



## Retention patches maintain diversity of epiphytic and epixylic indicator lichens more effectively than solitary trees

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### ABSTRACT

The effectiveness of retention trees and patches in preserving diversity of nine epiphytic and epixylic old-growth forest lichens was studied in north boreal spruce forests in Finland. We compared (1) 7–8-year-old retention cuts, with at least 5–10 living or dead retention trees per hectare, (2) 10–12-year-old clear-cuts, with some scattered living and dead retention trees on the sites, (3) old-growth spruce forests, and (4) 7–8-year-old retention patches (0.06–0.45 ha) representing the original tree species composition of old-growth forests. The occurrence of indicator lichens was studied on 150 deciduous trees and snags in each forest category. The species richness was significantly higher in old-growth forests than in the clear-cuts and retention cuts, but did not differ between old-growth forests and retention patches. Only three species were found in clear-cuts and two in retention cuts. Foliose cyanolichens *Leptogium saturninum* and *Nephroma bellum* thrived on solitary retention trees, whereas humidity-requiring pin lichens from the genus *Chaenotheca* were found only in old-growth forests and retention patches. Our results suggest that the ability of epiphytic and epixylic species to survive on retained trees depends on several factors: (1) substrate quality (tree species, tree type and diameter of a tree), (2) environmental factors (e.g. humidity, slope exposition), and (3) morphological and physiological characteristics of species. Besides of substrate trees, the retained conifers (esp. spruce) seem to be important in retention patches to provide the shading necessary to maintain humidity.

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### Introduction

Retention forestry was developed in north-western North America in the 1980s and 1990s as a response to even-aged forest regeneration and harvesting practices, which were shown to simplify forest structure and reduce biodiversity. Conventional harvesting practices, especially clear-cutting, were observed to result in forest structures that clash with the diverse structure of natural forests, such as multiple canopy layers, abundant woody debris on the forest floor, as well as snags and live trees of varied sizes and conditions (Franklin et al. 1997). The focus of retention forestry is on the structural elements of forests, such as individual trees, snags, logs, or small patches of forests, which are maintained for a long time after harvesting. Preserving these elements aims at increasing the structural variability of forest stands, providing habitats for forest species, achieving temporal and spatial continuity of elements and processes that are vital for many species, and increasing connectivity at the landscape level and, accordingly, enhancing the distribution of species. Furthermore, retention forestry may maintain ecosystem services of forests, mitigate environmental impacts of large-scale forestry (e.g. for water quality), and improve the aesthetics of harvested forests (Franklin et al. 1997; Gustafsson et al. 2013a). Retention forestry is currently applied in many countries in North and South America, Australia, Tasmania, and northern Europe. However, the quality, amount, and duration of retention elements vary considerably among the

countries: retention levels in Europe generally amount 1–10% of the harvested volume, whereas the figure in some forest areas in Tasmania and western Canada is 30–40% (Gustafsson et al. 2012).

There are contradictory results on the importance of retention elements on biodiversity. In general, retention forestry seems to help forest species to survive in harvested forests. In their review of 78 studies from North America and Europe, Fedrowitz et al. (2014) found that retention forests supported higher richness and abundance of forest species than clear-cuts. A review of 214 studies by Rosenvald and Löhmuß (2008) showed that birds and ectomycorrhizal fungi benefitted most from retention, and lifeboating was also successful for epiphytic lichens and small ground-dwelling animals, but not for forest bryophytes and vascular plants. Grouping together different species, species groups and retention levels may, however, hide the effects of retention forestry on specific species groups or individual species. Epiphytic lichens are slowly growing organisms, many of which are sensitive to environmental changes, e.g. to light and moisture conditions. The diversity of epiphytic lichens is enhanced by heterogeneous forests with old trees, which provide variable bark structure and an abundance of microhabitats (Ellis 2012; Nascimbene et al. 2013a). Forest harvesting has many negative effects on epiphytes, as it results in a lack of old trees and other substrates, a lack of structural diversity and forest continuity and either

excessive exposure to light and wind after harvesting, or excessive shadow when the canopy closes (Nascimbene et al. 2013b). Thus, epiphytic lichens may exhibit relatively quick responses to logging and also provide information on the role of retention trees in lifeboating these species over the regeneration phase. In his review analysis of boreal and temperate coniferous forests, Johansson (2008) concluded that logging had negative effects on the persistence, growth, and colonization of most epiphytic lichens, with the effects intensifying with logging severity. A relatively large number of studies have been conducted on the survival of epiphytic lichens on solitary retention trees (e.g. Löhmus et al. 2006; Jairus et al. 2009; Löhmus and Löhmus 2010; Runnel et al. 2013; Gustafsson et al. 2013b), many showing high survival of epiphytes on retention trees or in transplantation experiments in clear-cuts (Hazell and Gustafsson 1999; Hilmo 2002; Gauslaa et al. 2006; Lundström et al. 2013; Gustafsson et al. 2013b). However, most of these studies have thus far focused on the impacts of live tree retention on lichens, and only few (e.g. Runnel et al. 2013; Hämäläinen et al. 2014) have addressed the importance of retained dead wood for lichen diversity. Still fewer studies have been conducted on the survival of epiphytic and epixylic lichens in retention patches, especially in boreal forests (see, however, Perhans et al. 2009). Retention patches are retained forest lots varying in size from some 0.01 ha to several tens of hectares, usually representing the structures typical of the forest before logging. We still lack knowledge regarding the influence of retention scales on rare epiphytic and epixylic lichens, and the responses of individual species or species groups to different retention levels. In the present study, we aimed at seeking answers to these questions. We investigated the effectiveness of retention trees and patches in the preservation of nine old-growth forest epiphytic and epixylic lichens in the northern boreal zone in NE Finland in four different forest categories: (1) 7–8-year-old retention cuts, with at least 5–10 living or dead retention trees per hectare, (2) 10–12-year-old clear-cuts, with some scattered living and dead retention trees on the sites, (3) old-growth spruce forests, and (4) 7–8-year-old retention patches (0.06–0.45 ha), seeking specifically answers to the following questions:

- (1) How do the number of species and probability of occurrence of a species on a tree trunk differ in different forest categories?
- (2) What is the importance of different retention qualities (tree species, living and dead trees, broken-top snags, tree diameter, and decay stage) for species of conservation value? We wanted to study separately entire standing dead trees and broken-top snags (hereafter: snags), because of the lack of knowledge on the importance of these substrates for the studied species.
- (3) Do environmental factors (temperature, humidity, site exposition) affect the occurrence of those species?
- (4) Do specific species or species groups show different responses to retention levels (solitary trees vs. retention patches)?

## Materials and methods

### Study area and selection of sites

The study area is located in north-eastern Finland, in the municipality of Taivalkoski, and belongs to northern boreal forest zone (sensu Ahti et al. 1968). The area has been used for forestry since the beginning of the twentieth century, and prior to this slash and burn cultivation was relatively common in many forests nearby villages. Thus, the old-growth forests of the region are not in a completely natural state, and signs of old selective loggings were recognizable in most of the stands studied. The studied sites were selected from the archive files of Metsähallitus (state organization governing the area), with the criteria that the sites were, or had been, mesic forests dominated by Norway spruce (*Picea abies*, >80% of living-tree volume). Pubescent birch (*Betula pubescens*) and Scots pine (*Pinus sylvestris*) were the main admixture trees (5–19%, and 7–8% of living-tree volume) on the sites, with some percentages of aspen (*Populus tremula*), goat willow (*Salix caprea*), and rowan (*Sorbus aucuparia*). Our study comprised a total of 600 retention trees in four different forest categories (150 trees per category): (1) 7–8-year-old retention cuts, logged using new forest management methods with 5–10 retention trees (living or dead) left on the sites (retention cuts, RC, five replicates); (2) 10–12-year-old clear-cuts cuts, logged using old forest management methods with scattered living and dead trees left unlogged on the sites (clear-cuts, CC, five replicates); (3) old-growth spruce forests (old-growth, OG, five replicates); and (4) 7–8-year-old retention patches (RP, size 0.06–0.45 ha), left within retention cuts (12 replicates). The distances between the sites varied from 1 to 25 km.

Clear-cuts without retention trees were conducted about until the beginning of 1990s; in these “old type clear-cuts” only few living or dead trees were left occasionally at the sites. Retention cuts in our study were logged following the new management methods, implemented from mid 1990s, recommending at the time of logging (1995–1996) to leave 5–10 living or dead trees per hectare on the regeneration sites (Hallikainen et al. 2005). Retention patches were patches of old-growth forest left unlogged within the retention cuts, representing the original tree species composition of old-growth forests. Because the smallest retention patches contained typically only few trees matching our inventory tree schedule (see below), we had to include more replicates into this forest category than others, to reach the equal number of trees ( $n = 150$ ) to the other categories.

### Research design, lichen inventory, and tree measurements

We studied the occurrence of nine epiphytic or epixylic old-growth forest indicator lichens: *Arthonia incarnata* Th. Fr. ex Almq., *Chaenotheca brachypoda* (Ach.) Tibell, *C. furfuracea* (L.) Tibell, *C. gracillima* (Vain.) Tibell, *Leptogium saturninum* (Dicks.) Nyl., *Lobaria pulmonaria* (L.) Hoffm., *Nephroma bellum* (Spreng.) Tuck., *N. parile* (Ach.) Ach., and *N. resupinatum* (L.) Ach.; these species are commonly used as indicators of

forest continuity in boreal forest zone in Finland (see, e.g. Kuusinen 1996; Halonen and Jääskeläinen 2003). We included in the survey all living deciduous trees except for birch (*Betula pubescens* and *B. pendula*), because the target species occur very rarely on living birch, and all entire dead deciduous trees and the snags of deciduous trees (including birch). We selected 150 trees from each forest category using the following procedure: In the retention cuts, clear-cuts and old-growth forests, we established a 4-m-wide transect per site, the length varying from 100 to 480 m/site. The transect was randomly placed at a right angle to the longitudinal direction of the site, starting at least 50 m from its edge. All the trees meeting the study criteria were systematically studied when proceeding within the transect, until reaching 30 trees per transect. The study trees included (1) living deciduous trees (height > 130 cm) (excluding birch), (2) standing dead deciduous trees (height > 130 cm), and (3) snags of deciduous trees (snag = standing tree > 50 cm high with a broken top) (hereafter "tree types"). All the study trees were inventoried for lichen species, examining the tree from the base up to the height of 2 m. Five stands in each above mentioned forest category were inventoried for lichens, making altogether 150 trees per forest category.

As retention patches were too small for transects, we used circular plots with a diameter of 10 m for the investigation of study trees. On the small retention patches the perimeters of the circles touched, whereas on the larger ones the circular plots were placed along two lines with a distance of 30 m between their centres. The number of circular plots varied from 1 to 5 per site depending on the size of the site. On each plot, we investigated all the trees meeting the study criteria. The number of plots on the 12 retention patches totalled 33, and the number of studied trees per plot varied 0–9, the mean being 4.5 trees per plot. The total number of studied trees in retention patches totalled 150.

The diameter at breast height (DBH) and the length of the studied trees were measured, as well as decay stage of snags and standing dead trees, classified as follows: 1 = recently dead, wood hard, bark attached, 2 = partly decayed, knife penetrates at least 3–4 cm into the wood, bark partly detached, 3 = most of the wood soft, knife blade penetrates the wood entirely, 4 = very hard wood, bark detached. Decay stages 2 and 3 were recorded mainly among birch snags, which can stand up even as decayed, supported by the bark, which prevents the snag from collapsing (see Mäkinen et al. 2006). Decay stage 4 was relatively common among standing dead trees which had been completely dried after death. At the site level, the exposition of the site (0 = flat, 1 = N, 2 = NE, 3 = E, 4 = SE, 5 = S, 6 = SW, 7 = W, 8 = NW) was recorded. The distribution of studied trees by tree type, tree species, diameter class, decay stage, and exposition are given in Table 1.

In addition to the trees measured on the lichen inventory transects, the overall forest structure (living and dead trees) was measured for old-growth forest, retention cuts, and clear-cuts on five circular plots (radius 10 m) on each site (incl. 5 sites per forest category), totalling 25 plots per forest category. Respectively, the measurements were conducted in all the 12 retention patches, totalling 33 circular plots measured. Tree species and DBH of all living trees were

**Table 1.** The distribution of studied trees by tree type, species, diameter, decay stage and exposition in different forest categories.

	OG (%)	CC (%)	RC (%)	RP (%)
<i>Tree type</i>				
Living tree	27 (18.0)	20 (13.3)	73 (48.7)	13 (8.7)
Standing dead tree	28 (18.7)	54 (36.0)	3 (2.0)	47 (31.3)
Snag	95 (63.3)	76 (50.7)	74 (49.3)	90 (60.0)
<i>Tree species</i>				
Birch	76 (50.7)	44 (29.3)	69 (46.0)	119 (79.3)
Aspen	40 (26.7)	98 (65.3)	71 (47.3)	7 (4.7)
Goat willow	34 (22.6)	8 (5.4)	10 (6.7)	12 (8.0)
Rowan	0	0	0	12 (8.0)
<i>Diameter class (cm)</i>				
≤10	13 (8.7)	1 (0.7)	5 (3.3)	82 (54.7)
11–20	75 (50.0)	31 (20.7)	51 (34.0)	48 (32.0)
21–30	41 (27.3)	64 (42.6)	52 (34.7)	13 (8.7)
31–40	19 (12.7)	49 (32.7)	27 (18.0)	7 (4.6)
>40	2 (1.3)	5 (3.3)	15 (10.0)	0
<i>Decay stage</i>				
1	4 (2.7)	0	5 (3.3)	8 (5.4)
2	74 (49.3)	37 (24.7)	40 (26.7)	106 (70.6)
3	9 (6.0)	2 (1.3)	3 (2.0)	27 (18.0)
4	39 (26.0)	92 (61.3)	31 (20.7)	3 (2.0)
<i>Living tree</i>	24 (16.0)	19 (12.7)	71 (47.3)	6 (4.0)
<i>Exposition</i>				
Flat	30 (20.0)	0	120 (80.0)	80 (53.3)
N	0	30 (20.0)	0	20 (13.3)
NE	0	0	0	0
E	30 (20.0)	0	0	0
SE	30 (20.0)	30 (20.0)	0	14 (9.4)
S	0	0	30 (20.0)	0
SW	30 (20.0)	30 (20.0)	0	0
W	30 (20.0)	0	0	0
NW	0	60 (40.0)	0	36 (24.0)

Note: The percentage of each tree quality of all studied trees in the category ( $n = 150$ ) is in parenthesis. OG = old-growth forests, CC = clear-cuts, RC = retention cuts, RP = retention patches.

recorded, and the height of every fourth living tree was measured in order to calculate timber volume. All dead trees and pieces of coarse woody debris (both standing and downed) with a minimum base diameter of 5 cm or minimum length of 1 m were measured, and their decay stage was recorded using the classification described above.

### Temperature and humidity measurements

Measurements of temperature and relative air humidity were carried out at five points on each site about 1 m above the ground using a Vaisala HM34 humidity and temperature meter. In the retention cuts, clear-cuts, and old-growth forests, the measurements were made at 10 m intervals (at least 50 m from the edge of the site). On the retention patches, the measurements were made at the centres of the circular plots; where there were fewer than five circular plots on a patch, as many measurements as possible were made at the centres of the plots, the remaining being carried out on the perimeter. Measurements were conducted on three successive days, after a period of three rainless days, between 9 am and 5 pm. Microclimatic values of old-growth forests and retention patches were compared to those measured on the nearest clear-cut, and the measurements of the sites to be compared were all conducted within 1.5 h on the same day. As the absolute values measured on different days and at different times were not comparable, we calculated the differences in temperature and humidity between the old-growth forests or retention patches and the adjacent

clear-cuts, and used the differences as dependent variables in the analyses. For the clear-cuts and retention cuts, we calculated the total means of clear-cut and retention cut categories, and used the differences between each site mean and the total mean of both forest category as dependent variables in the analyses. This approach enabled us to compare whether the differences in the means within the clear-cuts or retention cuts differed from the differences in the means within old-growth forests or retention patches.

## Data analysis

### Site-level analyses

Site-level analyses were conducted for the living and dead tree volumes, and for the differences in the temperature and humidity. Differences in the volumes of living and dead trees were tested using one-way ANOVA. Tamhane's T2, a conservative test that does not assume equal variances, was used as a post-hoc test. Differences in the relative humidity and temperature between forest categories were examined using the non-parametric Kruskal-Wallis test.

### Modelling of the data at tree level

Data structure consisted of two levels: sample sites and trees nested within the sample sites; thus, the trees in each sample site were considered as correlated observations. Mixed models with sample site as a random factor were used to reduce pseudo-replication in the models. The variables in the models were included both at the sample site and tree levels.

The occurrence ("yes" or "no") of any of the indicator species, and two groups of the lichen species (*Nephroma* and *Chaenotheca* species), on the tree trunks was modelled using a binomial logistic model with sample site as a random factor. The data could be regarded as an inventory data, where the number of observations of different variables varied between the forest categories. However, the unbalanced structure of data could be overridden in the modelling, because the standard errors and the tests take into account the variation in the numbers of the observations among the categories. All the potential explanatory variables (= all the variables in Table 1, plus humidity and temperature difference) and their interactions were tested in all the models. Only the significant variables and their possible interactions under 5% risk level were kept in the final models.

In the model of *Chaenotheca* species, no observations of species were found in the trees belonging to the retention cuts and clear-cuts. This made the modelling of the four categories insecure, because of the biased estimates and their standard errors. Thus, the only way to model the occurrence of *Chaenotheca* species reliably in our data was to remove the retention cuts and clear-cuts from the model (see Allison 2012), and include only old-growth forest and retention patches.

The distribution of the number of indicator lichen species on the tree trunks was highly skewed, zero-inflated, and over-dispersed (variance larger than mean). Because of these characteristics, we modelled the number of species on a tree assuming a negative binomial distribution, which

takes the large proportion of zero values into account. In the negative binomial model, NB2 parameterization (Bolker et al. 2012) of the variance was used. The NB2 variance can be expressed as  $\text{variance} = \mu + (1 + \mu/k)$ , where  $\mu$  denotes expected value (mean) and  $k$  denotes a clumping parameter, also called *theta*. If  $k = 1$ , the distribution is a geometric one, and if  $k \rightarrow \infty$ , the distribution approaches a Poisson distribution. The zero-inflation coefficient was estimated in order to correct the bias caused by the great number of zeros (Fournier et al. 2012). The random part of the model was similar to that of the logistic model. Like in the logistic models, we included into the negative binomial models all the significant variables and their possible interactions under 5% risk level.

Finally, we used binomial logistic model to detect if the patch size influenced the probability of occurrence of the indicator species on a tree trunk in retention patches. The occurrence (yes or no) of any of the indicator species, and *Nephroma* and *Chaenotheca* species was modelled separately. Respectively, negative binomial model was used to detect if the patch size influenced the number of species on a tree trunk. The effect of retention patch size was tested both as the patch size as only explanatory variable in the models, and with all other significant explanatory variables.

The binomial model was computed using the R package MASS and its function `glmPQL` (Venables and Ripley 2002). The R package `glmmADMB` (Fournier et al. 2012) with its function `glmmadmb` was used in the estimation of the negative binomial model, because it could handle the zero-inflated responses in the mixed models by estimating the zero-inflated coefficient for the model. The predictions for the logistic models were calculated and plotted using the R package `effects` (Fox 2003). The predictions for the `glmmADMB` model were calculated using the coefficients of the model and the `lsmeans` package (Lenth 2016).

All the pairwise comparisons for the categorical variables were computed using the `lsmeans` package.

### Performance of the models

The performance of the logistic model was reasonably good considering the models for any of the species (receiver operating characteristic (ROC) = 0.80) and the *Nephroma* species (ROC = 0.76). ROC describes the classification efficiency of a logistic model. However, the model for the *Chaenotheca* species could not classify the events (occurrence of the lichens on the tree trunks) efficiently (ROC = 0.52), making the reliability of the model weak. The negative binomial model predicted correctly the values near the mean value of the response (observed mean = 0.19, predicted mean = 0.19 species), but could not predict correctly the extreme values: the observed values ranged from 0 to 4, but the predicted values from 0.01 to 2.61.

## Results

### Site-level results

#### Volumes of living and dead timber

The mean volume of living trees in the old-growth forests was 183.9 m<sup>3</sup> ha<sup>-1</sup> and the basal area 20.8 m<sup>2</sup> ha<sup>-1</sup> (spruce 16.6,

pine 0.8, birch 3.0 and aspen 0.2 m<sup>3</sup> ha<sup>-1</sup>). Because we had not measured the pre-harvest volumes of living trees in the clear-cuts or retention cuts, we compared the post-harvest volumes to the mean volume of the old-growth stands, which represent spruce forests typical of the area. In the clear-cuts, the mean volume for living trees was only 0.2 m<sup>3</sup> ha<sup>-1</sup>, representing 0.11% of the mean living-tree volume of the old-growth forests. In the retention cuts, the volume was 15.4 m<sup>3</sup> ha<sup>-1</sup>, representing 8.4% of the mean volume of old-growth forests. In the retention cuts with retention patches, the area retained varied from 3% to 8% of the logging unit, except for one area, where 25% of the area had been retained. In the retention patches, the mean living-tree volume was 125 m<sup>3</sup> ha<sup>-1</sup>, representing 68% of the volume of the old-growth stands. The differences between the categories were statistically significant ( $F = 22.19$ ,  $df = 3$ ,  $p = .000$ ). The dead-wood volumes varied from 32.8 m<sup>3</sup> ha<sup>-1</sup> in the old-growth forests to 23.8 m<sup>3</sup> ha<sup>-1</sup> in the retention cuts; the differences between the categories were not statistically significant ( $F = 0.558$ ,  $df = 3$ ,  $p = .648$ ).

### Temperature and humidity differences

The relative humidity in old-growth stands was on average 4.04 percentage points higher than in the nearby clear-cuts, and 1.66 percentage points higher in the retention patches than in the nearby clear-cuts (K-W test stat. 150.59,  $df = 3$ ,  $p = .000$ ). The humidity in the old-growth stands differed significantly from the retention cuts (OG-RC test stat. = -11.04,  $p = .000$ ) and from clear-cuts OG-CC, test stat. = -191.2,  $p = .000$ ), similarly, the humidity in retention patches was significantly higher than on the retention cuts (RP-RC, test stat. = -125.4,  $p = .000$ ) or clear-cuts (RP-CC, test stat. = -96.21,  $p = .000$ ). The difference between old-growth stands and retention patches was also significant (test stat. = 94.99,  $p = .000$ ), but no difference was found between the clear-cuts and retention cuts (test stat. = 19.96,  $p = .861$ ). No differences were found in temperature between the forest categories (test stat. = 5.19,  $df = 3$ ,  $p = .159$ ).

### Species richness and composition

All nine species studied occurred in the old-growth stands, and six of them in the retention patches, while only two species occurred in the retention cuts and three in the clear-cuts (Table 2). *Chaenotheca* species, which are epixylic

**Table 2.** Total number of species, and the number of inhabited trees by the studied species in different forest categories.

Species	OG	CC	RC	RP
<i>Arthonia incarnata</i>	1	0	0	0
<i>Chaenotheca brachypoda</i>	9	0	0	2
<i>C. furfuracea</i>	7	0	0	8
<i>C. gracillima</i>	2	0	0	2
<i>Leptogium saturninum</i>	1	4	6	0
<i>Lobaria pulmonaria</i>	1	0	0	0
<i>Nephroma bellum</i>	20	7	15	8
<i>N. parile</i>	8	0	0	1
<i>N. resupinatum</i>	9	1	0	1
Species (tot.)	9	3	2	6
No. of inhabited trees (tot.)	58	12	21	22

Note: The total number of studied trees in all forest categories is 150. OG = old-growth forests, CC = clear-cuts, RC = retention cuts, RP = retention patches.

old-growth forest indicator lichens mainly growing on birch snags, were completely lacking in the clear-cuts and retention cuts; by contrast, they occurred in retention patches about as frequently as in old-growth forests (Table 2). However, only *C. furfuracea* was found in the small patches (<0.4 ha), whereas *C. brachypoda* and *C. gracillima* were found exclusively in patches >0.4 ha. *Lobaria pulmonaria* and *Arthonia incarnata* occurred only in old-growth stands. Three species (*Leptogium saturninum*, *Nephroma bellum* and *N. resupinatum*) were found in clear-cuts and retention cuts, the two first being quite abundant (Table 2). Only minor differences were observed between retention cuts and clear-cuts regarding the composition of species, with retention cuts hosting more records of *Nephroma bellum* and clear-cuts hosting one occurrence of *N. resupinatum*, which was lacking in the retention cuts (Table 2).

### Predictions of the number of species at tree level (negative binomial models)

According to the negative binomial models, the factors that affected the number of indicator species at tree level were forest category, tree species, diameter, and tree type (Table 3). The predictions of the negative binomial models for the number of indicator species on a tree for the forest categories were highest for the old-growth forests (0.28 species per tree) and retention patches (0.21), and lowest for the clear-cuts (0.06) and retention cuts (0.07). The low mean values of the predictions are the result of the large number of trees without any lichens. The pairwise comparisons (Tukey-adjusted differences at the 5% risk level) showed that species richness of old-growth stands was significantly higher than richness of clear-cuts ( $p < .001$ ) or retention cuts ( $p < .001$ ), but no difference was observed to retention patches ( $p = .324$ , Table 3). Richness in retention patches was significantly higher than richness in retention cuts ( $p$

**Table 3.** Parameter estimates and likelihood ratio tests for the zero-inflated negative binomial model predicting the number of lichen species on a tree.

Variable, parameter	Estimate	Std. error	z- and chi-squared value	p
Intercept	-2.256	0.710	-3.18	.001
Treatment (ref. OG)			35.75 (3)	<.001
RC	-1.411	0.352	-4.01	<.001
CC	-1.549	0.378	-4.10	<.001
RP	-0.311	0.316	-0.99	.324
Tree species (ref. birch)			17.77 (3)	<.001
Aspen	0.405	0.347	1.16	.244
Goat willow	1.260	0.315	3.99	<.001
Rowan	0.315	1.109	0.28	.777
Tree type (ref. living tree)			12.18 (2)	.002
Standing dead	-1.508	0.438	-3.44	.001
Snag	-0.097	0.298	-0.33	.744
Diameter of tree	0.050	0.013	3.86	<.001
Random sample plot variance	0.040			
Negative binomial dispersion parameter	2.931	6.411		
Zero-inflation coefficient	0.062	0.390		

Note: Chi-squared values are the values of likelihood ratio tests. The reference category of each test is given in parentheses after the name of the test, and the degrees of freedom for likelihood ratio tests after each chi-squared value. OG = old-growth forests, CC = clear-cuts, RC = retention cuts, RP = retention patches.

= .013). No differences were found between the clear-cuts and retention cuts ( $p = .793$ ).

For different tree species, the prediction of the number of species per tree was clearly highest for goat willow (0.27 species), followed by aspen (0.11), rowan (0.10), and birch (0.07). The only significant difference at the 5% risk level was between goat willow and birch ( $p < .001$ , Table 3). The tree type affected the number of lichen species significantly. The predicted mean values per tree were 0.21 for living trees and 0.19 for snags, but only 0.05 for standing dead trees. Significant differences were found between living trees and standing dead trees ( $p = .001$ ) and standing dead trees and snags ( $p = .027$ ). The predicted number of species per tree increased remarkably with an increase in diameter; the values were 0.33 species for 10 cm DBH, 0.96 species for 30 cm DBH, and 2.95 species for a 50 cm DBH.

### Models predicting the probability of species occurrence at tree level (logistic models)

#### Models for the occurrence of any indicator species

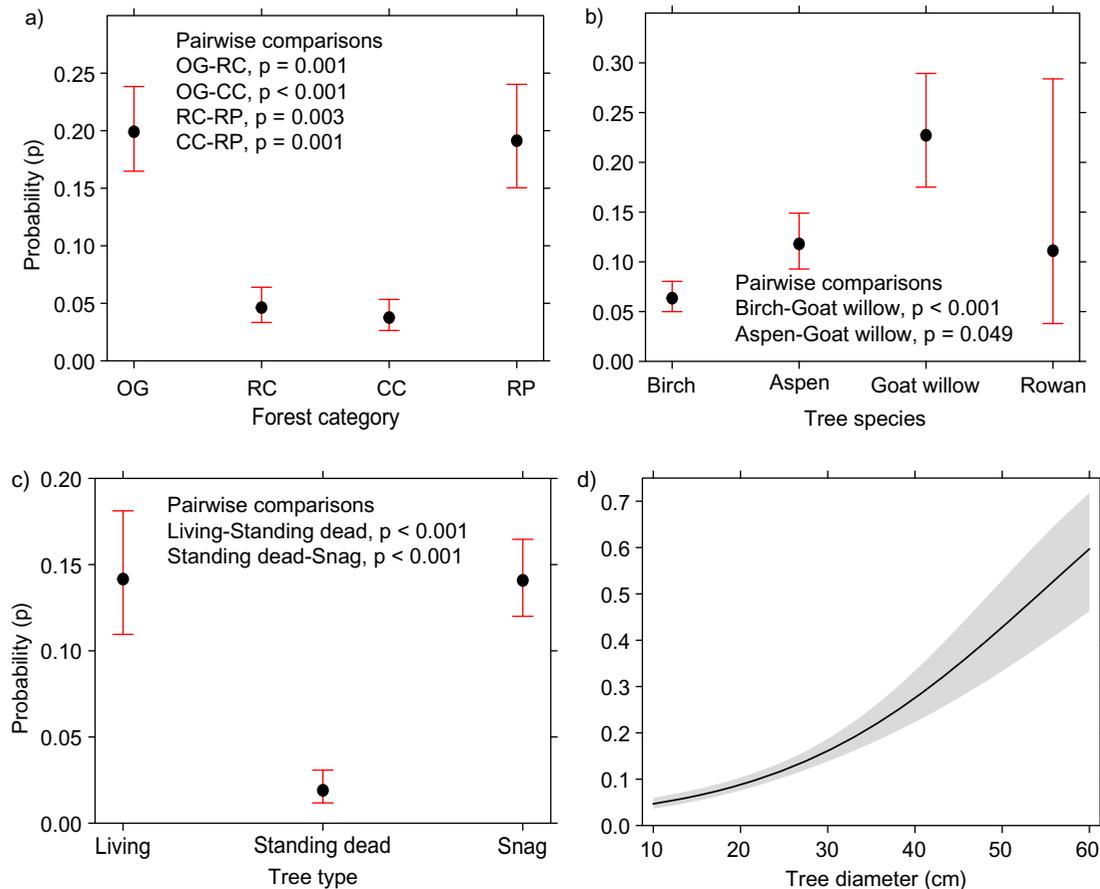
The probability of the occurrence of any of the indicator lichens in the forest category was about 20% for the old-growth forests and retention patches, but only 4–5% for the clear-cut and retention cut areas (Figure 1(a)). The categories differed significantly (Table 4); the pairwise test showed

**Table 4.** Parameter estimates and likelihood ratio tests of the binomial logistic models for the occurrence of any of the indicator species on a tree trunk.

Variable, parameter	Estimate	Std. error	t- and chi-squared value	p
Response: all the indicator species with Forest category in the model (df = 566, Treatment categories df = 23)				
Intercept	-2.749	0.563	-4.88	<.001
Forest category (ref. OG)			28.24 (3)	<.001
RC	-1.633	0.403	-4.05	.001
CC	-1.850	0.424	-4.36	<.001
RP	-0.049	0.368	-0.13	.895
Tree species (ref. birch)			14.23 (3)	.001
Aspen	0.680	0.394	1.73	.085
Goat willow	1.467	0.392	3.74	<.001
Rowan	0.612	1.186	0.52	.606
Tree type (ref. living)			18.40 (2)	<.001
Standing dead	-2.139	0.540	-3.96	<.001
Snag	-0.006	0.367	0.02	.987
Diameter of tree	0.068	0.015	4.65	<.001
Random plot variance (95% cl)	0.038 (2e - 4–8.713)			
Residual	0.906 (0.807–1.017)			

Note: Chi-squared values are for type III deviance tests. The reference category of each test is given in parentheses after the name of the test, and the degrees of freedom for deviance tests are presented in the parentheses after each chi-squared value. OG = old-growth forests, CC = clear-cuts, RC = retention cuts, RP = retention patches.

differences between old-growth stands and both clear-cut and retention cuts, as well as between retention patches and both clear- and retention cuts (Figure 1(a)). Among the



**Figure 1.** The predictions of the binomial logistic model for the probability of occurrence of any of the indicator species on a tree trunk, with point estimates and their standard errors. Significant differences of pairwise tests between the levels of categorical predictors (at  $p < .05$  risk level) are presented in the figures.

tree species, the highest probability of encountering any of the indicators was on goat willow (about 23%) and the lowest on birch (about 7%, Figure 1(b)); a significant difference was found between goat willow and birch (Table 4 and Figure 1(b)), and also between goat willow and aspen (Figure 1(b)). Among tree types, the probability was equally high for living trees and snags (about 14–15%), but only about 2% for standing dead trees (Figure 1(c)), the two first mentioned differing from standing dead trees (Figure 1(c)). An increase in the diameter of a tree increased the probability of occurrence of indicator lichens, from about 5% on a 10 cm DBH tree to about 40% on a 50 cm DBH tree (Figure 1(d)).

We also tested an alternative model where forest category was removed and humidity difference was included in the model. The probability of occurrence of a species increased almost three-fold (from 0.07 in clear-cuts to 0.18 in old-growth forests) when the humidity increased four percentage points; however, with these data, the humidity difference was not significant variable in the model (Chi sq. = 2.731, df = 1,  $p = .098$ ).

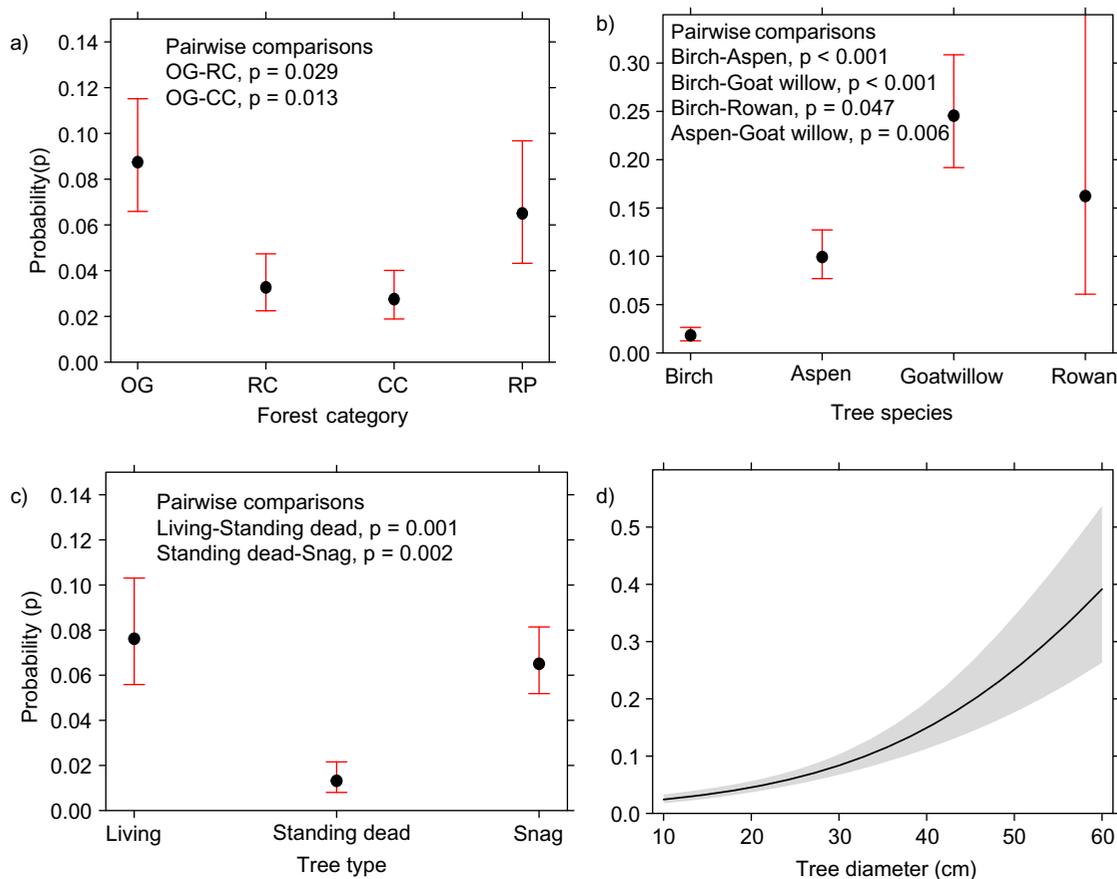
### Models for *Nephroma* species

The probability of encountering any of the three *Nephroma* species varied 7–9% in old-growth forests and retention patches, and 3–4% in clear-cuts and retention cuts (Figure 2(a)). A significant difference in the probability of encountering a species was found between old-growth stands and clear-

cuts, and old-growth stands and retention cuts (Figure 2(a) and Table 5). Of tree species, the highest probabilities for the occurrences of *Nephroma* species were on goat willow and rowan (20–25%), followed by aspen and, lastly, birch (about 1%) (Figure 2(b)). It has to be noted, however, that there was only one occurrence of *Nephroma* species on a total of 12 rowans, making the standard error very large. Significant differences were detected between goat willow and birch, aspen and birch (Figure 2(b) and Table 5) and goat willow and aspen (Figure 2(b)). In the case of tree type, the probability of occurrence was around 7% for snags and living trees, but only 1% for standing dead trees (Figure 2(c)); both living trees and snags differed significantly from standing dead trees. The diameter of a tree also affected the occurrence probability of *Nephroma* species, which increased from about 4% on a 20 cm DBH tree to about 25% on a 50 cm DBH tree (Figure 2(d)).

### Models for *Chaenotheca* species

The probability of occurrence of any of the three *Chaenotheca* species on a tree was modelled only for old-growth forests and retention patches, because the model could not perform the categories without any occurrences. The variables affecting the occurrence of *Chaenotheca* species significantly were tree species, diameter, and exposition of the site (Table 5). The highest probability of occurrence was on birch (13%); few occurrences were predicted for goat willow (1%).



**Figure 2.** The predictions of binomial logistic models for the probability of occurrence of the *Nephroma* species on a tree trunk, with point estimates and their standard errors. Significant differences of pairwise tests between the levels of categorical predictors (at  $p < .05$  risk level) are presented in the figures.

**Table 5.** Parameter estimates and likelihood ratio tests of the binomial logistic models for the occurrence of *Nephroma* and *Chaenotheca* species on a tree trunk.

Variable, parameter	Estimate	Std. error	t- and chi-squared value	p
Response: <i>Nephroma</i> species (df = 566, Forest categories df = 23)				
Intercept	-4.199	0.668	-6.29	<.001
Forest category (ref. OG)			9.18 (3)	.027
RC	-1.042	0.448	-2.32	.029
CC	-1.218	0.451	-2.70	.013
RP	-0.320	0.513	-0.62	.539
Tree species (ref. birch)			36.17 (3)	<.001
Aspen	1.782	0.490	3.64	<.001
Goat willow	2.864	0.483	5.93	<.001
Rowan	2.346	1.176	2.00	.047
Tree type (ref. living)			12.98 (2)	.002
Standing dead	-1.819	0.522	-3.48	.001
Snag	-0.169	0.371	-0.46	.648
Diameter of tree	0.065	0.016	4.15	<.001
Random plot variance (95% cl)	0.082 (0.002–3.798)			
Residual	0.804 (0.716–0.902)			
Response: <i>Chaenotheca</i> species (The forest categories of OG and RP, and tree species birch and goat willow included. df = 222, Exposition df = 9)				
Intercept	-3.349	0.588	-5.69	<.001
Tree species (ref. birch)			7.61 (1)	.006
Goat willow	-2.700	0.996	-2.71	.007
Exposition (ref. flat)			14.11 (6)	.028
North	-0.160	1.058	-0.15	.883
East	-0.696	1.023	-0.68	.513
South-East	1.587	0.524	3.03	.014
South-West	0.129	0.817	0.16	.878
West	0.673	0.672	1.00	.343
North-West	-0.076	0.785	-0.10	.925
Diameter of tree	0.074	0.028	2.63	.009
Random plot variance (95% cl)	1.996e - 8 (4.455e - 200–8.938e + 183)			
Residual	0.826 (0.691–0.988)			

Note: Chi-squared values are for the type III deviance tests. The reference category of each test is given in parenthesis after the name of the test, and the degrees of freedom for deviance tests are presented in parentheses after each chi-squared value. OG = old-growth forests, CC = clear-cuts, RC = retention cuts, RP = retention patches.

The occurrence was highest on sites with a southeast exposure (probability of occurrence 11%), differing significantly from the flat sites (Table 5). The probabilities of occurrence for other directions varied 1.3–4.9%. Tree diameter was also important for species occurrence in the case of *Chaenotheca* species: the probability of occurrence increased from 8% to 22% when the diameter increased from 15 to 30 cm. All *Chaenotheca* records except for one were made on birch and goat willow snags; the majority of records were made on decay stage 2 (72%) and 3 (21%, Table 6). The proportion of decay stage 2 varied 39–42% of all studied tree types in retention patches and old-growth forests, and 18–26% in clear-cuts and retention cuts (Table 6). Despite of suitable substrate in the two latter forest categories, no observations of species were encountered.

### Models for the influence of patch size

The zero-inflated negative binomial model found a significant effect between an increasing size of a retention patch and the number of indicator species on a tree trunk (Table 7). The

predicted number of species on a tree trunk increased from 0.28 in the patches of 0.1 ha to 0.6 in the patches of 0.3 ha, and 1.29 in the patches of 0.5 ha. The other factors affecting the number of species on a tree level in retention patches were tree species and the diameter of a tree (Table 7). On the contrary, the logistic models could not find any significant indication of the effect of patch size on the probability of occurrence of any of the indicator species, or the occurrence of *Nephroma* or *Chaenotheca* species on a tree in the retention patches.

### Discussion

Our results showed significantly higher species richness of the studied indicator lichens in the old-growth forests compared with clear-cuts and retention cuts, and the retention patches maintained the species diversity of studied lichens better than solitary retention trees. Tree species and type of retention trees were of crucial importance both for species richness

**Table 6.** Distribution of studied birch and goat willow snags to decay stages in different forest categories, and the number of *Chaenotheca* occurrences (occ *Chae* = number of trees inhabited by *Chaenotheca* species) per each decay stage.

	Decay 1	occ <i>Chae</i>	Decay 2	occ <i>Chae</i>	Decay 3	occ <i>Chae</i>	Decay 4	occ <i>Chae</i>
OG	4 (2.7)	0	63 (42.0)	16	8 (5.3)	1	11 (7.3)	1
CC	0	0	27 (18.0)	0	2 (1.3)	0	16 (10.7)	0
RC	5 (3.3)	0	39 (26.0)	0	1 (0.7)	0	25 (16.7)	0
RP	0	0	58 (38.7)	6	24 (16.0)	5	2 (1.3)	0

Note: The percentage of each decay stage of all the studied tree types in the category ( $n = 150$ ) is given in parenthesis. Note that the percentages are not summed to 100% because only birch and goat willow snags are shown in the table. One occurrence of *Chaenotheca* on living birch is not included into the table. OG = old-growth forests, CC = clear-cuts, RC = retention cuts, RP = retention patches.

**Table 7.** Parameter estimates and likelihood ratio tests for the zero-inflated negative binomial model for the number of lichen species on a tree in the retention patches.

Variable, parameter	Estimate	Std. error	z- and chi-squared value	<i>p</i>
Intercept	-4.248	0.808	-5.26	<.000
Tree species (ref. birch)			11.32 (3)	.010
Aspen	-0.527	1.096	-0.48	.631
Goat willow	1.726	0.550	3.14	.002
Rowan	-0.118	1.040	-0.11	.909
Diameter of tree	0.063	0.022	2.84	.005
Size of retention patch (ha)	3.850	1.760	2.19	.029
Random sample plot variance	1.753e - 07			
Negative binomial dispersion parameter	403.43	4.487		
Zero-inflation coefficient	1.000e - 06	1.068e - 05		

Note: Chi-squared values are the values of likelihood ratio tests. The reference category of tree species is birch. The degrees of freedom for likelihood ratio tests are given after chi-squared value.

and the probability of occurrence of species. Aspen has been found to be a hotspot tree for biodiversity in boreal forests in many studies (e.g. Esseen et al. 1997; Jüriado et al. 2003; Tikkanen et al. 2006), and in our study living aspen hosted most of the occurrences of lichens in the retention cuts and clear-cuts. However, in the old-growth stands goat willow was the most important tree species, hosting the largest number of species and having highest probability for the occurrence of any of the target species. Very little information exists on the importance of rowan for lichen diversity in boreal forests; it has been estimated that epiphyte diversity on rowan may be similar to that for aspen and goat willow (Väre and Kiuru 2006). Besides of living trees, our study emphasizes the importance of snags as retention elements for the studied epixylic species. Entire dead trees were of minor importance for the target species of our study; this does not, however, exclude their possible importance as a substrate for other epixylic cryptogams.

The species richness and probability of occurrence of indicator lichens exhibited a close connection with the diameter of a tree: the larger the tree, the more probably it hosted indicator lichens. The diameter and the age of a tree are strongly correlated, whereby older trees generally host more species than younger ones. This is attributed to factors such as the higher surface availability and increased number of microhabitats in larger trees, the increase in the variability of bark texture and structural stability, the variability in bark acidity and increase in its water-holding capacity, and favour in the establishment of species due to a longer time for colonization (see Ellis 2012 and references therein, Nascimbene et al. 2013a). Earlier studies indicate that decay stage is of importance for epixylic lichens (e.g. Söderström 1988); however, in our models, decay stage was neither a significant factor for the species richness, nor the probability of occurrence of any of the studied lichen, or epixylic *Chaenotheca* species. This may be related to structure of the data and the relatively low number of epixylic species. Overall, the results indicate that a varied tree species composition provides a diverse substrate supply, which maintains a diverse epiphytic and epixylic

flora. In our study, the number of species was limited to nine old-growth forest indicators; more extensive investigations of epiphytic and epixylic cryptogams have shown that stand-scale species richness is in general positively associated with increasing tree species diversity (Jüriado et al. 2003) and increasing diversity of tree qualities such as age and size (Brunialti et al. 2010).

Several studies show that many epiphytic and epixylic lichen species are sensitive to the environmental effects of logging (see Johansson 2008 and references therein), including increased irradiance level and wind exposure, which increase evaporation rates (e.g. Chen et al. 1995). Our results showed significant differences in humidity between clear-cuts and closed forests, and the probability of occurrence for the species studied increased from 7% to 18% when the difference in humidity increased four percentage points in the old-growth forests as compared to humidity in the clear-cuts. However, humidity was not a significant variable in the logistic model when predicting the species occurrence at tree level; this may be attributed to relatively small number of species occurrences and stand replicates in our data.

Different species and species groups showed differed tolerances to logging. The species thriving in clear-cuts were foliose cyanolichens (*Leptogium saturninum* and *Nephroma bellum*), which have a relatively thick upper cortex (Stenroos et al. 2011) reducing evaporation and thus enhancing their survival on exposed sites (e.g. Hedenås and Hedström 2007). Many epiphytic lichens have been found to survive for long periods in clear-cuts (at least 6–24 years, Perhans et al. 2009; Hedenås and Hedström 2007; Lundström et al. 2013). Some cyanolichens have been suggested to benefit from increased light due to the canopy opening (Hedenås and Ericson 2003; Hedenås and Hedström 2007), their survival being a balance between light availability and desiccation risk (Gauslaa et al. 2006). Furthermore, some lichen species have shown acclimatization to light and dry conditions in open areas by several physiological adaptations, such as thickening of the thallus and increased production of melanin (e.g. Gauslaa et al. 2006; Nybacken et al. 2007). However, all three epixylic crustose lichens in the genus *Chaenotheca* were absent from snags in clear-cuts and retention cuts. Similar results on the studied genera have been obtained by Perhans et al. (2009), who studied lichens and bryophytes over a 6-year period on retention patches 0.01–0.5 ha in size in boreal Sweden: they found out the cyanolichens *L. saturninum*, *N. bellum*, and *N. parile* increased in abundance, whereas *C. gracillima* decreased. Respectively, in the data of Lundström et al. (2013), *L. saturninum* and two *Nephroma* species increased in young forests (10–16 years old) compared with 0–4-year-old clear-cuts, but the few *Chaenotheca* occurrences disappeared. In our data, the number of snags with suitable decay stage (2–3) for *Chaenotheca* species varied about from 19% to 27% of the studied trees in clear-cuts and retention cuts. According to Mäkinen et al. (2006), it takes 9–11 years for birch snags to reach medium and very decayed stages (comparable to our decay stages 2 and 3) in southern and middle boreal forest zones. The retention cuts in our study were 7–8 years old, indicating that the birch snags on the sites originate from the time before logging. The presence

of *Chaenotheca* species in the retention patches, which originate from the same time than retention cuts, suggests that *Chaenotheca* species have most probably occurred on the snags in the retention cuts at the time of logging, but died out after logging. Thus, our results suggest that environmental circumstances rather than substrate availability are limiting factors for the occurrence of *Chaenotheca* species in retention cuts. Our findings on this genus are supported by earlier studies which show that many crustose species are vulnerable to logging (Hedenås and Ericson 2003; Hedenås and Hedström 2007), and microhabitat humidity is critical for several *Chaenotheca* species (Rikkinen 2003). Löhmus and Löhmus (2011) conclude that shade-tolerant wood dwellers such as *Chaenotheca* can inhabit clear-cuts only after the closing of the canopy.

The patch size affected the species richness of indicator lichens in retention patches, the predicted number of species on a tree trunk increasing with increasing patch size. This may be attributed to a larger number of suitable substrates in larger patches, which enables larger population sizes and enhances dispersal potential of species. However, the models did not find any significant indication of the effect of patch size on the probability of occurrence of species on a tree in the retention patches. These apparently conflicting findings may be due to the small number of the tree trunks that were inhabited by the lichens in our retention patch data, and further studies with larger data would be needed to reveal the linkages between species abundance and patch size. On the other hand, environmental circumstances, e.g. increased humidity, apparently allow a larger variety of species to survive in larger patches compared to smaller ones. In our data, *Chaenotheca furfuracea* was detected in patches as small as 0.07 ha, a finding that suggests that this species is less susceptible for environmental changes than *C. brachypoda* and *C. gracillima*, which were detected only in patches >0.4 ha.

The aspect of the site was significant in the case of *Chaenotheca* species, the highest number of occurrences being found on slopes facing southeast. The preference of many lichens for the northern side of the tree trunk has been documented in a number of studies, with connection to higher humidity and better survival of photobionts on the northern side of the trunk (e.g. Hazell and Gustafsson 1999; Hedenås et al. 2007), but less research has been done on the effect of site exposition on epiphytic and epixylic species. Löbel et al. (2012) found contrasting results to ours in their study of epiphytic bryophytes in boreo-nemoral forests in Sweden, showing that species at SE-facing edges had lowered shoot growth and vitality compared with NE-facing edges. The southern edges may, however, be favourable for some cryptogams, as indicated by Caruso et al. (2011).

What is notable in our study sites is that the majority of retained trees in the patches were spruce, which effectively shade the retained deciduous trees. Thus, not only do the deciduous tree species hosting the epiphyte species play an important role in retention patches, but also the surrounding conifers which provide continuous shade and help in keeping higher humidity are crucial for the survival of shade-requiring

epiphytic and epixylic lichens. Similar effects have been found by Caruso et al. (2011), who noted that increased shade increased the occurrence of forest-interior cryptogams in forest edges compared to open habitats of young forests.

Another important consideration for the long-time persistence of epiphytes is continuous availability of suitable substrates. Mortality of trees can be relatively high among retention trees, and solitary trees in particular are susceptible to strong winds (Heikkala et al. 2014; Hallinger et al. 2016). The rotation times of modern forestry practices appear to be too short for many epiphytic lichens: Aude and Poulsen (2000) concluded from their data that several epiphytic species are unable to colonise trunks within a management cycle of 100–130 years. Johansson (2008) suggests that very long times are needed for epiphytic lichens to recover from disturbances: more than 300 years for cyanolichens and 200–300 years for alectorioid lichens. Normal forestry practices do not allow for rotation times of such length without special arrangements, for example, leaving some of the retention patches unlogged over several management cycles. Furthermore, barriers to dispersal and colonization may turn out crucial for the long-term survival of epiphytic lichens at the landscape scale. Even though solitary retention trees can help individual species, in many countries a considerable proportion of the diversity will be lost without increased retention levels. For instance in Finland, the average proportion of retained timber volume is only 1–3%, and the retained area within cutting areas 1–5%, whereas strict minimum for retention levels, recommended by experts are 5–10% of the logging area or harvested volume (Gustafsson et al. 2012).

To summarize, a variety of tree species are needed as retention trees to fulfil the substrate needs and ecological requirements of different epiphytic and epixylic lichen species in boreal forests. Large-diameter living trees and dead wood especially in the form of snags, as well as high site humidity, enhance species richness and occurrence. Our results show that solitary retention trees lifeboat only a small fraction of rare epiphytic and epixylic lichens, whereas retention patches can also maintain species richness of shade-demanding species. Long-term retention of some patches over several management cycles would enhance the persistence of slowly-dispersing species.

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