

Growth form matters – crustose lichens are sensitive to forest management on dead wood

Annina Kantelinen¹, Jenna Purhonen^{2,3,4}, Panu Halme^{2,5}, Leena Myllys¹

¹ Botany Unit, Finnish Museum of Natural History, P.O. Box 7, FI-00014 University of Helsinki, Finland.

² Department of Biological and Environmental Science, University of Jyväskylä, P.O. Box 35, FIN-40014 University of Jyväskylä

³ Biodiversity Unit, University of Turku, FI-20014 Turku, Finland.

⁴ Zoology Unit, Finnish Museum of Natural History, P.O. Box 7, FI-00014 University of Helsinki, Finland.

⁵ School of Resource Wisdom, University of Jyväskylä, P.O. Box 35, FIN-40014 University of Jyväskylä

Abstract

Lichens have a vital role in forest ecosystems and they are a threatened group in boreal forests. However, the conservation ecology of the total lichen community has very rarely been studied. Here we studied lichen species and communities, including macrolichens (= foliose and fruticose growth forms) and rarely studied crustose lichens, on decaying wood in boreal spruce-dominated forests in Finland. We also studied obligate lignicoles that grow only on dead wood and are mostly crustose in growth form. Species richness and community composition were examined on decaying logs and natural or cut stumps of *Picea abies* at different decay stages (2–5) in 14 stands, half of which were natural or seminatural and half recently managed. We used thorough search to yield a species list as close to complete as possible. Our study questions were: 1) Are species richness and lichen communities different in natural and managed forests, and if so, are there differences between macrolichens, crustose lichens and obligate lignicoles in how they respond to forest management? 2) How does the decay stage and dead wood type affect the lichens, i.e. are there differences between stumps and logs? We found a total of 127 lichen species. Most (75%) of the recorded lichen species were crustose. With a generalized linear model we found that crustose lichens and obligate lignicoles had a higher species richness in natural than managed forests, but macrolichen richness was not significantly affected by forest management. Utilizing non-metric multidimensional scaling we discovered that site level community composition of macrolichens, crustose lichens and obligate lignicoles was also significantly different between natural and managed forests. We found that on dead wood unit level the decay stage had a significant effect on species richness and community composition, so that the species richness of all studied groups declined during the decay process. The dead wood type (stump vs. log) had a significant effect on species richness of macrolichens and obligate lignicoles, as well as on the communities of crustose lichens.

Introduction

Dead wood is crucially important for forest biodiversity (e.g. Löhmus & Löhmus 2001; Siitonen 2001; Stokland et al. 2012), but in managed forests its amount, quality and dynamics have changed significantly compared to natural forests (Angelstam 1997; Linder & Östlund 1998; Wilhere 2003). For instance in Fennoscandia, forest management has dramatically altered the environment for wood-inhabiting species, which constitute 25-30% of all forest species and include many fungi, bryophytes,

insects and lichens (Siitonen 2001). The most conspicuous practice of forest management is the removal of trees. This action has decreased the amount of large-diameter dead wood to a fraction of that in natural forests (Fridman & Walheim 2000; Siitonen 2001; Brassard & Chen 2006).

In their comprehensive review, Spribille et al. (2008) concluded that as many as 550 species of lichens occupy dead wood in Fennoscandia and Pacific Northwest of North America, which have one of the best known lichen floras in the world. Of these species, 132 were regarded as obligate lignicoles not known from other substrata and 418 as facultative lignicoles that alternatively occupy bark, rock or soil. Among wood-inhabiting lichens many are dependent on old-growth forests and constant canopy coverage (Spribille et al. 2008; Löhmus & Löhmus 2011; Malíček et al. 2019), and lichens are considered to be one of the most reliable indicators of forest-continuity and forest quality (Johansson & Gustafsson 2001; Paillet et al. 2010). However, there are also some species that inhabit stumps or slash in young managed forests (Kantvilas & Minchin 1989; Caruso et al. 2008; Rudolphi & Gustafsson 2011; Svensson et al. 2015; Kantvilas & Jarman 2006), making these species vulnerable to the increasing demand of energy wood.

Lichen species richness is generally considered to increase with increasing stand age (Selva 1994; Ulizcka & Angelstam 1999; Hilmo et al. 2009; Lommi et al. 2010; Nascimbene et al. 2010; Malíček et al. 2019; Nirhamo et al. 2021). There are two main reasons for this: firstly, old-growth forests harbor a rich diversity of microhabitats, including higher diversity and volume of dead wood, that have evolved during the long time available; secondly, the microclimate is more stable and suitable for lichens (e.g. Hyvärinen et al. 1992; Kuusinen 1996; Hilmo et al. 2009; Löhmus & Löhmus 2011; Bäcklund et al. 2016). In managed forests lichens appear to be particularly vulnerable to thinning of forest canopy (Bunnell et al. 2008; Löhmus & Löhmus 2011). This exposes lichens to prolonged desiccation via the increase of radiation, maximum air temperatures and wind speed, and also decreases the humidity of the site (Lange et al. 1999; Gauslaa & Solhaug 2000; Sillett & Antoine 2004; Gauslaa et al. 2006). For wood-inhabiting lichens in managed forests, the lower amount and diversity of dead wood is a major threat as it jeopardizes the continuity of their resource availability both in space and time (Kuusinen & Siitonen 1998; Caruso et al. 2008; Saine et al. 2018; Pykälä et al. 2019).

A decline in wood-inhabiting species has been recorded widely in the world (Angelstam 1997; Linder & Östlund 1998; Wilhere 2003; Stokland *et al.* 2012; Boch et al 2013; Ardelean et al. 2015). Similar trend is evident also in Finland where the Red List evaluations show an increase in the amount of endangered lichen species within the last 20 years, and report that forest management is the most important threat for 40 % of the threatened lichen species including many facultative and obligate lignicoles (Pykälä et al. 2019). Especially highly specialized species, such as obligate lignicoles, likely have a high extinction risk (Spribille et al. 2008; Vamosi et al. 2014; Resl et al. 2018; Launis & Myllys 2019). However, evaluating the extinction risk of wood inhabiting lichens is challenging, as the majority of them are poorly known microlichens (Spribille et al. 2008). These small crustose lichens appear to be especially sensitive to environmental changes, probably because they are so closely associated with their substratum and the microclimate (Tibell 1992; Selva 2003).

Although the ecology of lichens occupying dead wood has been studied quite extensively in northern Europe, Baltic states (Tibell 1992; Krüys & Jonsson 1997; Crites & Dale 1998; Forsslund & Koffman 1998; Krüys et al 1999; Löhmus & Löhmus 2001; Jüriado et al. 2003; Caruso et al. 2008; Spribille et al. 2008; Löhmus & Löhmus 2011; Svensson et al. 2015) and North America (Selva 1994; Bunnell et al. 2008; Spribille et al. 2008), the research has mostly focused on limited assembly of lichen

groups such as macrolichens or calicioid fungi leaving out much of the inconspicuous diversity of the crustose lichens. Only a few studies have included all lichen groups on dead wood and compared the species composition in managed and natural forests (Forsslund & Koffman 1998; Bunnell et al. 2008). Fewer still have examined both the significance of decay class and the amount of dead wood for the species composition (Forsslund & Koffman 1998).

In this study, we explored lichens on decaying logs and natural or cut stumps of Norway spruce (*Picea abies*) in Finland, including all lichen groups and different decay stages between 2–5 (Renvall 1995). We focused on spruce because it is a dominant species in natural and managed forests in southern and central Finland, and it has been reported to have higher number of unique species (Kuusinen & Siitonen 1998), as well as to host higher diversity of crustose lichens compared to the other dominant tree species *Pinus sylvestris* (Halonen et al. 1991; Hyvärinen et al. 1992). We examined the following questions: 1) Are species richness and lichen communities different in natural and managed forests, and if yes, are there differences between macrolichens, crustose lichens and obligate lignicoles in how they respond to forest management? 2) How does the decay stage and dead wood type affect the lichens, i.e. are there differences between stumps and logs? Answering these questions increases our knowledge of lichen diversity on dead wood, and also gives us important information on how forestry affects the crustose lichens.

Material and methods

2.1. Study regions

The study was conducted in southern boreal zone in southern Finland and middle boreal zone in central Finland. The selected forests were managed monocultures or alternatively natural or seminatural mixed stands with *Pinus sylvestris* or *Picea abies* as a dominant species together with deciduous trees such as *Betula* spp. and *Populus tremula*. In southern and central Finland, the landscape is dominated by managed forests that typically undergo one to three thinnings before a clear-felling at the age of 70-100 years. Ca. 4 % of forests in southern and central Finland are legally protected (Vaahtera et al. 2018).

The selected forest stands were mostly dominated by *Picea abies* (L.) H. Karst, with mixed *Pinus sylvestris* L. and *Betula* spp. The dominant forest types were a herb-rich *Oxalis-Myrtillus* and a mesic *Myrtillus* type (MT) in the stands located in the southern boreal zone and the corresponding forest types in the middle boreal zone (see Kalela 1961 for details).

2.2. Study site selection, study plot positioning and sampling

Study site selection

Fieldwork was conducted in July 2012 and between May to October 2013. A total of 14 stands were selected for the study to represent spruce-dominated managed forests (7 stands) and natural forests (7 stands). Natural sites were selected based on expert evaluation to represent the most valuable natural or seminatural forests in southern and southeastern Finland for spruce-inhabiting lichen diversity. After selecting the natural sites, the potential managed study sites were searched by using map services that show the age and tree species composition of forests and the presence of dead wood

(Ministry of the Environment, Finnish Environment Institute and Metsähallitus). We searched one potential managed study site close to each natural site included in the study.

Managed and natural forests were defined based on forest structure so that natural stands had only little signs of earlier human influence such as cut stumps whereas managed stands were subjected to forestry during the late 20th century. In reality, the natural stands are more correctly seminatural, because human influence is present everywhere in Finland.

Stand age varied between 40 and 85 years in the managed forests, and 80 to 150 years in the natural forests (Table 1). Stand age was determined from forest cover maps for the study areas located in state owned lands. For private lands the information was obtained directly from forest owners who had received it from the Finnish Forest Center.

The southern boreal zone study stands were situated in Tavastia australis province (4 stands) and Nylandia province (4 stands). The middle boreal zone study stands were situated in Karelia borealis province (4 stands, border of southern and middle boreal zones) and Ostrobothnia kajanensis province (2 stands, middle boreal zone) located in eastern Finland (Ahti et al. 1968) (Fig. 1).

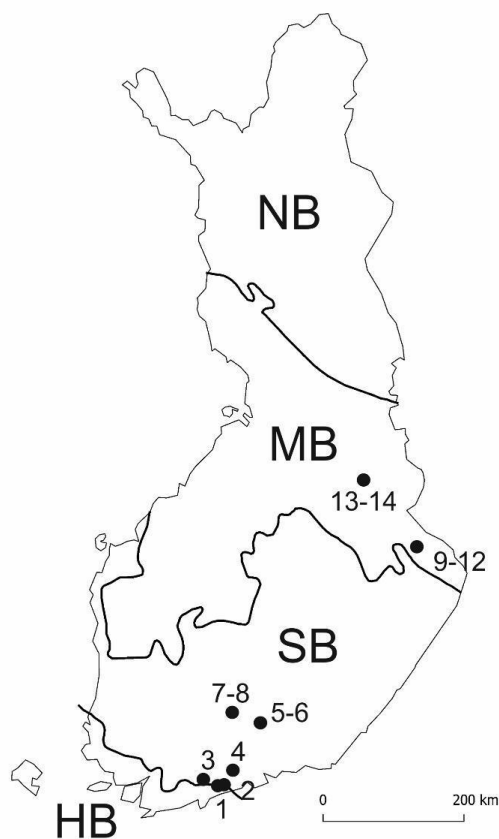


Fig 1. Vegetation zones and the locations of the 14 studied forest areas. HB = hemiboreal, SB = southern boreal, MB = middle boreal, and NB = northern boreal zone.

Table 1. Site information.

	Site	Municipality	Forest age (years)	Forest type	Number of species
1	Herukkapuro	Vantaa	81-100	Natural	44 (one cf.)
2	Korso	Vantaa	61-80	Managed	26
3	Nuukio	Kirkkonummi	61-80	Managed (lately protected)	40
4	Röstrand	Sipoo	61-80	Natural	18
5	Iitti2	Iitti	61-80	Managed	30
6	Iitti	Iitti	41-60	Managed	25
7	Kotinen	Hämeenlinna	126-150	Natural	30
8	Evo	Hämeenlinna	81-100	Managed (lately protected)	43
9	Koli1	Lieksa	126-150	Natural	53 (one cf.)
10	Koli2	Lieksa	126-150	Natural	43
11	Koli3	Lieksa	41-60	Managed	28 (one cf.)
12	Koli4	Lieksa	41-60	Managed	19
13	Rommakkovaara	Sotkamo	126-150	Natural	32 (one cf.)
14	Vuokatti	Sotkamo	over 150	Natural	47 (one cf.)

Study plot positioning

Sampling was performed in study plots of 50 m x 20 m. Our selection of the study plots resembles that of the subjective selection methods described by Vondrák et al. (2018) and applied by Malíček et al. (2019) and Vondrák et al. (2019), as also our major aim was to yield a species list as close to complete as possible. As previous studies have shown, the species richness of epiphytic lichens is not uniformly distributed but much greater in hotspots (Neitlich et al. 1999; Vondrák et al. 2015). Therefore, a comprehensive inventory of species diversity is difficult to obtain via random sampling. For wood-inhabiting lichens the amount and diversity of dead wood is crucial, therefore our main criterion to select the study plots was that it included as much dead wood as could be found within the site. Especially in managed forests the amount and diversity of dead wood is often low, and therefore we actively sought dead wood in order to find some. This method prevents most of the plot-level statistical analyses because the dead wood volume is manipulated via plot selection process but it has been shown to be useful for unveiling high lichen species richness in forests (Vondrák et al. 2018).

Sampling

Study plots in natural forests were surveyed for 10–16 hours and in managed forests 6–10 hours. This included the selection of the study plot within an appropriate forest site and additional ecological

measurements. In each study plot, tree species and diameter at breast height (dbh) were recorded for all live and dead trees (standing trees, downed logs and cut stumps) with dbh \geq 3 cm. Decay class (2–5) was estimated by knife for all dead trees (Renvall 1995). The difference in survey times between managed and natural stands is explained mostly by that the differences in the size of dead wood units (DWU from hereafter) that were generally smaller in the managed study plots.

Within the study plots, lichens were sampled from three decaying *Picea abies* DWU of each decay class (2–5), target being 12 units per study plot. We did not study DWU in decay stage 1, because those are usually completely covered with bark (e.g. Löhmus & Löhmus 2001). The uncorticated hard snags, on the other hand, have been studied before quite extensively (Tibell 1992; Löhmus & Löhmus 2001; Rikkinen 2003; Selva 2003; Löhmus & Löhmus 2011). Especially in managed stands, the amount of sampled DWUs was sometimes less than 12 because of the scarcity of the DWU in different decay stages. In total, 121 DWUs were inventoried, including downed logs and natural or cut stumps. Sampled DWUs were selected as follows: 1) Sampling was primarily focused on downed logs. However, stumps were selected if the occurrence of downed logs was \leq 3 per decay class; 2) If more than three logs per decay class occurred in the study plot, logs with the highest lichen coverage were selected (estimated by eye).

2.3. Species data and identification

All lichen species were inventoried and/or collected from the selected trees. Species were inventoried from the whole length of the sampled tree or stump (excluding branches). The study species represent macro- and crustose lichens, including all three lichen growth forms, i.e. fruticose, foliose and crustose. The essential difference between macrolichens (fruticose and foliose) and crustose lichens is how they grow and utilize their substrata: macrolichens are not tightly bound whereas crustose lichens adhere strongly to the substrate, making separation from the substrate impossible without destruction. Most of the obligate lignicoles are crustose lichens (Table 2 on pages 23-25) and they are not known from other substrata (Spribille et al. 2008). Only two of the nineteen obligate lignicoles in our data are macrolichens (genus *Cladonia*).

Morphological studies

Specimens were identified with a dissecting (Leica S4E) or compound microscope (Leica CME) using relevant literature (e.g. Coppins 1983; Foucard 2001; Czarnota 2007; Smith et al. 2009; Spribille et al. 2014). Anatomical characters and ascospore dimensions were measured in water. Secondary metabolites of the specimens were identified using chemical spot tests and thin-layer chromatography (TLC). For spot tests we used 10 % potassium hydroxide (K) and sodium hypochlorite (C) (Orange et al. 2010). For TLC a small piece of thallus was removed from the specimen and placed in a microcentrifuge tube. Secondary compounds were extracted using acetone and the extracts were spotted on 10 × 20 cm Merck silica gel 60 F-254 pre-coated glass plates with 75 mm/75 μ L Haematocrit capillaries (Hirschmann Laborgeräten). Extracts were run in solvent systems A and B (Culbertson & Kristinsson 1970; Orange et al. 2010).

Molecular studies

Some of the specimens were examined using molecular characters for reliable species identification. Total genomic DNA was extracted from lichen structures (apothecia, pycnidia or thallus). Extractions

were conducted using DNeasy® Blood & Tissue kit by Qiagen following the protocol described in Myllys et al. (2011).

For the ITS region, PCR was run under the following conditions: initial denaturation for 5 min at 95 C followed by five cycles of 30 s at 95 C (denaturation), 30 s at 58 C (annealing), and 1 min at 72 C (extension); for the remaining 40 cycles, the annealing temperature was decreased to 56 C; and the PCR program ended with a final extension for 7 min at 72 C. Primers ITS1-LM (Myllys et al. 1999) and ITS4 (White et al. 1990) were used both for PCR amplification and sequencing.

For the mtSSU gene, PCR was run under the following conditions: initial denaturation for 10 min at 95 C followed by six cycles of 1 min at 95 C (denaturation), 1 min at 62 C (annealing), and 105 s at 72 C (extension); for the remaining 35 cycles, the annealing temperature was decreased to 56 C; and the PCR program ended with a final extension of 10 min at 72 C. Primers mrSSU1 and mrSSU3R (Zoller et al. 1999) were used both for PCR amplification and sequencing.

PCR products were cleaned and sequenced by Macrogen Inc., Amsterdam (www.macrogen.fi).

2.4. Statistical analysis

We studied the effect of forest management to stand level species richness by calculating species accumulation curves for macrolichens, crustose lichens and obligate lignicoles in different forest types (natural and managed). We further investigated this relationship by fitting a generalized linear model with negative binomial regression, in which stand level species richness was the dependent variable and forest type the explanatory variable.

We also studied the relationship of the species richness on each studied DWU with stand- and DWU-level variables by fitting generalized linear mixed models with negative binomial regression. Here we included forest type, decay stage and dead wood type as explanatory variables. To account for the stand-level hierarchy of the study design (DWU within stand) we included site identity as a nested random effect. We utilized the “glmmTMB” function of the package “glmmTMB” to perform both the generalized linear and mixed models (Mollie et al. 2017).

We used Nonmetric Multidimensional Scaling (NMDS) to study the differences in community composition according to different environmental variables, separately for macrolichens, crustose lichens and obligate lignicoles. We performed the analysis on two levels, at stand-level in which case we used species level abundance data for each study site, and at DWU-level in which presence-absence data for each species per DWU was used. Prior to the analysis we removed all DWU that had less than two species occurring to avoid the problem of no convergence. Bray-Curtis dissimilarities were calculated for each community pair with the function “metaMDS” of the “vegan” package (Oksanen et al. 2019). We performed three-dimensional scaling on each occasion.

We further investigated the relationship of environmental variables with community dissimilarity axes with permutation test using the function “envfit” of the “vegan” package (Oksanen et al. 2019). At site level we included the forest type (categorical, natural/managed) and stand identity (categorical, site id) as for environmental variables. For DWU level, we included the following environmental variables; decay stage (continuous, 2-5), dead wood type (categorical, log/stump), the forest type (categorical, natural/managed) and the site identity (categorical, site id). All data analyses were conducted with R software version 3.5.1 (R Core Team 2021).

3. Results

We recorded 3254 observations of lichen thalli belonging to 127 species among the ca. 4000 samples collected. 95 of these species were crustose lichens and 32 macrolichens (Table 2). 19 species were obligate lignicoles. Of these, 17 were crustose lichens belonging to the genera *Absconditella*, *Chaenotheca*, *Micarea*, *Thelocarpon* and *Xylographa*, and 2 were macrolichens belonging to the genus *Cladonia* (Table 2). Three taxa showed unique morphological, chemical and DNA-level characters, and likely represent scientifically undescribed species (*Micarea nigella* clades 1, 3 and 4). In addition, eleven taxa could not be identified with certainty and they are marked as 'agg.', 'cf.', 's. lato' or 'sp.'. In both forest classes, decay stages 2 and 3 were the most common. In managed forest stands 34 of the studied DWU were logs and 25 were human made stumps, and in natural forest stands 46 were logs and 16 were natural stumps. We found altogether 24 red listed species for Finland.

3.1 Species richness

The mean number of species per DWU was 3.3 for macrolichens, 5.8 for crustose lichens and 1,4 for obligate lignicoles (Appendix). 31 % (n=44) of the species occurred only once in our sampling. 63,4 % (n=90) of the species had 5 or fewer occurrences, and 69,1 % (n=98) had 10 or fewer occurrences. The most common species in our dataset was a macrolichen species *Cladonia coniocrea* (n=83), followed by crustose species *Micarea prasina* (n=74), *Placynthiella dasae* (n=60), *Placynthiella icmalea* (n=57) and *Lepraria jackii* (n=55) (see Table 2). The two forest types shared the most common species, however in managed forest sites *Vulpicida pinastri* (macrolichen) was the third most common species whereas in natural forest sites the third most common species was a crustose lichen *Lepraria jackii* (Table 2).

We identified 101 species in the natural forest sites and 83 in the managed sites. Koli National Park (site 10) and Vuokatti (site 14) in eastern Finland, had the highest species richness, with 52 and 46 species, respectively. On the contrary, a young natural forest in Southern Finland Rörstrand (site 4) and a managed forest in Eastern Finland near Koli National Park (site 12) harbored the lowest species richness with 18 and 19 species, respectively (Table.1). Altogether 38 of the observed species were unique to natural forest sites and 18 were unique to managed forest sites.

Our results show that on site level, crustose lichens and obligate lignicoles are more species rich in natural than managed forests. Macrolichens, however, are not significantly affected by forest management practices (Fig. 2, Table 3). The accumulation curves indicate rather high number on undetected species of crustose lichens.

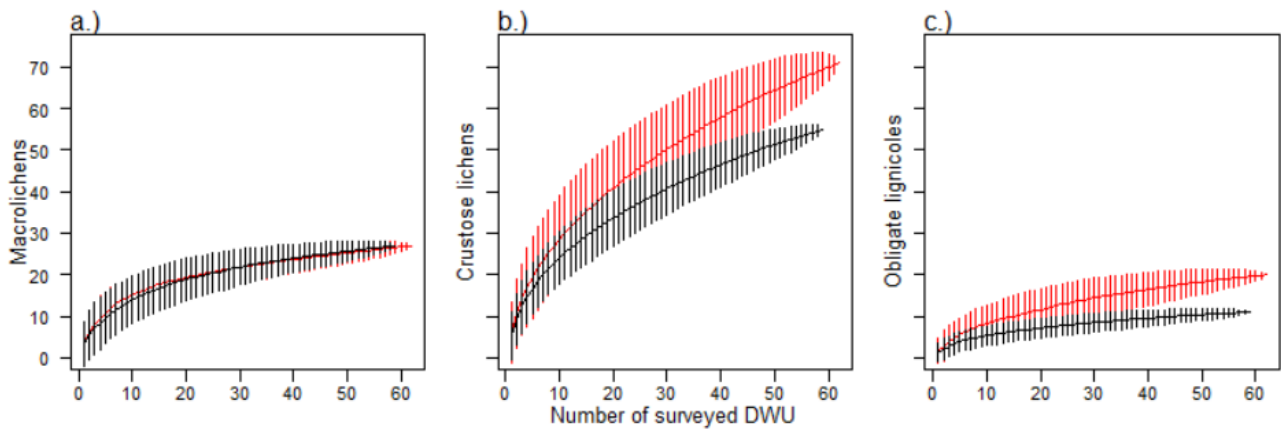


Fig. 2 (a-c). Species accumulation curves for a.) macrolichens, b.) crustose lichens, and c.) obligate lignicoles in different forest types, namely spruce-dominated natural forests (red colour) and managed forests (black colour). The higher and lower 95% confidence intervals are presented with vertical lines. The elevation of the curves indicates differences in the number of detected species and the slope reveals the likelihood of undetected species and the effects of sampling effort.

Table 3. Site-level statistics of generalized linear model for species richness, separately for macrolichens, crustose lichens and obligate lignicoles. Asterisk indicate P-values as follows: *** = $P \leq 0.000$, ** = $0.000 < P \leq 0.01$, * = $0.01 < P \leq 0.05$, · = $0.05 < P \leq 0.1$.

Macro	Estimate Std.	Error z	value	Pr(> z)
(Intercept)	2.645	0.439	6.033	<0.000 ***
Forest type	-0.137	0.279	-0.490	0.624
Crustose				
(Intercept)	3.462	0.234	14.789	<0.000 ***
Forest type	-0.267	0.152	-1.757	0.079 ·
Obligate				
(Intercept)	2.353	0.344	6.838	<0.000 ***
Forest type	-0.449	0.234	-1.921	0.055 ·

On DWU-level, forest type did not have significant relationship with any of the studied lichen groups (Table 4). Dead wood type had significant negative relationship with macrolichen and obligate lichen species richness being smaller on stumps than logs, while for crustose lichens there was no significant relationship. We also studied the effect of decay stage to species richness. We identified on the average 2.0 species per DWU belonging to decay stage 2 (762 observations, 84 species on 41 units). On decay stage 3 we identified on the average 2.1 species (782 observations, 75 species on 35 units), on decay stage 4 we identified on the average 1.9 species (535 observations, 62 species on 32 units) and on decay stage 5 we identified on the average 2.2 species (105 observations, 29 species on 13 units) (Table 5 on page 26-27). With the generalized mixed linear modeling we found that on DWU-level species richness decreased during the decay process for all of the studied lichen groups (Table 4).

Table 4. DWU-level statistics of generalized linear mixed model for species richness, separately for macrolichens, crustose lichens and obligate lignicoles. Asterisk indicate P-values as follows: *** = $P \leq 0.000$, ** = $0.000 < P \leq 0.01$, * = $0.01 < P \leq 0.05$.

Macro	Estimate	Std. Error	z value	Pr(> z)	
(Intercept)	1.770	0.564	3.137	0.002	**
Decay	-0.138	0.057	-2.410	0.016	*
Forest type	-0.086	0.343	-0.251	0.802	
Dead wood type	-0.530	0.140	-3.787	0.000	***
Crustose					
(Intercept)	2.548	0.251	10.157	<0.000	***
Decay	-0.176	0.053	-3.347	0.000	***
Forest type	-0.157	0.131	-1.199	0.231	
Dead wood type	-0.170	0.116	-1.471	0.141	
Obligate					
(Intercept)	1.218	0.426	2.856	0.004	**
Decay	-0.177	0.083	-2.126	0.034	*
Forest type	-0.194	0.230	-0.847	0.397	
Dead wood type	-0.478	0.203	-2.357	0.018	*

3.2 Community composition

Most of the recorded lichen species were crustose (75 %). Also, of the 10 most common species (with more than 30 occurrences) most were crustose lichens (70%). Of the uncommon species with five or fewer occurrences, 72,2 % (n=65) were crustose lichens, and most of them occurred only or more frequently in natural sites (Table 2).

On site level, forest type explained best the community composition of crustose lichens whereas the macrolichen communities were similarly explained by forest management type and site. For obligate lignicoles, the site identity explained the community composition better than forest type (Fig. 3).

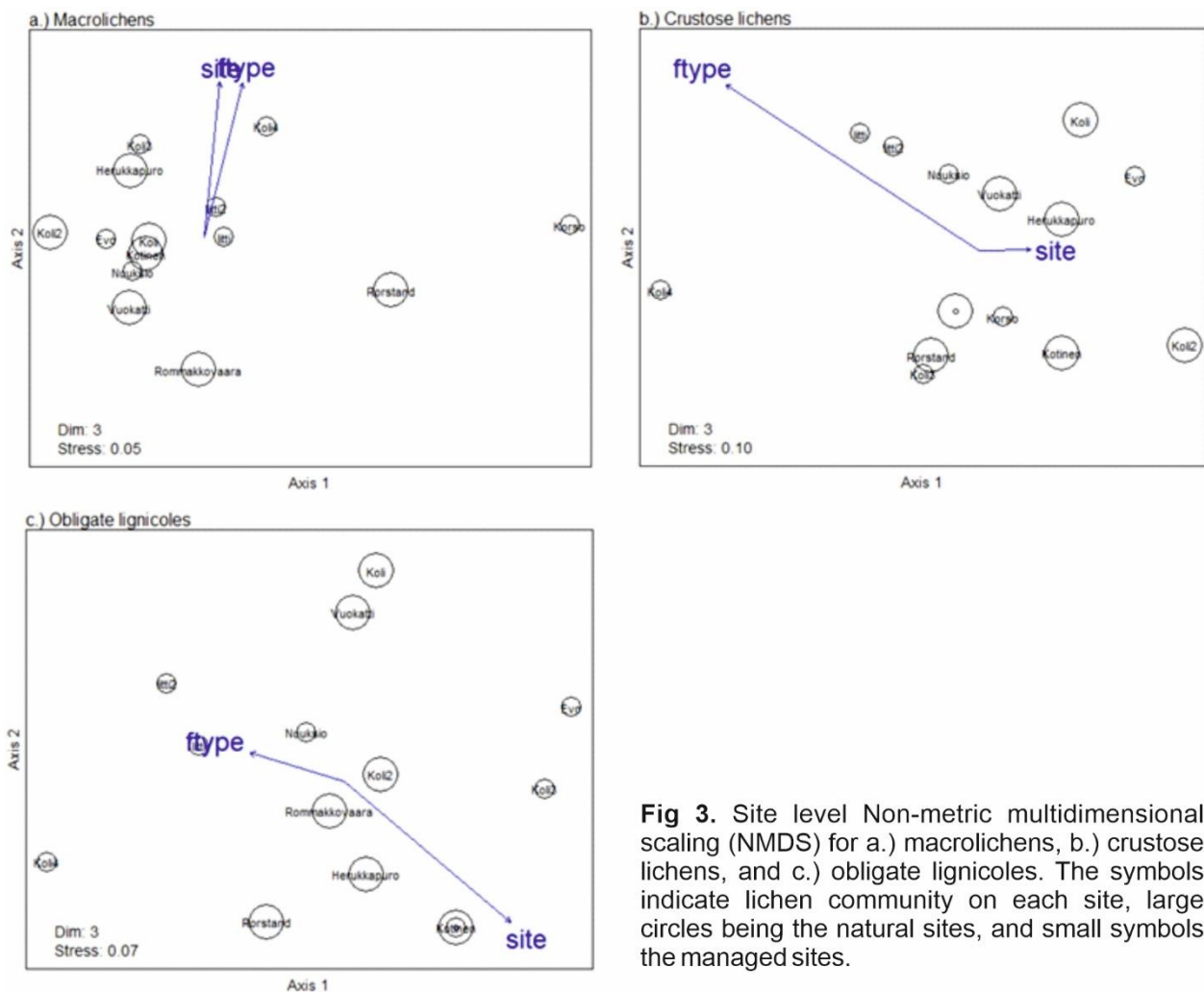


Fig 3. Site level Non-metric multidimensional scaling (NMDS) for a.) macrolichens, b.) crustose lichens, and c.) obligate lignicoles. The symbols indicate lichen community on each site, large circles being the natural sites, and small symbols the managed sites.

On DWU level, differences in macrolichen community composition were best explained by decay stage. Site, dead wood type (log or stump) and decay stage were significant variables for crustose lichen composition (Fig 4). Forest type (natural/managed) explained best the community composition of obligate lignicoles. We also found that certain species were clearly specialized on specific decay stages. E.g. species in the genus *Xylographa* occurred on early decay stages, whereas *Micarea hedlundii* occurred on late decay stages wood (Table 5).

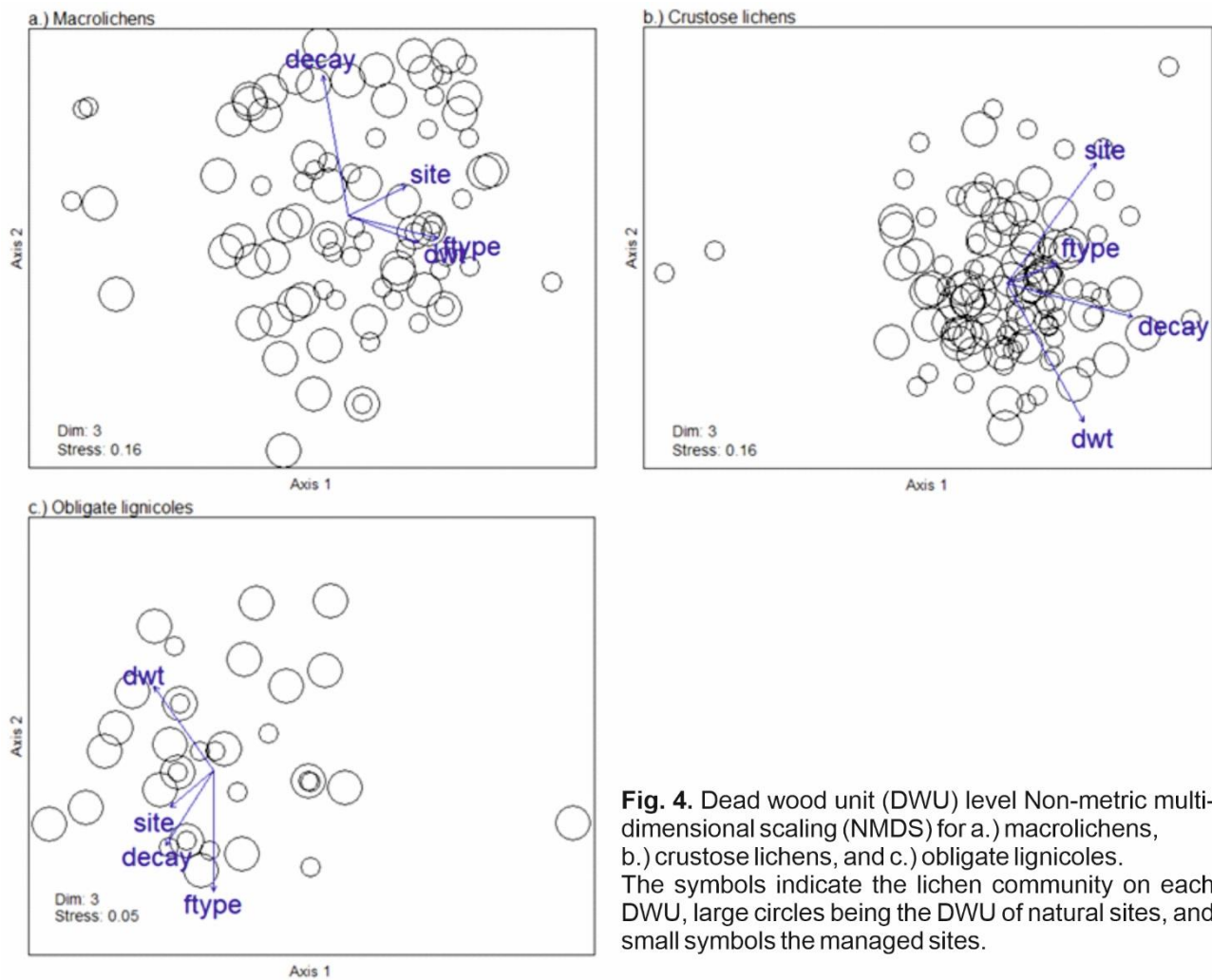


Fig. 4. Dead wood unit (DWU) level Non-metric multi-dimensional scaling (NMDS) for a.) macrolichens, b.) crustose lichens, and c.) obligate lignicoles. The symbols indicate the lichen community on each DWU, large circles being the DWU of natural sites, and small symbols the managed sites.

4. Discussion

4.1 Species richness

One of the key results of our study is that on site level crustose lichens and obligate lignicoles have higher species richness in natural forests than in managed forests. Macrolichens, however, are not similarly affected by forest management. This indicates that growth form has a crucial effect on the biology and conservation requirements of lichens (regarding that obligate lignicoles are mostly crustose). Also, previous ecological studies in boreal forests have shown that crustose lichens and macrolichens differ in some of their responses: crustose lichens seem to be more shade tolerant than macrolichens (Löhmus & Löhmus 2011; Bäcklund et al. 2016), and they are more substrate specific

between spruce and pine, probably because of their sensitivity to differences in bark pH (Hyvärinen et al. 1992).

The macrolichen species in our study are mostly generalists that occur on various substrates and habitats, whereas the crustose species are more often specialists that are restricted to certain habitats such as old-growth forests and dead wood (e.g. Smith et al. 2009; Stenroos et al. 2016). In previous studies, crustose lichens have also been considered more sensitive to environmental changes (Tibell 1992; Selva 2003). The differences in the volume of dead wood and ecological continuity could explain why crustose lichens in our study are more species rich in natural than managed forests. In the natural forest sites, the DWUs are larger than in the managed forest sites where dead wood is mainly human-made stumps or small logs. In addition, the natural forest sites are older, likely providing forest continuity and a higher number of different microhabitats that benefit specialists.

Microclimate might also influence why crustose lichens are more species rich in natural forest sites. The removal of forest canopy due to thinning is known to change microclimatic features by decreasing humidity levels and increasing maximum temperatures, wind speed and the amount of light (Yarranton 1972; Sillett & Antoine 2004; Gauslaa et al. 2006). As most lichens do not have effective structures for water storage, they are sensitive to prolonged desiccation and exposure to light (Lange et al. 1999; Gauslaa & Solhaug 2000). Many of the dominant crustose lichens on dead wood are soredious or goniocystoid in structure, meaning that they are “powdery-like” and lack a protective cortex layer (i.e. *Lepraria* spp., *Micarea* spp. and *Placynthiella* spp.). Macrolichens, on the other hand, typically have a protective cortex (Smith et al. 2009). We hypothesize that this structural difference makes crustose lichens on dead wood more vulnerable to microclimatic changes compared to macrolichens.

The three lichen growth forms (i.e. fruticose, foliose and crustose) have been associated with different ecological strategies. Based on Grime’s (1979) triangular ordination model, foliose and fruticose growth forms of macrolichens have been linked to a competitive strategy while a crustose growth form has been connected to stress tolerant and ruderal strategies (Rogers 1988, 1990). Crustose lichens have generally been considered as poor competitors because of their small size, slow growth rate and because they are easily overgrown by macrolichens and bryophytes. Given that, it is interesting that ours, as well as previous studies (Bunnell et al. 2008; Spribille et al. 2008), have revealed that most lichen species on dead wood are in fact crustose. This could be explained by at least two hypotheses: First, their better tolerance for shade might be crucially important in spruce – dominated areas where fallen trees and stumps at the forest understory are typically poorly lit. Second, the ephemeral nature of the growing substrata probably favors species with ruderal and stress tolerant strategies.

We found that the number of unique species is twice as high in natural forests than managed forests. This result is in line with previous studies (Selva 1994; Ulizcka & Angelstam 1999; Hilmo et al. 2009; Lommi et al. 2010; Nascimbene et al. 2010; Malíček et al. 2019) and is likely explained by the combination of natural forests having more dead wood, wider diversity of microhabitats, and more stable microclimatic conditions. Boreal lichen communities have also been considered as additive systems where early colonizers persist and new species are added without replacing the old ones (Ulizcka & Angelstam 1999; Hilmo et al 2009).

In addition to the site-level analyses, we studied environmental effects on DWU-level. We found that the decay stage has a significant effect on species richness so that richness declines during the decay process. This trend is evident in all groups, i.e. crustose lichens, obligate lignicoles and macrolichens. The peak of lichen richness is centered around decay stages 2 and 3, which is the time after bark loss and before bryophyte colonization. During this period wood becomes soft and starts to lose form. Later, the changes in wood structure and the colonization of bryophytes alter dead wood into unfavorable substratum to most lichen species. These results are in line with previous studies reporting patterns of succession of lichens on down wood in North America and Europe (McCullough 1948; Muhle & LeBlanc 1975; Jansová & Soldán 2006).

The dead wood type (logs vs. stumps), has also a significant effect on lichen species richness on DWU-level. This is especially evident for the macrolichens and obligate lignicoles, both for which species richness is higher on logs than on stumps. For macrolichens, this might simply be because logs are larger units than stumps and hence offer more space to grow on. For obligate lignicoles, on the other hand, the reasons for higher species richness on logs might be more complex. In general, the obligate lignicoles are specialist crustose species. In our data, the number of records of obligate lignicoles is substantially higher in natural forest sites than in managed forest sites, meaning that these species probably benefit from higher diversity and amount of dead wood.

By comparing how many records per species were made on logs and stumps, we found out that several lichen species on dead wood prefer either stumps or logs as their growing substratum (Table 6 in supporting info). *Absoconditella lignicola*, *Micarea anterior*, *Micarea contexta*, *Micarea misella*, *Placynthiella dasae*, *P. icmalea*, *Thelocarpon intermediellum*, *Trapeliopsis flexuosa* and *Xylographa soralifera*, that are all crustose species, have distinctly more records on logs than on stumps. The Calicioids, on the other hand, were found only on dead standing trees. *Cladonia digitata*, *Coenogonium pineti* and *Lepraria jackii* are common on logs and stumps.

4.2 Community composition

On site level, lichen communities on dead wood are influenced mainly by two parameters: site and forest management. Macrolichen communities are influenced significantly by both parameters, crustose lichen communities by forest management and obligate lignicoles mostly by site. This shows that especially for macrolichens and obligate lignicoles, the selected study sites represent diverse habitats and that these communities are not only affected by management history and spruce-dominance, but that other parameters likely play an important role. Such parameters are not the focus of this study, but we can hypothesize that they are related to the age of site, geography and dead wood diversity. Forest management also plays an important role for the community structure of macrolichens and crustose lichens. Our results show that even though species richness of macrolichens is not significantly different between managed and natural sites, the communities in fact are. Crustose lichens, on the other hand, are affected by forest management on both levels, species richness and community.

On dead wood level, lichen communities are influenced mostly by decay stage, dead wood type (log vs. stump), and site. Macrolichen communities are explained especially by decay stage, whereas crustose lichen communities are explained by three parameters that are dead wood type, site and decay stage. Obligate lignicoles are affected mostly by forest management (tendency). In our view, the reason why crustose and macrolichen communities on dead wood level are affected significantly by decay stage is mainly because they have to compete with bryophytes. The amount and coverage of bryophytes increases during the decay process and lichens lose the competition for space. Dead wood type is also a significant parameter for the communities of crustose lichens. This may indicate that the species are more sensitive to environmental conditions such as light and moisture that are likely different between logs and stumps.

Finally, contrary to site level, forest management does not appear to have a significant effect on lichen communities on DWU level. This means that lichens can utilize dead wood in managed and natural forests, but that on site-level, the communities become significantly different.

4.3 Species diversity and threat status

Every 5th species found in our study are red-listed in Finland (24 species of the total 127). Ten are classified as vulnerable, eleven as near threatened and three as data deficient (Hyvärinen et al. 2019). Of these, nine were found only from natural forests and fifteen from both managed and natural forests. None of the red listed species were found only from managed forests, a result in line with e.g. Malíček et al. (2019).

Interestingly, our study also revealed that two red listed species are in fact more common than was previously known -- *Micarea anterior* (Nyl.) Hedl. and *M. contexta* Hedl. were found frequently from natural and managed forests. This is probably explained by the inconspicuousness of these species, but also by the rarity of specialists who can identify them.

During this project, seven species were recorded new to Finland (Myllys and Launis 2018) and in addition seven species have lately been described as new to science (Guzow-Krzemińska et al. 2016; Launis et al. 2019 a, b). In addition, three taxa in our data set represent possibly still undescribed species (*Micarea nigella* clades 1, 2, 4; Kantelinen & Myllys manuscript). Eleven taxa could not be identified with certainty; these specimens either represent groups that have taxonomic unclarities or specimens show morphological and sometimes also chemical characters that differ from known species descriptions. DNA-data of these specimens is insufficient for further identifications. This reveals that even in Fennoscandia, dead wood hosts a considerable amount of lichen diversity that was previously unknown.

5. Conclusions

We show that on dead wood the number of crustose lichen species is significantly higher than the number of macrolichen species. One of our key results is that management practices affect species richness of crustose lichens but do not similarly affect macrolichens. This indicates that crustose

lichens on dead wood are sensitive to factors that differ between natural and managed forests such as quantity and diversity of dead wood, stand continuity and microclimate. On a community assembly level, both the macrolichens and crustose lichens are affected by forest management.

We also found that decay stage and dead wood type (stump vs logs) matter to lichens on dead wood. This result is important for conservation planning when aiming to increase species diversity in managed forests.

Acknowledgements

We thank prof. Otso Ovaskainen, PhD Nerea Abrego and the other members of the Predictive Community Ecology Group, as well as PhD researcher Aleksi Nirhamo for their helpful comments to the manuscript. This research was financially supported by the Finnish Ministry of Environment as a part of the research programme on deficiently known and threatened forest species (grant YTB067), a postdoctoral fellowship of the Finnish Museum of Natural History and Societas pro Fauna et Flora Fennica (a personal grant for the first author), and a postdoctoral grant from Alfred Kordelin Foundation (a personal grant for the second author).

References

- Ahti, T., Hämet-Ahti, L., Jalas J., 1968. Vegetation zones and their sections in northwestern Europe. *Ann Bot Fenn.* 5, 169–211.
- Angelstam, P., 1997. Landscape analysis as a tool for the scientific management of biodiversity. *Ecological Bulletins* 46, 140–170.
- Ardelean, I.V., Keller, C., Scheidegger, C., 2015. Effects of management on lichen species richness, ecological traits and community structure in the Rodnei Mountains National Park (Romania). *PLoS ONE*. <https://doi.org/10.1371/journal.pone.0145808>
- Boch, S., Prati, D., Hessenmöller, D., Schulze, E.D., Fischer, M., 2013. Richness of lichen species, especially of threatened ones, is promoted by management methods furthering stand continuity. *PLoS ONE*. <https://doi.org/10.1371/journal.pone.0055461>
- Brassard, B.W., Chen, H.Y.H., 2006. Stand structural dynamics of North American boreal forests. *Crit. Rev. Plant Sci.* 25, 115e137.
- Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M., Bolker, B.M., 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal* 9, 378–400.
- Bunnell, F., Spribille, T., Houde, I., Goward, T., Björk, C., 2008. Lichens on down wood in logged and unlogged forest stands. – *Canadian Journal of Forest Research* 38, 1033–1041
- Caruso, A., Rudolphi, J., Thor, G., 2008. Lichen species diversity and substrate amounts in young planted *Picea abies* forests: a comparison between slash and stumps of *Picea abies*. *Biol. Conserv.* 141, 47e55.
- Colwell R.K. 2013. EstimateS: statistical estimation of species richness and shared species from samples. Version 9. User guide and application. <http://viceroy.eeb.uconn.edu/estimates/index.html>.
- Coppins, B.J., 1983. A taxonomic study of the lichen genus *Micarea* in Europe. *Bulletin of the British Museum (Natural History), Botany series* 11, 17–214.
- Crites, S., Dale, M.R.T., 1998. Diversity and abundance of bryophytes, lichens, and fungi in relation to woody substrate and successional stage in aspen mixedwood boreal forests. *Can. J. Bot.* 76, 641–651. doi:10.1139/cjb-76-4-641.
- Culberson, C.F., Kristinsson, H.D., 1970. A standardized method for the identification of lichen products. *Journal of Chromatography A* 46, 85–93.
- Czarnota, P., 2007. The lichen genus *Micarea* (Lecanorales, Ascomycota) in Poland. *Polish Botanical Studies* 23, 190 p.
- Forsslund, A., Koffman, A., 1998. Species diversity of lichens on decaying wood: a comparison between old-growth and managed forest. *Växt-ekologi, Botaniska Institutionen, Stockholms Universitet*. pp. 1–40.
- Foucard, T., 2001. Svenska skorplavar och svampar som växer på dem. *Stenströms Bokförlag*, pp. 392.

- Fridman, J., Walheim, M., 2000. Amount, structure and dynamics of dead wood on managed forestland in Sweden. *Forest Ecology and Management* 131, 23–36.
- Gauslaa, Y., Solhaug, K.A., 2000. High-light-intensity damage to the foliose lichen *Lobaria pulmonaria* within a natural forest: the applicability of chlorophyll fluorescence methods. *Lichenologist* 32, 271–289. doi:10.1006/lich.1999.0265.
- Gauslaa, Y., Lie, M., Solhaug, K.A., Ohlson, M. 2006. Growth and ecophysiological acclimation of the foliose lichen *Lobaria pulmonaria* in forests with contrasting light climates. *Oecologia (Berl.)*, 147, 406–416. doi:10.1007/s00442-005-0283-1
- Guzow-Krzemińska, B., Czarnota, P., Łubek, A., Kukwa, M. 2016. *Micarea soralifera* sp. nov., a new sorediate species in the *M. prasina* group. *Lichenologist* 48: 161–169.
- Graham, D.J., Midgley, N.G. 2000. Graphical representation of particle shape using triangular diagrams: an Excel spreadsheet method. *Earth. Surf. Proc. Land.*, 25, 1473-1477.
- Halme, P., Ódor, P., Christensen, M., Piltaver, A., Veerkamp, M., Walley, R., Siller, I., Heilmann-Clausen, J. 2013. The effects of habitat degradation on metacommunity structure of wood-inhabiting fungi in European beech forests. *Biological Conservation* 168, 24–30. 10.1016/j.biocon.2013.08.034.
- Halonen, P., Hyvärinen, M., Kauppi, M., 1991. The Epiphytic Lichen Flora on Conifers in Relation to Climate in the Finnish Middle Boreal Subzone. *The Lichenologist* 23, 61–72. doi:10.1017/S0024282991000117
- Herben, T., Rydin, H., Söderström, L., 1991. Spore establishment probability and the persistence of the fugitive invading moss, *Orthodontium lineare*: a spatial simulation model. *Oikos* 60, 215–221.
- Hilmo O, Holien H, Hytteborn H, Ely-Aalstrup H., 2009. Richness of epiphytic lichens in differently aged *Picea abies* plantations situated in the oceanic region of central Norway. *Lichenologist* 41, 97–108.
- Hyvärinen, M., Halonen, P., Kauppi, M., 1992. Influence of stand age and structure on epiphytic lichen vegetation in middle-boreal forests of Finland. *Lichenologist* 24, 165–180.
- Hyvärinen, E., Juslén, A., Kemppainen, E., Uddström, A., Liukko, U.-M. 2019. The 2019 Red List of Finnish Species. Ministry of the Environment & Finnish Environment Institute. Helsinki. 704 p.
- Jansová, I., Soldán, Z., 2006. The habitat factors that affect the composition of bryophyte and lichen communities on fallen logs. *Preslia (Prague)* 78, 67–86
- Johansson, P., Gustafsson, L., 2001. Red-listed and indicator lichens in woodland key habitats and production forests in Sweden. *Can J For Res.* 31, 1617–1628.
- Jüriado, I., Paal, J., Liira, J., 2003. Epiphytic and epixylic lichen species diversity in Estonian natural forests. *Biodiversity and Conservation* 12, 1587–1607. 10.1023/A:1023645730446.
- Kalela, A. 1961. Waldvegetationszonen Finnlands und ihre Klimatischen paralleltypen. *Archiv. Soc. Zool. Bot. Fenn. Vanamo* 16: 65-83.
- Kantvilas, G., Minchin, P., 1989. An analysis of epiphytic lichen communities in Tasmanian cool temperate rainforest. *Vegetatio*. 84, 99–112. 10.1007/BF00036510.

- Kantvilas, G., Jarman, S.J., 2006. Recovery of lichens after logging: preliminary results from Tasmania's wet forests. *Lichenologist* 38, 383–394.
- Kruys, N., Jonsson, B.G., 1997. Insular patterns of Calicioid lichens in a boreal old-growth forest-wetland mosaic. *Ecography* 20, 605–613. doi:10.1111/j.1600-0587.1997.tb00429.x.
- Kruys, N., Fries, C., Jonsson, B.G., Lamas, T., Stal, G., 1999. Wood-inhabiting cryptogams on dead Norway spruce (*Picea abies*) trees in managed Swedish boreal forests. *Can. J. For. Res.* 29, 178–186. doi:10.1139/cjfr-29-2-178.
- Kuusinen, M., 1996. Epiphyte flora and diversity on basal trunks of six old-growth forest tree species in southern and middle boreal Finland. *Lichenologist* 28, 443–463. doi:10.1006/lich.1996.0043
- Kuusinen, M., Siitonen, J., 1998. Epiphytic lichen diversity in old-growth and managed *Picea abies* stands in southern Finland. *J Veg Sci.*, 9, 283–292.
- Lange, O.L., Leisner, J.M.R., Bilger, W., 1999. Chlorophyll fluorescence characteristics of the cyanobacterial lichen *Peltigera rufescens* under field conditions. II. Diel and annual distribution of metabolic activity and possible mechanisms to avoid photoinhibition. *Flora* 194, 413–430.
- Launis, A., Myllys, L., 2019. *Micarea fennica*, a new lignicolous lichen species from Finland. *Phytotaxa* 409, 179–188.
- Linder, P., Östlund, L., 1998. Structural changes in three mid-boreal Swedish forest landscapes, 1885-1996. *Biological Conservation* 85, 9–19.
- Lommi, S., Berglund, H., Kuusinen, M., Kuuluvainen, T., 2010. Epiphytic lichen diversity in late-successional *Pinus sylvestris* forests along local and regional forest utilization gradients in eastern boreal Fennoscandia. *Forest Ecology and Management* 259, 883–892. <https://doi.org/10.1016/j.foreco.2009.11.028>
- Lõhmus, P., Lõhmus, A., 2001. Snags and their lichen flora in old Estonian peatland forests. – *Annales Botanici Fennici* 38, 265-280.
- Lõhmus, A., Lõhmus, P., 2011. Old-forest species: the importance of specific substrata vs. stand continuity in the case of calicioid fungi. *Silva Fenn.* 45, 1015e1039.
- Malíček, J., Palice, Z., Vondrak, J., Kostovcik, M., Lenzová, V., Hofmeister, J., 2019. Lichens in old-growth and managed mountain spruce forests in the Czech Republic: assessment of biodiversity, functional traits and bioindicators. *Biodiversity and Conservation* 1–32. 10.1007/s10531-019-01834-4.
- McCullough, H.E., 1948. Plant succession on fallen logs in a virgin spruce-fir forest. *Ecology* 29, 508–513. doi:10.2307/1932645.
- Muhle, H., LeBlanc, F., 1975. Bryophyte and lichen succession on decaying logs. 1. Analysis along an evaporational gradient in eastern Canada. *J. Hattori Bot. Lab.* 39, 1–33.
- Myllys, L., Lohtander, K., Källersjö, M., Tehler, A., 1999. Sequence insertion and ITS data provide congruent information in *Rocella canariensis* and *R. tuberculata* (Arthoniales, Euascomycetes) phylogeny. *Molecular Phylogenetics and Evolution* 12, 295–309.

- Myllys, L., Velmala, S., Holien, H., Halonen, P., Wang, L.S., Goward, T., 2011. Phylogeny of the genus *Bryoria*. *Lichenologist* 43, 617–638.
- Myllys, L., Launis, A., 2018. Additions to the diversity of lichens and lichenicolous fungi living on decaying wood in Finland. *Graphis scripta* 30, 78–87.
- Nascimbene, J., Marini, L., Nimis, P.L., 2010. Epiphytic lichen diversity in old-growth and managed *Picea abies* stands in Alpine spruce forests. *For Ecol Manage.* 260, 603–609.
- Neitlich, P.N., McCune, B., 1997. Hot-spots of Epiphytic Lichen Diversity in Two Young Managed Forests. *Conserv Biol.* 11, 172–182.
- Nirhamo, A., Pykälä, J., Halme, P., Komonen, A., 2021. Lichen communities on *Populus tremula* are affected by the density of *Picea abies*. *Appl. Veg. Sci.* 24, 1–9.
<https://doi.org/10.1111/avsc.12584>
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2019. *vegan*: Community Ecology Package. R package version 2.5-6. <https://CRAN.R-project.org/package=vegan>
- Orange, A., James, P.W., White, F.J., 2010. Microchemical methods for the identification of lichens. *British Lichen Society* 44–45.
- Paillet, Y., Bergès, L., Hjältén, J., Odor, P., Avon, C., Bernhardt-Römermann, M., 2010. Biodiversity Differences between Managed and Unmanaged Forests: Meta-Analysis of Species Richness in Europe. *Conserv Biol.* 24, 101–112. <https://doi.org/10.1111/j.1523-1739.2009.01399.x> PMID: 20121845
- Podani, J., Schmera, D. 2011. A new conceptual and methodological framework for exploring and explaining pattern in presence–absence data. *Oikos* 120, 1625–1638.
- Pykälä, J., Jääskeläinen, K., Rämä, H., Launis, A., Vitikainen, O. & Puolasmaa, A., 2019. Lichens. In: Hyvärinen, E., Juslén, A., Kemppainen, E., Uddström, A. & Liukko, U.-M. (eds.) 2019. The 2019 Red List of Finnish Species. Ministry of the Environment & Finnish Environment Institute. Helsinki. P. 263–312.
- Renvall, P. 1995. Community structure and dynamics of wood-rotting Basidiomycetes on decomposing conifer trunks in northern Finland. *Karstenia* 35, 1–51.
- Resl, P., Fernández-Mendoza, F., Mayrhofer, H., Spribille, T., 2018. The evolution of fungal substrate specificity in a widespread group of crustose lichens. *Proc. R. Soc. B.* 285, 20180640. <http://dx.doi.org/10.1098/rspb.2018.0640>
- Rikkinen, J., 2003. Calicioid lichens and fungi in the forests and woodlands of western Oregon. *Acta Bot. Fenn.* 175, 1–41.
- Rogers, R. W., 1990. Ecological strategies of lichens. *Lichenologist* 22, 149–162.
- Rogers, R. W., Barnes, A., 1986. Leaf demography of the rain forest shrub *Wilkiea macrophylla* and its implications for the ecology of foliicolous lichens. *Australian journal of Ecology* 11, 341–345.

- Rudolphi, J., Gustafsson, L., 2011. Forests regenerating after clear-cutting function as habitat for bryophyte and lichen species of conservation concern PLoS One 6, e18639
- Saine, S., Aakala, T., Purhonen, J., Launis, A., Tuovila, H., Kosonen, T., & Halme, P., 2018. Effects of local forest continuity on the diversity of fungi on standing dead pines. *Forest Ecology and Management* 409, 757–765. <https://doi.org/10.1016/j.foreco.2017.11.045>
- Selva, S.B., 1994. Lichen diversity and stand continuity in the northern hardwoods and spruce-fir forests of northern New England and western New Brunswick. *Bryologist*, 97, 424–429. doi:10.2307/3243911.
- Selva, S.B., 2003. Using calicoid lichens and fungi to assess ecological continuity in the Acadian Forest Ecoregion of the Canadian Maritimes. *Forestry Chron.* 79, 550–558.
- Siitonen, J., 2001. Forest management, coarse woody debris, and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological Bulletins* 49, 11–41.
- Sillett, S.C., McCune, B., Peck, J.E., Rambo, T.R., Ruchty, A., 2000. Dispersal limitations of epiphytic lichens result in species dependent on old-growth forests. *Ecol. Appl.* 10, 789–799. doi:10.1890/1051-0761(2000)010[0789:DLOELR]2.0.CO;2.
- Sillett, S.C., Antoine, M.E., 2004. Lichens and bryophytes in forest canopies. In *Forest canopies*. 2nd ed. Edited by M.D. Lowman and H.B. Rinker. Elsevier Academic Press, Oxford, UK. pp. 151–174.
- Smith, C.W., Aptroot, A., Coppins, B.J., Fletcher, A., Gilbert, O.L., James, P.W., Wolseley, P.A. (eds.). 2009. *The Lichens of Great Britain and Ireland*. British Lichen Society, pp. 1046.
- Spribile, T., Thor, G., Bunnell, F.L., Goward, T., Björk, C.R., 2008. Lichens on dead wood: species-substrate relationships in the epiphytic lichen floras of the Pacific Northwest and Fennoscandia. *Ecography* 31, 741–750.
- Spribile, T., Resl, P., Ahti, T., Pérez-Ortega, S., Mayrhofer, H., Lumbsch, H.T., 2014. Molecular systematics of the wood-inhabiting, lichen-forming genus *Xylographa* (Baeomycetales, Ostropomycetidae) with eight new species. *Symbolae Botanicae Upsalienses* 37, 1–87.
- Stenroos, S., Velmala, S., Pykälä, J., Ahti, T., 2016. *Lichens of Finland*. Finnish Museum of Natural History, pp. 895.
- Stokland, J.N., Siitonen, J., Jonsson, B.G., 2012. *Biodiversity in dead wood*. Cambridge University Press, Cambridge, pp. 412.
- Svensson, M., Johansson, V., Dahlberg, A., Frisch, A., Thor, G., 2016. The relative importance of stand and dead wood types for wood-dependent lichens in managed boreal forests. *Fungal Ecology* 20: 166–174.
- Tibell, L., 1992. Crustose lichens as indicators of forest continuity in boreal coniferous forests. *Nord J Bot.* 12, 427–450.
- Ulizcka, H., Angelstam, P., 1999. Occurrence of epiphytic macrolichens in relation to tree species and age in managed boreal forest. *Ecography* 22, 396–405.
- Yarranton, G. A., 1972. Distribution and succession of epiphytic lichens on Black Spruce near Cochrane, Ontario. *Bryologist* 75, 462–480.

- Vaahtera, E., Aarne, M., Ihalainen, A., Mäki-Simola, E., Peltola, A., Torvelainen, J., Uotila, E., Ylitalo, E. eds. 2018. Finnish Forest Statistics. Helsinki: Natural Resources Institute Finland (Luke), Available online: <http://urn.fi/URN:NBN:fi-fe201902043966>
- Vamosi, J.C., Armbruster, W.S., Renner, S.S., 2014. Evolutionary ecology of specialization: insights from phylogenetic analysis. *Proc. R. Soc. B.* 281, 20142004. doi:10.1098/rspb.2014.2004
- Vondrák, J., Malíček, J., Šoun, J., Pouska, V., 2015. Epiphytic lichens of Stučica (E Slovakia) in the context of Central European old-growth forests. *Herzogia* 28, 104–126.
- Vondrák, J., Malíček, J., Palice, Z., Bouda, F., Berger, F., Sanderson, N., Acton, A., Pouska, V., Kish, R., 2018. Exploiting hot-spots; effective determination of lichen diversity in a Carpathian virgin forest. *PLoS ONE*. <https://doi.org/10.1371/journal.pone.0203540>
- Vondrák, J., Urbanavichus, G., Palice, Z., Malíček, J., Urbanavichene, I., Kubásek, J., Ellis, J. 2019. The epiphytic lichen biota of Caucasian virgin forests: a comparator for European conservation. *Biodivers Conserv* 28, 3257–3276. <https://doi.org/10.1007/s10531-019-01818-4>
- Walser, J.C., Zoller, S., Büchler, U., Scheidegger, C., 2001. Species-specific detection of *Lobaria pulmonaria* (lichenized ascomycete) diaspores in litter samples trapped in snow cover. *Mol. Ecol.* 10, 2129–2138. doi:10.1046/j.1365-294X.2001.01353.x.
- White, T.J., Bruns, T., Lee, S., Taylor, J.W., 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis, M.A., Gelfand, D.H., Sninsky, J.J., White, T.J., eds. *PCR protocols: A guide to the methods and applications*. New York, NY: Academic Press. p. 315–322.
- Wilhere, G.F., 2003. Simulations of snag dynamics in an industrial douglas-fir forest. *Forest Ecology and Management* 174, 521–539.
- Zoller, S., Scheidegger, C., Sperisen, C., 1999. PCR primers for the amplification of mitochondrial small subunit ribosomal DNA of lichen-forming ascomycetes. *Lichenologist* 31, 511–516.

Table 2. List of species on decaying *Picea abies*, their growth form and ecology based on literature, Finnish Red List assessment 2019 (Pykälä et al.) and number of occurrences in managed (MF) and natural forests (NF).

Species	Growth form	Ecology based on literature	Red List assesment	Number of logs on which found		
				MF	NF	Total
<i>Absconditella lignicola</i>	Crustose	Obligate	LC	20	19	39
<i>Biatora chrysantha</i>	Crustose	Facultative	LC	3	0	3
<i>Biatora efflorescens</i>	Crustose	Facultative	LC	4	2	6
<i>Biatora fallax</i>	Crustose	Facultative	VU	1	4	5
<i>Biatora globulosa</i>	Crustose	Facultative	LC	2	1	3
<i>Biatora helvola</i>	Crustose	Facultative	LC	5	1	6
<i>Biatora cf. helvola</i>	Crustose	not known	not assessed	1	2	3
<i>Biatora meiocarpa</i>	Crustose	Facultative	LC	0	1	1
<i>Biatora ocelliformis</i>	Crustose	Facultative	LC	1	1	2
<i>Calicium viride</i>	Crustose	Facultative	LC	1	0	1
<i>Cetrariella delisei</i>	Macro: fruticose	Facultative	LC	0	1	1
<i>Chaenotheca brunneola</i>	Crustose	Obligate	LC	0	2	2
<i>Chaenotheca chlorella</i>	Crustose	Facultative	NT	0	1	1
<i>Chaenotheca chrysocephala</i>	Crustose	Facultative	LC	0	2	2
<i>Chaenotheca ferruginea</i>	Crustose	Facultative	LC	2	1	3
<i>Chaenotheca gracillima</i>	Crustose	Facultative	NT	0	1	1
<i>Chaenotheca laevigata</i>	Crustose	Facultative	VU	0	1	1
<i>Chaenotheca stemonea</i>	Crustose	Facultative	VU	0	1	1
<i>Chaenotheca trichialis</i>	Crustose	Facultative	LC	1	0	1
<i>Chaenothecopsis consociata</i>	Crustose	Lichenicolous	LC	0	1	1
<i>Chaenothecopsis pusilla</i>	Crustose	Facultative/lichenicolous	LC	0	1	1
<i>Chaenothecopsis savonica</i>	Crustose	Lichenicolous/facultative	LC	0	2	2
<i>Chaenothecopsis sp.</i>	Crustose	Not known	not assessed	1	0	1
<i>Chaenothecopsis viridireagens</i>	Crustose	Lichenicolous/facultative	NT	1	1	2
<i>Cladonia arbuscula</i>	Macro: fruticose	Facultative	LC	7	6	13
<i>Cladonia bacilliformis</i>	Macro: foliose	Obligate	LC	1	1	2
<i>Cladonia botrytes</i>	Macro: foliose	Facultative	LC	12	4	16
<i>Cladonia carneola</i>	Macro: foliose	Facultative	LC	3	0	3
<i>Cladonia cenotea</i>	Macro: foliose	Facultative	LC	4	8	12
<i>Cladonia chlorophaea</i>	Macro: foliose	Facultative	LC	0	4	4
<i>Cladonia cf. chlorophaea</i>	Macro: foliose	Not known	not assessed	0	2	2
<i>Cladonia coniocrea</i>	Macro: foliose	Facultative	LC	38	45	83
<i>Cladonia crispata</i>	Macro: fruticose	Facultative	LC	1	0	1
<i>Cladonia cyanipes</i>	Macro: foliose	Facultative	LC	1	0	1
<i>Cladonia deformis</i>	Macro: foliose	Facultative	LC	2	0	2
<i>Cladonia digitata</i>	Macro: foliose	Facultative	LC	15	17	32
<i>Cladonia fimbriata</i>	Macro: foliose	Facultative	LC	14	10	24
<i>Cladonia gracilis</i>	Macro: foliose	Facultative	LC	3	0	3
<i>Cladonia grayi</i>	Macro: foliose	Facultative	LC	10	6	16

<i>Cladonia macilenta</i>	Macro: foliose	Facultative	LC	2	1	3
<i>Cladonia norvegica</i>	Macro: foliose	Facultative	NT	8	13	21
<i>Cladonia ochrochlora</i>	Macro: foliose	Facultative	LC	0	1	1
<i>Cladonia parasitica</i>	Macro: foliose	Obligate	VU	1	1	2
<i>Cladonia pyxidata</i>	Macro: foliose	Facultative	LC	1	1	2
<i>Cladonia rangiferina</i>	Macro: fruticose	Facultative	LC	1	0	1
<i>Cladonia squamosa</i>	Macro: foliose	Facultative	LC	2	8	10
<i>Cladonia sulphurina</i>	Macro: foliose	Facultative	LC	2	7	9
<i>Cladonia symphycarpa</i>	Macro: foliose	Facultative	LC	0	1	1
<i>Coenogonium pineti</i>	Crustose	Facultative	LC	14	11	25
<i>Epigloea urosperma</i>	lichenicolous	Lichenicolous	LC	9	10	19
<i>Fellhanera subtilis</i>	Crustose	Facultative	LC	1	2	3
<i>Frutidella pullata</i>	Crustose	Facultative	LC	1	1	2
<i>Hypocenomyce scalaris</i>	Crustose	Facultative	LC	1	3	4
<i>Hypogymnia physodes</i>	Macro: fruticose	Facultative	LC	6	16	22
<i>Icmadophila ericetorum</i>	Crustose	Facultative	LC	0	1	1
<i>Lecania furfuracea</i>	Crustose	Facultative	not assessed	0	1	1
<i>Lecanora pulicaris</i>	Crustose	Facultative	LC	1	0	1
<i>Lecanora symmicta</i>	Crustose	Facultative	LC	1	0	1
<i>Lecidea albofuscescens</i> s.lato	Crustose	Facultative	NT	0	1	1
<i>Lecidea leprarioides</i>	Crustose	Facultative	LC	0	1	1
<i>Lecidea nylanderii</i>	Crustose	Facultative	LC	1	1	2
<i>Lecidea turgidula</i>	Crustose	Facultative	LC	1	1	2
<i>Lepraria caesioalba</i>	Crustose	Facultative	LC	0	4	4
<i>Lepraria elobata</i>	Crustose	Facultative	LC	6	0	6
<i>Lepraria finkii</i>	Crustose	Facultative	LC	0	2	2
<i>Lepraria incana</i>	Crustose	Facultative	LC	0	2	2
<i>Lepraria jackii</i>	Crustose	Facultative	LC	20	35	55
<i>Lepraria sp 3</i>	Crustose	not known	not assessed	1	0	1
<i>Lepraria sp 1</i>	Crustose	not known	not assessed	0	2	2
<i>Lepraria sp 2</i>	Crustose	not known	not assessed	0	4	4
<i>Loxospora elatina</i>	Crustose	Facultative	LC	0	2	2
<i>Micarea anterior</i>	Crustose	Obligate	NT	9	13	22
<i>Micarea byssacea</i>	Crustose	Facultative	LC	2	10	12
<i>Micarea contexta</i>	Crustose	Obligate	NT	7	19	26
<i>Micarea denigrata</i>	Crustose	Obligate	LC	3	2	5
<i>Micarea elachista</i>	Crustose	Facultative	VU	2	2	4
<i>Micarea globulosella</i>	Crustose	Facultative	NT	2	6	8
<i>Micarea hedlundii</i>	Crustose	Obligate	VU	2	2	4
<i>Micarea melaena</i>	Crustose	Facultative	LC	6	10	16
<i>Micarea melaeniza</i>	Crustose	Obligate	DD	0	1	1
<i>Micarea micrococca</i>	Crustose	Facultative	LC	13	8	21
<i>Micarea micrococca</i> agg.	Crustose	Facultative	not assessed	1	0	1
<i>Micarea misella</i>	Crustose	Obligate	LC	24	17	41
<i>Micarea nigella</i> s.str. (clade 3)	Crustose	Obligate	DD	2	3	5
<i>Micarea nigella</i> -group (clade 1)	Crustose	not known	not assessed	1	1	2
<i>Micarea nigella</i> -group (clade 2)	Crustose	not known	not assessed	2	0	2
<i>Micarea nigella</i> -group (clade 4)	Crustose	not known	not assessed	5	4	9

<i>Micarea nowakii</i>	Crustose	Obligate	DD	1	1	2
<i>Micarea peliocarpa</i>	Crustose	Facultative	LC	0	1	1
<i>Micarea prasina</i>	Crustose	Facultative	LC	32	42	74
<i>Micarea pusilla</i>	Crustose	Facultative	not assessed	2	0	2
<i>Micarea fallax</i>	Crustose	Facultative	not assessed	3	5	8
<i>Micarea microareolata</i>	Crustose	Facultative	not assessed	0	1	1
<i>Micarea laeta</i>	Crustose	Facultative	not assessed	4	1	5
<i>Micarea pseudomicrococca</i>	Crustose	Facultative	not assessed	0	1	1
<i>Micarea czarnotae</i>	Crustose	Facultative	not assessed	1	0	1
<i>Micarea</i> sp 1	Crustose	not known	not assessed	1	0	1
<i>Micarea</i> sp 2	Crustose	not known	not assessed	1	0	1
<i>Micarea</i> sp 3	Crustose	not known	not assessed	0	1	1
<i>Micarea tomentosa</i>	Crustose	Obligate	VU	0	2	2
<i>Mycoblastus affinis</i>	Crustose	Facultative	LC	1	0	1
<i>Mycoblastus sanguinarius</i>	Crustose	Facultative	LC	0	0	1
<i>Ochrolechia androgyna</i>	Crustose	Facultative	LC	0	4	4
<i>Ochrolechia microstictoides</i>	Crustose	Facultative	LC	0	1	1
<i>Opegrapha niveoatra</i>	Crustose	Facultative	NT	0	1	1
<i>Parmeliopsis ambigua</i>	Macro: foliose	Facultative	LC	13	13	26
<i>Parmeliopsis hyperopta</i>	Macro: foliose	Facultative	LC	4	16	20
<i>Peltigera degenii</i>	Macro: foliose	Facultative	LC	0	1	1
<i>Peltigera praetextata</i>	Macro: foliose	Facultative	LC	0	1	1
<i>Placynthiella dasae</i>	Crustose	Facultative	LC	27	33	60
<i>Placynthiella icmalea</i>	Crustose	Facultative	LC	27	30	57
<i>Platismatia glauca</i>	Macro: foliose	Facultative	LC	4	9	13
<i>Puttea margaritella</i>	Crustose	Facultative	NT	1	3	4
<i>Steinia geophana</i>	Crustose	Facultative	LC	0	1	1
<i>Thelocarpon depressellum</i>	Crustose	Obligate	VU	0	1	1
<i>Thelocarpon intermediellum</i>	Crustose	Facultative	NT	10	2	12
<i>Thelocarpon lichenicola</i>	Crustose	Facultative	LC	2	0	2
<i>Thelocarpon strasseri</i>	Crustose	Obligate	VU	1	4	5
<i>Trapeliopsis flexuosa</i>	Crustose	Facultative	LC	14	17	31
<i>Trapeliopsis granulosa</i>	Crustose	Facultative	LC	1	0	1
<i>Vulpicida pinastri</i>	Macro: foliose	Facultative	LC	28	21	49
<i>Xylographa parallela</i>	Crustose	Obligate	LC	0	1	1
<i>Xylographa soralifera</i>	Crustose	Facultative	LC	11	18	29
<i>Xylographa trunciseda</i>	Crustose	Obligate	VU	0	2	2
<i>Xylographa vitiligo</i>	Crustose	Obligate	LC	0	7	7
<i>Xylopsora friesii</i>	Crustose	Obligate	LC	0	1	1

Table 5. Lichen species on *Picea abies* found on decay stages 2-5.

Decay stage 2 (82 taxa)	Decay stage 3 (74 taxa)	Decay stage 4 (62 taxa)	Decay stage 5 (31 taxa)
Absconditella lignicola	Absconditella lignicola	Absconditella lignicola	Absconditella lignicola
Biatora cf. helvola	Biatora chrysantha	Biatora chrysantha	Cladonia coniocrea
Biatora chrysantha	Biatora efflorescens	Biatora efflorescens	Cladonia deformis
Biatora efflorescens	Biatora globulosa	Biatora fallax	Cladonia digitata
Biatora fallax	Biatora helvola	Biatora ocelliformis	Cladonia grayi
Biatora globulosa	Chaenotheca chlorella	Chaenotheca chrysocephala	Cladonia macilenta
Biatora helvola	Chaenotheca chrysocephala	Chaenothecopsis savonica	Cladonia norvegica
Biatora ocelliformis	Chaenotheca gracillima	Chaenothecopsis viridireagens	Cladonia rangiferina
Calicium viride	Chaenothecopsis consociata	Cladonia arbuscula	Cladonia symphylicarpa
Cetrariella delisei	Chaenothecopsis savonica	Cladonia botrytes	Coenogonium pineti
Chaenotheca brunneola	Cladonia arbuscula	Cladonia cenotea	Epigloea urosperma
Chaenotheca ferruginea	Cladonia bacilliformis	Cladonia chlorophaea	Hypocenomyce scalaris
Chaenotheca trichialis	Cladonia botrytes	Cladonia coniocrea	Hypogymnia physodes
Chaenothecopsis sp	Cladonia carneola	Cladonia digitata	Lepraria jackii
Cladonia arbuscula	Cladonia cenotea	Cladonia fimbriata	Micarea denigrata
Cladonia bacilliformis	Cladonia chlorophaea	Cladonia gracilis	Micarea hedlundii
Cladonia botrytes	Cladonia coniocrea	Cladonia grayi	Micarea melaena
Cladonia carneola	Cladonia cyanipes	Cladonia norvegica	Micarea melaeniza
Cladonia cenotea	Cladonia digitata	Cladonia ochrochlora	Micarea micrococca
Cladonia coniocrea	Cladonia fimbriata	Cladonia pyxidata	Micarea misella
Cladonia crispata	Cladonia gracilis	Cladonia squamosa	Micarea nigella clade 2
Cladonia deformis	Cladonia grayi	Cladonia sulphurina	Micarea nigella clade 3
Cladonia digitata	Cladonia macilenta	Coenogonium pineti	Micarea nigella str.
Cladonia fimbriata	Cladonia norvegica	Epigloea urosperma	Micarea prasina
Cladonia grayi	Cladonia pyxidata	Hypocenomyce scalaris	Micarea sp. 1
Cladonia macilenta	Cladonia squamosa	Hypogymnia physodes	Micarea tomentosa
Cladonia norvegica	Cladonia sulphurina	Lepraria caesioalba	Placynthiella dasae
Cladonia parasitica	Coenogonium pineti	Lepraria elobata	Placynthiella icmalea
Cladonia squamosa	Epigloea urosperma	Lepraria jackii	Thelocarpon intermediellum
Cladonia sulphurina	Fellhanera subtilis	Micarea anterior	Trapeliopsis flexuosa
Cladoniasulphurina	Hypogymnia physodes	Micarea byssacea	Vulpicida pinastri
Coenogonium pineti	Lecanora symmicta	Micarea contexta	
Epigloea urosperma	Lecidea turgidula	Micarea czarnotae	
Fellhanera subtilis	Lepraria caesioalba	Micarea fallax	
Frutidella pullata	Lepraria elobata	Micarea globulosella	
Hypocenomyce scalaris	Lepraria finkii	Micarea hedlundii	
Hypogymnia physodes	Lepraria jackii	Micarea laeta	
Icmadophila ericetorum	Lepraria sp 2	Micarea melaena	
Lecania furfuracea	Micarea anterior	Micarea microareolata	
Lecanora pulicaris	Micarea byssacea	Micarea micrococca	
Lecidea			
albofuscenscens.lato	Micarea contexta	Micarea misella	
Lecidea nylanderii	Micarea contexta	Micarea nigella clade 2	
Lecidea turgidula	Micarea denigrata	Micarea prasina	
Lepraria elobata	Micarea fallax	Micarea sp 3	
Lepraria incana	Micarea globulosella	Mycoblastus sanguinarius	
Lepraria jackii	Micarea hedlundii	Ochrolechia androgyna	

Lepraria sp 1	Micarea laeta	Opegrapha niveoatra
Lepraria sp 2	Micarea melaena	Parmeliopsis ambigua
Loxospora elatina	Micarea micrococca	Parmeliopsis hyperopta
Micarea anterior	Micarea misella	Peltigera degenii
Micarea byssacea	Micarea nigella clade 2	Peltigera praetextata
Micarea contexta	Micarea nigella clade 4	Placynthiella dasae
Micarea elachista	Micarea nigella str.	Placynthiellaicmalea
Micarea fallax	Micarea nowakii	Platismatia glauca
Micarea globulosella	Micarea prasina	Steinia geophana
Micarea laeta	Micarea pseudomicrococca	Thelocarpon intermediellum
Micarea melaena	Micarea tomentosa	Thelocarpon lichenicola
Micarea micrococca	Mycoblastus sanguinarius	Thelocarpon strasseri
Micarea nigella clade 3	Parmeliopsis ambigua	Trapeliopsis flexuosa
Micarea nigella str.	Parmeliopsis hyperopta	Vulpicida pinastri
Micarea nowakii	Placynthiella dasae	Xylographa soralifera
Micarea peliocarpa	Placynthiellaicmalea	Xylographa vitiligo
Micarea prasina	Platismatia glauca	
Micarea pusilla	Puttea margaritella	
Micarea soralifera	Thelocarpon intermediellum	
Micarea sp 2	Thelocarpon lichenicola	
Mycoblastus affinis	Thelocarpon strasseri	
Mycoblastus sanguinarius	Trapeliopsis flexuosa	
	Trapeliopsis	
Parmeliopsis ambigua	pseudogranulosa	
Parmeliopsis hyperopta	Vulpicida pinastri	
Placynthiella dasae	Xylographa parallela	
Placynthiella icmalea	Xylographa soralifera	
Platismatia glauca	Xylographa trunciseda	
Thelocarpon depressellum	Xylographa vitiligo	
Thelocarpon intermediellum		
Thelocarpon strasseri		
Trapeliopsis flexuosa		
Vulpicida pinastri		
Xylographa soralifera		
Xylographa trunciseda		
Xylographa vitiligo		
Xylopsora friesii		