both groups and that the strength of the response does not differ between the taxa, (4) that summed richness across both taxa consequentially is highest in forests with a combination of a relatively larger stem diameter, a more open overstory and a more dense understory, and (5) epiphytic lichen and bird richness is not correlated across forests with varying understory/overstory densities. We examined these predictions for three different 'height breaks', to find the height above ground which defines a meaningful functional border between the forest's understory and overstory for epiphytic lichens and birds. We also assessed whether any particular tree species was correlated with understory/overstory densities at these different height breaks.

2. Material and methods

2.1. Study site

The study site is located east of Uppsala in Sweden (59.84, 17.96, Fig. S.1) where the forests and the silviculture are a typical example of young coniferous dominated managed stands in Fennoscandia. Forestry here is based on 80–100 year cycles, with one cycle consisting of clear cutting, replanting and one to three thinning's, predominantly from below, during which a large part of the vegetation in the understory is removed (Holm, 2015). The reduction of tree density also contributes to reducing the amount of vegetation in the overstory to a varying degree. The tree species are predominantly Scot's pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), with deciduous species, mostly birch (*Betula* spp.) and aspen (*Populus tremula*) being more rare (Holm, 2015). The landowner (forest company Holmen AB) provided us with 250 ha of forests at an age of 40 to 70 years which were managed for the production of pine and ready for thinning. These forests were distributed along a gradient from low to high understory/overstory densities, where forests offered a dense understory in combination with an open or dense overstory as well as vice versa (Minimum and maximum densities in Table 1). For this study we placed 58 plots with a radius of 50 m in the forests, excluding bogs, lakes and forestry roads. For the forest descriptive measurements and the epiphytic lichen survey, we placed three 10 m radius subplots within each plot (one in the plot centre, and 25 m to the east and west of the centre). The minimum distance between two plot centres was 100 m, the mean 8.6 km, and the maximum 20 km (Fig. S.1).

2.2. Data collection

2.2.1. Bird data collection

The survey plots were visited between April 1 and June 21, five times in 2017 and five times in 2018; all surveys occurred between 30 min before sunrise and six hours after. We noted the occurrence of all bird species, except flyby birds, heard or seen within 50 m from the plot centre, during two five minute sessions at every visit. The break between sessions was 20 min in 2017 and 5 min in 2018. Of the 58 plots, 32 were affected by thinning management that occurred in the winter of 2017/2018 and were therefore not surveyed for this study in 2018. Point count surveys were always performed by the same observer (JK). We recorded 2297 bird occurrences of 33 species, among which 4 bird species are red-listed in Sweden: *Chloris chloris* (EN), *Ficedula hypoleuca* (NT), *Tetrastes bonasia* (NT), *Poecile montanus* (NT), and *Poecile palustris* (NT) (SLU Artdatabanken, 2020). A species list with the number of observations per species is provided in Table A1.

Table 1
Summary of all forest variables used in this study and of both the scaled and expected species richness of epiphytic lichens and birds (2017 data). The unit for the vegetation densities is the percentage of laser reflections below (understory) and above (overstory) the indicated height break (Fig. 1).

	min	1st quantile	mean	3d quantile	max
vegetation density (% laser returns)					
overstory > 3 m	42.3	47.3	52.2	57.5	70.5
overstory > 5 m	31.5	43.6	48.5	53.4	64.0
overstory > 7 m	15.7	38.2	43.1	49.6	61.6
understory < 3 m	1.5	2.7	3.9	4.5	9.4
understory < 5 m	2.7	4.5	7.7	8.8	26.2
understory < 7 m	4.1	7.7	13.0	14.3	46.7
diameter at breast height (cm)					
remotely sensed DBH	12.2	18.4	20.2	22.1	28.3
field DBH	11.2	16.5	19.1	22.2	28.8
number of trees per hectare					
deciduous	0	42	189	220	1783
Scot's pine	11	170	387	560	881
Norway spruce	11	138	370	409	1592
understory spruce	42	514	791	976	2610
expected species numbers (absolute and scaled)					
epiphytic lichen richness	15	30	35	39	75
epiphytic lichen richness (scaled)	−2.9	−0.7	0	0.6	5.8
bird richness	5	12	13.9	16	25
bird richness (scaled)	−3.8	−0.7	0	0.7	3.7

2.2.2. Epiphytic lichen data collection

In all 58 plots, we randomly chose one of the three subplots for the epiphytic lichen inventory. The presence of all epiphytic lichen species on the stem and the branches (including wood) below 2 m above ground were surveyed by a lichenologist (GT) in the spring of 2018. We surveyed only epiphytic lichens as other lichen types were not abundant enough to study them. The survey technique used a constant survey time per basal tree area to avoid survey bias associated with different stem-diameter trees. We included all live trees with a diameter at breast height (DBH) of at least 10 cm. This restricted survey area on these trees < 2 m is likely to capture the true richness for epiphytic lichens since it has been shown that in boreal forests, richness is either constant along the tree's height gradient or maximised in this lower section of the tree (Caruso and Thor, 2007). In the plots where thinning occurred in the winter of 2017/2018, epiphytic lichens were inventoried only on the remaining stems. Because the inventory took place only months after the thinning, the epiphytic lichen community could still be
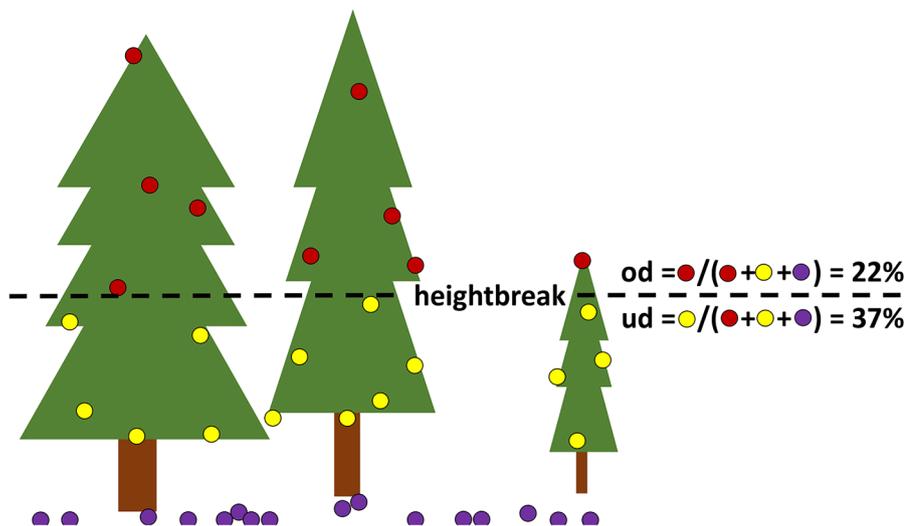
attributed to the forest structure before the thinning (Johansson et al., 2018). We noted 13 928 epiphytic lichen occurrences of 116 species on 1101 trees, among which no epiphytic lichens were red-listed in Sweden (SLU Artdatabanken, 2020). A species list with the number of observations per species and details on species identification is provided in Table A2.

2.2.3. Forest data collection

To analyse the importance of the density of the forest vegetation for birds and epiphytic lichens, we used LiDAR-derived metrics representing understory and overstory density. LiDAR data is a 3D co-ordinate informed point cloud in which every point represents a reflection of light, emitted by an airborne (here airplane) laser scanner, either on the ground or on the vegetation (including stems; Lefsky et al., 2002). The data in this study were collected in April 2011 by the Swedish Land Survey (Lantmäteriet, 2016; Density = 0.5–1 point/m^2, Precision = 3.1 cm vertical & 25 cm horizontal). This was 7 years before the species data collection. However vegetation growth, particularly in the supressed understory, is slow in this region (6.6 m^3/(ha * year); Swedish National Forest Inventory (NFI), 2019) and we therefore assume that possible changes in forest structure are small and neglectable given the coarse laser resolution. For every plot we calculated the percentage of laser reflections between 0.5 m and a height break (understory density) and above a height break (overstory density), using Fusion (Schematic figure of this metric in Fig. 1; McGaughey, 2015). A definition for the height break that separates the understory from the overstory in a forest does not exist. Therefore and to find the height break which is functionally meaningful for epiphytic lichens and birds, we set the height break to either 3, 5 or 7 m, with 7 m being the apparent natural upper limit for the understory (average forest height = 14 m; Fig. 1). The understory density was not correlated with the overstory density for the 3 and 5 m height break (Pearson correlation coefficient (Pcc) = 0.05 and −0.35), but correlated for the height break at 7 m (Pcc = -0.7).

In autumn 2017 and in the forest, we measured the tree DBH (diameter breast height at 130 cm) and noted the species of all live trees with a diameter of at least 5 cm on all subplots on each plot. We measured the DBH because we assumed it would have a strong influence on richness and because it is a metric that is also available as remote sensing data for Swedish forests (Reese et al., 2003; Pcc between field data DBH and remote sensing DBH in this study location = 0.87). We counted the number of trees to clarify whether the understory/overstory densities, measured by LiDAR, were shaped by the numbers of any tree species in particular. A summary of all the measurements is in Table 1.

od = ●/(● + ○ + ●) = 22%
ud = ○/(● + ○ + ●) = 37%

Fig. 1. Schematic figure serving as an example showing how the understory/overstory densities are calculated from the LiDAR data. Every point represents a laser return on any plant/tree object. Yellow points are below the chosen height break and red ones above. Purple points represent laser returns on the ground. The overstory density (od) and understory density (ud) are then calculated as shown in the picture. Because a definition for the height break that separates the understory from the overstory in a forest does not exist as well as to find the height break which is functionally meaningful for epiphytic lichens and birds, we set the height break above to either 3, 5 or 7 m, with 7 m being the natural upper limit for the understory (average forest height = 14 m). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.3. Statistical analysis

2.3.1. Bird model

To model expected bird richness, we fitted a Bayesian multi species occupancy model to account for incomplete detection (Fig. S.2). We used a multivariate normal distribution because of the possibility that the rate of detection and occupancy were correlated (i.e. a higher occupancy probability is often associated with a higher species abundance, which increases the detection probability; Kéry and Royle, 2008). The number of surveys per bird species varied between 6 and 10, depending on the arrival date of that species at the site, with us using species-specific arrival dates to adjust the number of potential surveys for detection in the model. The mean and SD of bird richness (the sum of all predicted species occupancies) was then extracted from the model for every plot and both survey years (Fig. S.2). Some bird species were excluded from our analyses because their presence could not be definitively associated with the forest structure of the survey plot: i.e. birds not breeding in the area (*Fringilla montifringilla, Acanthis flammea*), birds not breeding during the survey period (*Loxia* spp.), and birds of prey (*Buteo buteo, Accipiter gentilis* and *nisus*) and ravens (*Corvus corax*) with home ranges much larger than the plot scale.

2.3.2. Epiphytic lichen model

Because the large variation of tree numbers among subplots would result in a sampling bias, we used species accumulation curves based on the number of trees surveyed per subplot and the occurrences of epiphytic lichen species per tree to model the expected richness on each plot. To do this we pooled the epiphytic lichen species found per stem and branch to species occurrence per tree, then reshuffled the order of all inventoried trees 100 times for every plot and created 100 species accumulation curves (Gotelli and Colwell, 2001). We then extracted the mean and the SD of the expected richness across all species accumulation curves for every plot (Fig. S.2). The species accumulation curves were modelled with a Michaelis-Menten function with the asymptote being the expected epiphytic lichen richness per plot and the half saturation parameter the number of trees needed to reach half of the expected plot richness. The accumulated number of unique species observed on a certain sampled tree of a certain species accumulation curve was modelled with a Poisson distribution.

2.3.3. Combined and summed richness model

To answer the question of how the richness of epiphytic lichens and birds responds to understory and overstory densities as well as the stem DBH and to answer whether the response differs between the two taxa, we combined epiphytic lichen and bird richness estimates from the respective species group models (above) into a new model according to Kéry and Royle (2016; Fig. A.2) with the species group as an interaction term (*combined richness model*). Because these methods are Bayesian, we could include the uncertainty from the taxon-specific richness model estimates (above) into this new model. Epiphytic lichen richness, and hence also its variance, is generally much larger than bird richness, making a direct comparison of the taxa's richnesses hard to interpret. To account for this, we used scaled richness values (Z-score Normalisation). To compare scaled values to raw values and to be able to interpret the order of magnitude of a change, we provide quantiles of both scaled and unscaled expected richness values in Table 1 and detailed comparison figures for every plot in the supplementary material (Fig. S.3). We analysed also the response of the summed richness across both taxa to the understory/overstory densities and stem DBH (*summed richness model*; Fig. S.2). To avoid epiphytic lichen richness dominating the sum we used the sum of the scaled richness values also in this analysis. Both analyses (*combined* & *summed richness models*) were performed for each of our three height breaks between the understory and the overstory, once with the bird data from 2017 and once with the bird data 2018. We evaluated the models according to their ability to predict the mean, coefficient of variance and the residuals of the original data

(posterior predictive checks; see Hooten et al., 2015). Using the posterior distribution, we predicted the change in richness due to the understory - and overstory density, and visualised this with the package *ggplot2* (Wickham, 2009) in R. For this visualisation, we back-transformed the scaled richness in the figure showing the results of the *combined richness model*.

2.3.4. Correlation among forest variables and taxa

We calculated the Pearson correlation coefficients (Pcc) between the understory/overstory densities and the amount of different tree species in the forest, to see if the amount of a tree species in particular was correlated with the understory/overstory densities at different height intervals. For a direct comparison of the two taxa, we calculated the Pcc between the mean expected absolute richness values for birds and epiphytic lichens and visualised this comparison with *ggplot*.

2.3.5. Model specifications

The whole data analysis process followed a Bayesian hierarchical framework in JAGS (Just another Gibbs sampler; Plummer, 2003) in R (R Development Core Team, 2013) with the packages *rjags* (Plummer, 2015) and *CODA* (Plummer et al., 2006). For all models, three MCMC chains with different initial values were run until convergence and good mixing was achieved. Subsequently 100 000 samples with a thinning interval of 50 were taken. All continuous explanatory variables were scaled to improve model performance and facilitate interpretability of model outputs. Flat priors were used for all estimated parameters, unless specified otherwise. While we ran all models with bird data from 2017 and 2018, the visualisations are with bird data from 2017 only. The analyses together with the data can be downloaded (http://doi.org/10.5281/zenodo.3899847).

3. Results

3.1. Combined richness model

3.1.1. The response of birds to the forest variables

A denser understory up to 3 and 5, but not up to 7 m, was associated with higher bird richness. A denser overstory defined by all of the three height breaks, on the other hand, had an overall negative effect on bird richness, although with high associated uncertainties (Fig. 2). Birds showed a positive response to the DBH in the models with the 5, and 7, but not the 3 m height break (Table 2).

3.1.2. The response of epiphytic lichens to the forest variables

A denser overstory above all three height breaks had a strongly negative effect on epiphytic lichen richness, while a denser understory below the 5 and 7, but not 3 m height break had a marginally negative effect on epiphytic lichens (Fig. 2). Epiphytic lichen richness showed a clear increase with an increasing stem DBH in all models (Table 2).

3.1.3. The response of the two taxa compared

The two taxa differed only in their response to the understory density up to 5 and 7 m, with epiphytic lichens showing a clear negative response in contrast to the positive response of bird richness to a denser understory (Table 2).

3.2. Summed richness model

The summed richness of birds and epiphytic lichens per plot was strongly positively related to DBH (Table 3) and negatively related to the overstory density above all three height breaks (Fig. 3). The understory density had only a marginally positive effect on the summed richness when its defining height break was 3 m (Fig. 3). To get an impression of the magnitude of change in absolute richness, see Fig. S.3.
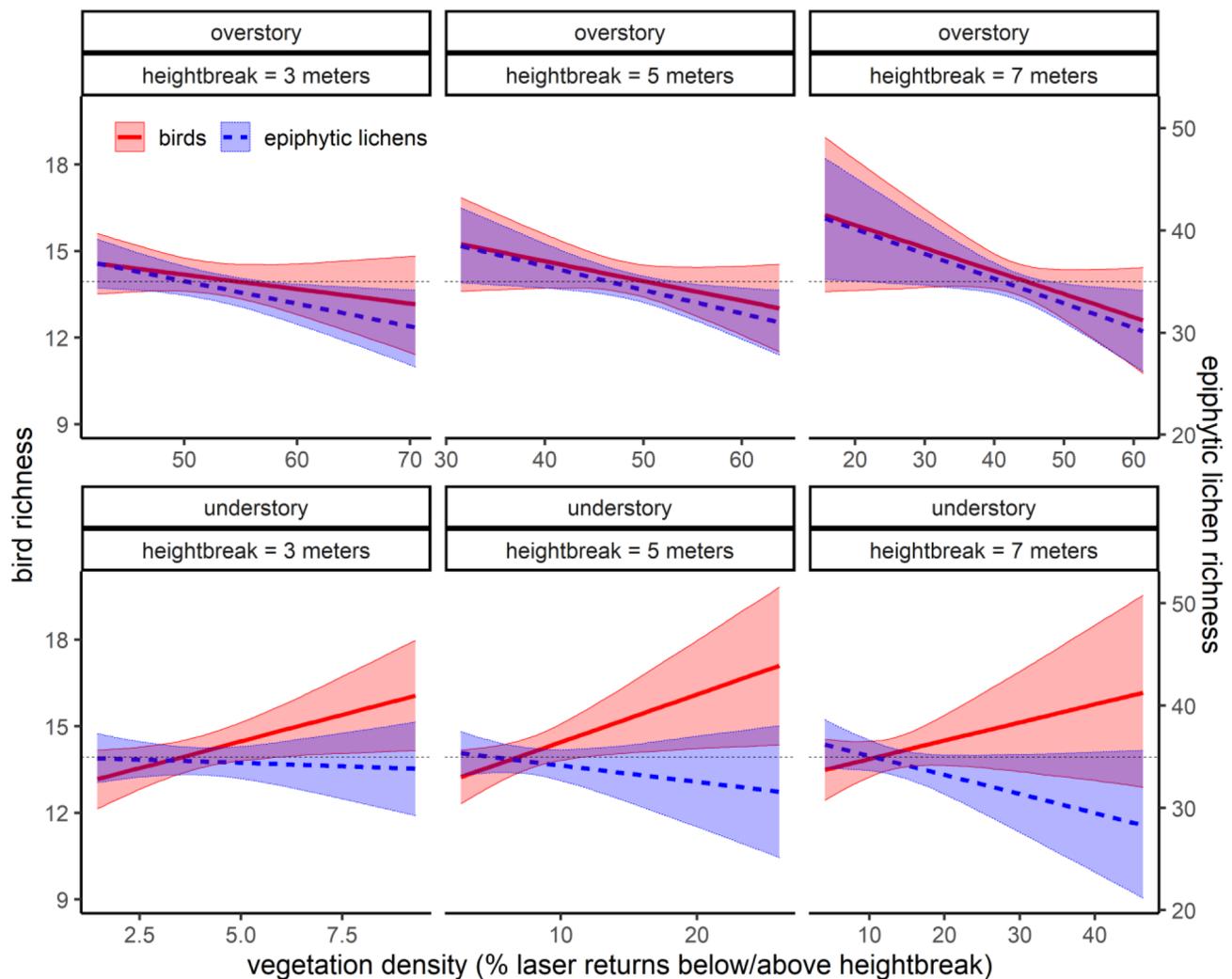
Fig. 2. The predicted richness of both epiphytic lichens (red) and birds (blue) is shown for the three height breaks between the understory and overstory density (*combined richness model*). The displayed richness values are back-transformed from the scaled richness values used in the statistical model. Lines are medians with their 95% CIs. Note that vegetation density values are on different scales. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.3. Differences between years and correlations

All results described above arise from the models using bird data from all 58 plots from 2017. The 2018 results from only 26 plots of bird data showed the same direction of effects, although with much larger uncertainties (Tables 2 & 3). Epiphytic lichen richness was not correlated with bird richness (Pearson correlation coefficient = 0.12, Fig. S.4), when comparing the complete data from 2017. The overstory density was not correlated with the amount of any tree species in particular, no matter the defining height break (Table 4). However, the understory density defined by all three height breaks was correlated with: (i) the number of deciduous trees, (ii) the total number of spruce trees, and (iii) the number of understory spruce trees. The number of pine trees was not correlated with any of the understory/overstory densities (Table 4).

4. Discussion

4.1. Scope of the study

This is the first study to combine observations of epiphytic lichens (sessile) and forest-dwelling birds (mobile) from the same commercially managed boreal forest stands to explain the relative importance of understory and overstory density on taxon-specific and summed richness. For this, we provide an applied example of an integrated multi-hierarchical modelling approach that incorporates the observational error for both organism groups into the covariates model in which both groups are modelled simultaneously. Our results show that the different taxa are not correlated and have contrasting vegetation density requirements and that to concurrently maintain a higher richness of both taxa in forests, forest managers must walk a fine line between leaving and removing too much biomass in different vertical layers of the forest. We elaborate in detail below.

4.2. Understory and overstory density

The density in the forest understory has been previously linked to species richness in mobile organisms like birds (Lindberg et al., 2015) and mammals (Carey and Johnson, 1995). A more complex and dense understory provides a greater variety of potential nesting sites for birds as well as more protection from predators for both birds and mammals while foraging on or close to the ground. The above-ground height which delineates the understory density has previously been either not defined (Carey and Johnson, 1995; Hart and Chen, 2006) or defined without assessing how the understory/overstory definition affects the conclusions (Aubin et al., 2000; Lindberg et al., 2015). We show in this

Table 2
Results from the three models (*combined richness model*) with the understory/overstory densities at all three height breaks (3 m, 5 m, 7 m), which separate the understory from the overstory. Results with the bird data from N = 58 plots in 2017 and N = 26 in 2018 are shown separately. The modelled variable is richness per plot (scaled for both taxa separately) with the mean and the 95% credible intervals of the posterior distribution for all models. To get an impression of the magnitude of change in absolute richness, see Fig. S.3.

y = specific richness		height break 3 m			height break 5 m			height break 7 m		
		mean	2.5%	97.5%	mean	2.5%	97.5%	mean	2.5%	97.5%
2017 bird data (N = 58)	intercept	0.05	−0.17	0.27	0.05	−0.17	0.27	0.05	−0.18	0.27
	epiphytic lichens	−0.11	−0.40	0.19	−0.12	−0.40	0.18	−0.11	−0.41	0.17
	understory density	0.27	0.02	0.53	0.30	0.03	0.59	0.22	−0.11	0.56
	understory density (epiphytic lichens)	−0.30	−0.63	0.02	−0.41	−0.77	−0.06	−0.45	−0.88	−0.02
	overstory density	−0.12	−0.36	0.10	−0.19	−0.44	0.07	−0.29	−0.63	0.05
	overstory density (epiphytic lichens)	−0.08	−0.38	0.22	−0.04	−0.35	0.29	−0.02	−0.47	0.41
	average DBH	0.15	−0.11	0.41	0.28	−0.03	0.59	0.36	0.02	0.71
	average DBH (epiphytic lichens)	0.17	−0.16	0.50	0.05	−0.35	0.45	−0.01	−0.46	0.44
	SD residual error	0.53	0.39	0.69	0.52	0.38	0.67	0.52	0.38	0.68
2018 bird data (N = 26)	intercept	0.03	−0.34	0.40	0.03	−0.33	0.39	0.03	−0.35	0.40
	epiphytic lichens	−0.21	−0.69	0.29	−0.21	−0.71	0.28	−0.21	−0.70	0.31
	understory density	0.45	−0.04	0.94	0.25	−0.35	0.84	0.14	−0.55	0.86
	understory density (epiphytic lichens)	−0.57	−1.25	0.08	−0.33	−1.14	0.46	−0.34	−1.32	0.57
	overstory density	−0.17	−0.54	0.20	−0.17	−0.61	0.28	−0.24	−0.95	0.41
	overstory density (epiphytic lichens)	−0.03	−0.53	0.44	−0.09	−0.7	0.49	−0.25	−1.20	0.65
	average DBH	0.45	−0.05	0.93	0.40	−0.20	1.00	0.44	−0.24	1.16
	average DBH (epiphytic lichens)	−0.06	−0.73	0.60	0.12	−0.72	0.94	0.23	−0.69	1.14
	SD residual error	0.72	0.50	0.97	0.74	0.52	1.01	0.74	0.52	0.99

study that this choice of 'height break' between under- and overstory can strongly influence the conclusions on the importance of understory density for different taxonomic groups. For the overstory however, the height break delineation in this study did not qualitatively influence our conclusions regarding the positive relationship between a more open overstory and epiphytic lichen or bird richness. Epiphytic lichens (Vondrák et al., 2019) together with vascular plants (Tonteri et al., 2016; Widenfalk and Weslien, 2009) and insects (Koivula, 2002) thrive more in open forests where additional light for photosynthesis and a warmer microclimate is available. For epiphytic lichens, this has also been shown experimentally where forest thinning in western US was associated with an improved habitat quality for epiphytic lichens, as long as key substrates (e.g. old and hardwood tree species) were retained (Root et al., 2010).

4.3. Average stem DBH and tree species composition

It is important to note that the effect of the average stem DBH on the summed richness was markedly higher than its effect on richness separated by organism groups. The capacity of a forest to host many species of different taxa is thought to be strongly dependent on the time since the last major disruption to the forest (McGarigal and Fraser, 1984; Nordén and Paltto, 2001); this is because the amount and variety of macro- and micro-structures increases over time (Brassard et al., 2008). This is especially important in early successional stages, as in our study area, where this time effect predominantly manifests itself through factors related to a larger stem DBH.

At the stand level, epiphytic lichen richness depends also on the tree species composition (Kuusinen, 1996; McMullin et al., 2010), humidity (Gauslaa and Solhaug, 1996) and dead wood (Santaniello et al., 2017; Svensson et al., 2016). While the host tree species can be expected to play an important role for tree-dependent epiphytic lichens (Bäcklund et al., 2016), this effect is expected to be much weaker for birds. Bird diversity is more likely to be influenced by the trees' effects on the vertical distribution and density of the forest vegetation, rather than the tree species per se (Müller et al., 2010). Although we did not directly test this, we did look at how understory/overstory densities at different height levels in the forest (as a way of relating these to the overstory/

Table 3
Results from the three models (*summed richness model*) with the understory/overstory densities at all three height breaks (3 m, 5 m, 7 m), which separate the understory from the overstory. The modelled variable is the sum of the epiphytic lichen and bird richness per plot (scaled for both taxa separately and then summed). Results with the bird data from N = 58 plots in 2017 and N = 26 in 2018 are shown separately, with the mean and the 95% credible intervals of the posterior distribution for all models. To get an impression of the magnitude of change in absolute richness, see Fig. S.3.

y = summed richness		height break 3 m			height break 5 m			height break 7 m		
		mean	2.5%	97.5%	mean	2.5%	97.5%	mean	2.5%	97.5%
2017 bird data (N = 58)	intercept	0.00	−0.30	0.30	−0.01	−0.30	0.29	−0.01	−0.31	0.29
	understory density	0.25	−0.10	0.59	0.20	−0.17	0.58	−0.01	−0.45	0.42
	overstory density	−0.34	−0.64	−0.04	−0.42	−0.75	−0.10	−0.61	−1.06	−0.16
	average DBH	0.45	0.11	0.79	0.60	0.20	1.00	0.71	0.26	1.16
	SD residual error	0.77	0.45	1.12	0.76	0.41	1.08	0.74	0.40	1.08
2018 bird data (N = 26)	intercept	−0.14	−0.65	0.38	−0.13	−0.64	0.38	−0.13	−0.64	0.38
	understory density	0.32	−0.36	1.00	0.16	−0.65	0.99	−0.10	−1.09	0.90
	overstory density	−0.37	−0.89	0.15	−0.46	−1.10	0.14	−0.78	−1.73	0.16
	average DBH	0.84	0.12	1.57	0.94	0.10	1.81	1.16	0.08	2.09
	SD residual error	1.04	0.58	1.61	1.05	0.60	1.63	1.03	0.57	1.61
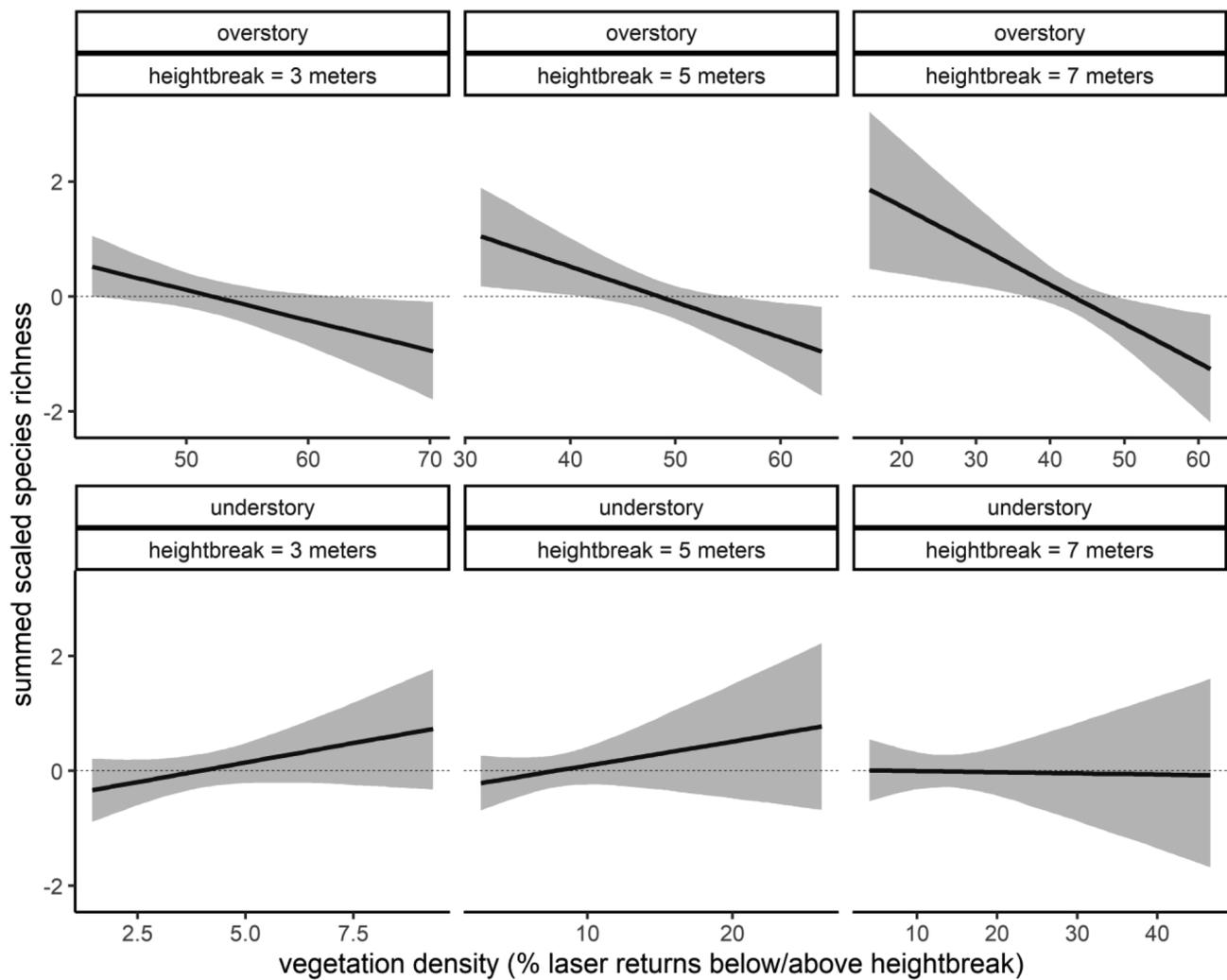
Fig. 3. The predicted sum of the scaled richnesses of epiphytic lichens and birds is shown for the three height breaks between the understory and overstory density (*summed richness model*). Lines are medians with their 95% CIs. Note that vegetation density values are on different scales. To get an impression of the magnitude of change in absolute richness, see Fig. S.3.

Table 4
Pearson correlation coefficients between the understory/overstory densities at different height breaks and the number of trees of different tree species per survey plot. Understory spruces are spruces that have live branches between 0 and 2 m from the ground.

		number of trees per hectare			
		deciduous	Scot's pine	Norway spruce	understory spruce
vegetation density (% laser returns)	overstory > 3 m	0.03	−0.29	0.48	0.32
	overstory > 5 m	−0.18	−0.11	0.11	0.04
	overstory > 7 m	−0.34	0.04	−0.31	−0.20
	understory < 3 m	0.51	−0.41	0.58	0.62
	understory < 5 m	0.51	−0.40	0.74	0.63
	understory < 7 m	0.49	−0.35	0.81	0.59

understory height break categories) were correlated with the tree species composition. Here our results indicate that understory density was largely driven by deciduous trees and Norway spruce: the number of Scot's pines was not associated with understory/overstory densities. The importance of deciduous trees (Reunanen et al., 2000) as well as understory Norway spruces (Eggers and Low, 2014) for forest dwelling organisms has been highlighted in other contexts.

4.4. Comparable studies and limitations

Our study is one of very few to have compared how organism groups with a very different biology simultaneously react to different forest structural variables. In contrast to our results, Sabatini et al. (2016) found little effect of structural heterogeneity (except dead wood) on the diversity in birds, epiphytic lichens, beetles and fungi. A likely

explanation for this discrepancy is that they evaluated richness relationships in a natural structurally complex forest system. We suggest that the effect of different forest structural attributes may be easier to detect in structurally simpler forest ecosystems, where, like in this study, a small change in the forest structural attributes can result in relatively larger differences in the species community. However Sabatini et al. (2016) studied *Fagus sylvatica* forests which might not be comparable to boreal forest ecosystems. We therefore call for more studies with a multi-taxa focus when evaluating the effects of forest structural elements on biodiversity, especially from the boreal forest.

In this study we excluded birds of prey and ravens as they have home ranges much larger than the size of the studied forest plots. Thus the results of this study should not be generalised to this group of birds. In fact, birds of prey might benefit from more open forests in general, as this can make it easier to find their prey (Hakkarainen et al., 2004; von Blotzheim et al., 1994). Further, we focus on general patterns of across taxa richness, which might not always fit specific forest species: including rare species whose responses to forest structure might be masked in these general patterns. While we consider a diverging effect of rare species to be unlikely since a higher richness often also includes more rare species (Prendergast et al., 1993), we encourage an extension of this study to include species-level responses to these forest variables and potentially include larger spatial scales for birds of prey, to be able to give more specific recommendations to managers.

4.5. Epiphytic lichens and forest-dwelling birds: A general lack of correlation

We did not detect a direct correlation between epiphytic lichen species per tree and bird richness per plot within the study area. This is in line with our finding that the forests vegetation density can have a diverging effect on richness in the two organism groups. However, it has previously been suggested that epiphytic lichen and bird richness should be correlated, because the abundance and richness of epiphytic lichens and invertebrates are correlated in a number of studies (Gunnarsson et al., 2004; Pettersson et al., 1995). This correlation was then extrapolated to suggest birds should also co-vary with these species because of birds' high dependency on insect food during breeding. While such relationships may exist in our system, this effect is largely overshadowed by the vertical distribution and density of the forest vegetation. Here, epiphytic lichens and birds are only expected to show positive covariation in richness under very specific forest conditions. Even if more epiphytic lichens support more insects, if the understory is too open for birds and this reduces their nesting and sheltering opportunities, any increase in insect abundance appears not to compensate for this.

5. Conservation and management implications

Our study shows that for forest managers to combine biomass extraction during thinning with conserving the richness of epiphytic lichens and forest-dwelling birds, they need to: (i) create a mosaic of different forest understory and overstory densities based on the needs of birds (dense understory < 5 m) in some areas, and epiphytic lichens (open overstory > 3 m) in others, and/or (ii) to adopt a narrow range of understory/overstory thinning practices that support the biodiversity of both taxa (i.e. dense vegetation < 3 m and an open vegetation > 3 m). In either situation, increasing the average stem diameter of the remaining trees is expected to lead to additional gains in richness in both taxa. This management suggestion partly follows a previously

developed thinning method, *understory retention thinning* (Eggers and Low, 2014), where the understory 2–3 m above ground is largely maintained. Here the authors claim that this method is economically feasible and implementable under current thinning regimes; thus we used measures in our study that are available to forest managers in Sweden and possibly in other boreal nations to ensure any relationships we found could be easily incorporated into thinning management. By retaining a high proportion of deciduous trees and/or Norway spruce that contribute to the understory below 3 m above ground, this could be an effective way of achieving our suggested vegetation density distribution for supporting biodiversity. It is possible that the overstory thinning that we recommend is already largely implemented under current thinning regimes in Sweden (Fig. S.5). This is because commercial thinning in Sweden not only removes small trees (reducing understory density), but also removes large trees, which reduces overstory density (Fig. S.5; Holm, 2015). Because the planning of forestry thinning interventions are now commonly done with remote sensing tools at a large scale, often without field visits (Wulder et al., 2012), it is important to have understory/overstory thinning recommendations that can be measured using these tools. Here we demonstrate how one such tool, LiDAR, together with nationwide forest maps of the tree stem diameter can be used to locate and quantify in detail the key forest structural elements that are drivers of biodiversity across taxa, while also assessing biomass production. Measuring vegetation density with LiDAR irrespective of the tree species composition, together with the average stem DBH, would enable managers to apply our results to large scale planning of forest thinning that supports biodiversity retention. In addition, the clear overall positive effect of the average stem DBH on richness supports: (i) at the stand level, maintaining an older stand age which allows for high diameter trees (e.g. high percentage of green tree retention; Gustafsson et al., 2010), or (ii) at the landscape scale, prolonging forestry cycles. This, in combination with our clear recommendations for understory retention thinning, should allow forestry managers to better balance biomass extraction with biodiversity conservation. However this study cannot provide specific guidelines for the conservation of singular focal species. Nevertheless, a forest structure that results in a larger richness in general is likely to also be beneficial for non-generalist species, i.e. including rare taxa (Prendergast et al., 1993), and increase ecosystem resilience (Loreau and de Mazancourt, 2013).

Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A

See complete lists of the species observed in this study in Table A1 and Table A2.

Table A1
We show the names of all bird species, their abbreviations used in the data and the analysis, and the number of times they were observed during 2017 and 2018 together.

latin name	abbreviation	number of observations
Anthus trivialis	trapa	16
Certhia familiaris	trake	40
Chloris chloris	gronk	3
Coccothraustes coccothraustes	stenk	3
Columba palumbus	ringa	9
Corvus cornix	kraka	1
Cuculus canorus	gok	1
Cyanistes caeruleus	blams	214
Dendrocopos major	stort	15
Erithacus rubecula	rodhe	330
Ficedula hypoleuca	svare	29
Ficedula parva	minde	2
Fringilla coelebs	bofik	478
Garrulus glandarius	notsa	13
Lophophanes cristatus	tofss	118
Muscicapa striata	grafe	10
Parus major	talge	381
Periparus ater	svars	59
Phylloscopus trochilus	lovse	60
Poecile montanus	talla	82
Poecile palustris	entia	3
Prunella modularis	jarnv	37
Pyrrhula pyrrhula	domhe	4
Regulus regulus	kungl	178
Scolopax rusticola	morka	1
Sitta europaea	notva	34
Sylvia atricapilla	svara	21
Sylvia borin	trase	1
Tetrastes bonasia	jarpe	2
Troglodytes troglodytes	gardg	48

Table A2
The nomenclature follows Nordin et al. (2019). All lichen species observed during this study and the number of observations per tree are shown. Specimens that could not be determined in the field were collected and determined later by microscopic examination and/or by high performance thin layer chromatography (HPTLC). Undeterminable lichens (too small or in bad condition) were excluded. *Fuscidea pusilla* and *Ropalospora viridis* were frequently present with small specimens and therefore not possible to separate and treated as a collective taxon. Also *Physcia adscendens* and *Physcia tenella* were present with small specimens and therefore not possible to separate and treated as a collective taxon. For the same reason and due to the lack of apothecia, also *Micarea prasina* grp. was treated as a collective taxon. Within the investigated area, *M. micrococca* might be the most common species in the *M. prasina* grp. *Cladonia* spp. is frequently occurring without podetia (only with phyllocladia) and if these react PD + red (fumarprotocetraric acid), they are not possible to determine and treated as a collective taxon. *Lepraria* spp. include all species but *L. lobificans*. These are often not possible to determine without performing thin layer chromatography and, at least include *L. elobata*, *L. incana* and *L. jackii*. *Cladonia pyxidata*, as treated here include specimens with other chemistry than only fumarprotocetraric acid (rarely occurring). These specimens are currently difficult to name (T. Ahti, pers. comm.). A reference collection of the majority of species is at the UPS herbarium in Uppsala, Sweden.

latin name	no. observations	latin name continued	no. observations
Absconditella lignicola	2	Lecanora subrugosa	30
Acrocordia gemmata	1	Lecanora symmicta	41
Anaptychia ciliaris	6	Lecidea erythrophaea	2
Anisomeridium polypori	1	Lecidea nylanderi	1155
Arthonia vinosa	1	Lecidea turgidula	335
Bacidia arceutina	4	Lecidella elaeochroma	19
Bacidia beckhausii	1	Lepraria lobificans	3
Biatora efflorescens	36	Lepraria spp.	902
Biatora helvola	4	Loxospora elatina	1
Bryoria capillaris	17	Melanelixia glabratula	12
Bryoria fuscescens	116	Melanelixia subaurifera	4
Bryoria implexa	7	Micarea denigrata	174
Buellia griseovirens	5	Micarea lignaria	1
Calicium glaucellum	1	Micarea melaena	1
Calicium parvum	9	Micarea misella	52
Caloplaca cerina	1	Micarea peliocarpa	1
Candelariella xanthostigma	1	Micarea prasina grp.	330
Catillaria erysiboides	1	Mycobilimbia epixanthoides	5
Catinaria atropurpurea	4	Mycoblastus alpinus	1
Chaenotheca chrysocephala	12	Mycoblastus sanguinarius	2

(*continued on next page*)

Table A2 (*continued*)

latin name	no. observations	latin name continued	no. observations
Chaenotheca ferruginea	14	Ochrolechia androgyna	18
Chaenotheca furfuracea	3	Ochrolechia arborea	2
Chaenotheca trichialis	7	Ochrolechia microstictoides	97
Cladonia arbuscula	8	Parmelia saxatilis	3
Cladonia botrytes	1	Parmelia sulcata	216
Cladonia cenotea	245	Parmeliopsis ambigua	879
Cladonia chlorophaea	1	Parmeliopsis hyperopta	100
Cladonia coniocraea	708	Peltigera membranacea	6
Cladonia cornuta	9	Peltigera praetextata	3
Cladonia deformis	2	Pertusaria amara	4
Cladonia digitata	323	Pertusaria borealis	20
Cladonia fimbriata	636	Phaeophyscia orbicularis	1
Cladonia floerkeana	2	Phlyctis argena	192
Cladonia macilenta	7	P. adscendens / tenella	14
Cladonia pyxidata	53	Physcia aipolia	2
Cladonia rangiferina	5	Physconia distorta	4
Cladonia sulphurina	1	Placynthiella icmalea	2
Cladonia squamosa	26	Platismatia glauca	312
Cladonia spp. phyllocladia PD + red	214	Polycauliona polycarpa	1
Coenogonium pineti	204	Pseudevernia furfuracea	283
Evernia prunastri	75	Pseudoschismatomma rufescens	1
Fuscidea arboricola	5	Pycnora sorophora	3
Graphis scripta	2	Ramalina farinacea	10
Gyalolechia flavorubescens	3	Ropalospora viridis / Fuscidea pusilla	1143
Hypocenomyce scalaris	41	Scoliciosporum chlorococcum	13
Hypogymnia farinacea	17	Scoliciosporum pruinosum	1
Hypogymnia physodes	1706	Scoliciosporum sarothamni	2
Hypogymnia tubulosa	301	Stenocybe pullatula	1
Imshauguia aleurites	16	Toniniopsis subincompta	2
Japewia subaurifera	4	Trapeliopsis flexuosa	248
Lecanora albellula	302	Trapeliopsis granulosa	1
Lecanora carpinea	2	Tuckermannopsis chlorophylla	100
Lecanora chlarotera	6	Usnea dasypoga	14
Lecanora expallens	1	Usena hirta	118
Lecanora hypoptella	48	Violella fucata	627
Lecanora pulicaris	559	Vulpicida pinastri	604
Lecanora sambuci	1	Xanthoria parietina	6
Lecanora subintricata	8	Xylopsora friesii	8

Appendix B. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118327.

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