

<https://helda.helsinki.fi>

---

## Growth form matters-Crustose lichens on dead wood are sensitive to forest management

Kantelinen, Annina

2022-11-15

---

Kantelinen , A , Purhonen , J , Halme , P & Myllys , L 2022 , ' Growth form matters-Crustose lichens on dead wood are sensitive to forest management ' , Forest Ecology and Management , vol. 524 , 120529 . <https://doi.org/10.1016/j.foreco.2022.120529>

---

<http://hdl.handle.net/10138/350455>

<https://doi.org/10.1016/j.foreco.2022.120529>

---

cc\_by

publishedVersion

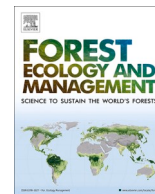
---

*Downloaded from Helda, University of Helsinki institutional repository.*

*This is an electronic reprint of the original article.*

*This reprint may differ from the original in pagination and typographic detail.*

*Please cite the original version.*



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

Annina Kantelinen<sup>a,\*</sup>, Jenna Purhonen<sup>b,c,d,e</sup>, Panu Halme<sup>c,e</sup>, Leena Myllys<sup>a</sup>

<sup>a</sup> Botany Unit, Finnish Museum of Natural History, P.O. Box 7, FI-00014 University of Helsinki, Helsinki, Finland

<sup>b</sup> Biodiversity Unit, University of Turku, FI-20014 Turku, Finland

<sup>c</sup> Department of Biological and Environmental Science, University of Jyväskylä, P.O. Box 35, FIN-40014 Jyväskylä, Finland

<sup>d</sup> Zoology Unit, Finnish Museum of Natural History, P.O. Box 7, FI-00014 University of Helsinki, Helsinki, Finland

<sup>e</sup> School of Resource Wisdom, University of Jyväskylä, P.O. Box 35, FIN-40014 University of Jyväskylä, Jyväskylä, Finland

### ARTICLE INFO

#### Keywords:

Wood-inhabiting species

Conservation

Red listed lichens

Boreal forests

### 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, both for which species richness was higher on logs than on stumps, as well as on the communities of crustose lichens.

### 1. Introduction

Dead wood is crucially important for forest biodiversity (e.g. Löhmus and 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 and 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 and Walheim, 2000; Siitonen, 2001; Brassard and 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; Malíček et al., 2019), and

\* Corresponding author.

E-mail address: [annina.kantelinen@helsinki.fi](mailto:annina.kantelinen@helsinki.fi) (A. Kantelinen).

<https://doi.org/10.1016/j.foreco.2022.120529>

Received 10 May 2022; Received in revised form 5 September 2022; Accepted 7 September 2022

Available online 18 September 2022

0378-1127/© 2022 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

lichens are considered to be one of the most reliable indicators of forest-continuity and forest quality (Johansson and Gustafsson, 2001; Paillet et al., 2010). However, there are also some species that inhabit stumps or slash in young managed forests (Kantvilas and Minchin, 1989; Caruso et al., 2008; Rudolphi and Gustafsson, 2011; Svensson et al., 2016; Kantvilas and 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 and 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; Lohmus and Lohmus, 2011; Bäcklund et al., 2016). In managed forests lichens appear to be particularly vulnerable to thinning of forest canopy (Bunnell et al., 2008; Lohmus and Lohmus, 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 and Solhaug, 2000; Sillett and 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 and 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 and 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 and 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; Krusys and Jonsson, 1997; Crites and Dale, 1998; Forsslund and Koffman, 1998; Krusys et al., 1999; Lohmus and Lohmus, 2001; Jürjado et al., 2003; Caruso et al., 2008; Spribille et al., 2008; Lohmus and Lohmus, 2011; Svensson et al., 2016) 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 and Koffman, 1998; Bunnell et al., 2008). 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 and 5 (Renvald, 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 and 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 knowledge of lichen diversity on dead wood, and also gives important information on how forestry affects crustose lichens.

## 2. 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 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-Myrtilus* and a mesic *Myrtilus* 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

#### 2.2.1. 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, we searched potential managed study sites close to each natural site included in the study. The 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 favored sites with relatively easy access. The managed study sites represent middle-aged *Picea abies* -dominated forests that have a thinning history. Similar to natural forest sites, we looked for sites that include dead wood (the amount is on average lower in managed versus natural forests).

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 80–150 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 kajanaensis province (2 stands, middle boreal zone) located in eastern Finland (Ahti et al., 1968), (Fig. 1).

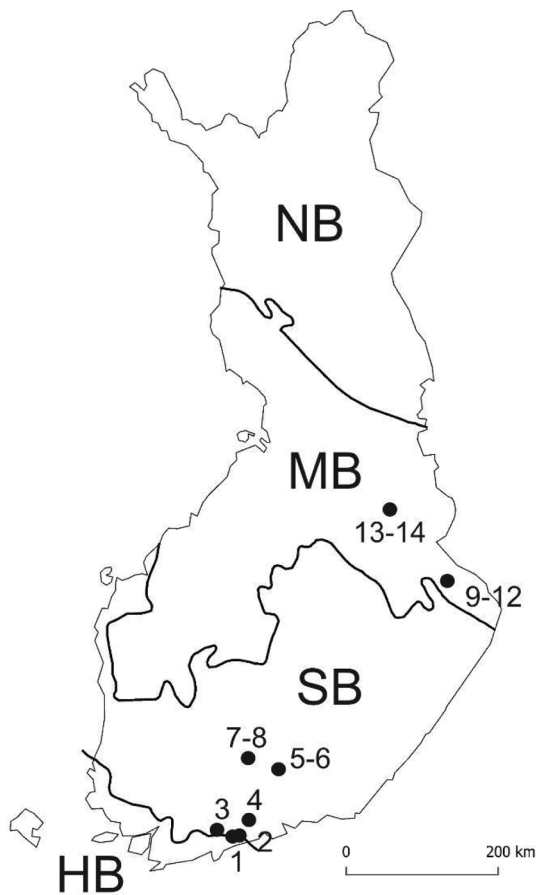
#### 2.2.2. Study plot positioning

Sampling was performed in study plots of 50 m × 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)

**Table 1**

Site information. The consecutive number relates to the site numbers in the Fig. 1. The number in brackets () relates to the geographical grouping used in the analyses. See further information on the dead wood characteristics in the **Supplementary information Table 2**.

	Site	Municipality	Forest age (years)	Forest type	Number of CWD	Number of species	
1	(1)	Herukkapuro	Vantaa	81–100	Natural	41	44 (one cf.)
2	(1)	Korso	Vantaa	61–80	Managed	17	26
3	(1)	Nuuksio	Kirkkonummi	61–80	Managed (lately protected)	34	40
4	(1)	Rörstrand	Sipoo	61–80	Natural	32	18
5	(2)	Iitti2	Iitti	61–80	Managed	20	30
6	(2)	Iitti1	Iitti	41–60	Managed	16	25
7	(2)	Kotinen	Hämeenlinna	126–150	Natural	21	30
8	(2)	Evo	Hämeenlinna	81–100	Managed (lately protected)	10	43
9	(3)	Koli1	Lieksa	126–150	Natural	46	53 (one cf.)
10	(3)	Koli2	Lieksa	126–150	Natural	49	43
11	(3)	Koli3	Lieksa	41–60	Managed	1	28 (one cf.)
12	(3)	Koli4	Lieksa	41–60	Managed	4	19
13	(3)	Rommakkovaara	Sotkamo	126–150	Natural	NA	32 (one cf.)
14	(3)	Vuokatti	Sotkamo	over 150	Natural	27	47 (one cf.)



**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.

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 & McCune, 1997; 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 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).

### 2.2.3. Sampling

Study plots in natural forests were surveyed for 10–16 h and in managed forests 6–10 h. 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, this data missing for site 13) 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; Table 2 in the Supplementary info). The difference in survey times between managed and natural stands is explained mostly by the differences in the size of dead wood units (DWU from hereafter) being 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 and Löhmus, 2001). The uncorticated hard snags, on the other hand, have been studied before quite extensively (Tibell, 1992; Löhmus and Löhmus, 2001; Rikkinen, 2003; Selva, 2003; Löhmus and Löhmus, 2011). Especially in managed stands, the amount of sampled DWUs was sometimes  $<12$  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. Most of the obligate lignicoles are crustose lichens (Table 3 on pages 23–25) that are not known from other substrata (Spribile et al., 2008).

#### 2.3.1. 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; Spribile et al., 2014). Anatomical characters and ascospore dimensions were measured in water. Secondary metabolites of the specimens were identified using

Table 3

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>Absonditella 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 macilentata</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 symphyocarpa</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 s.lato</i>	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

(continued on next page)

Table 3 (continued)

Species	Growth form	Ecology based on literature	Red List assesment	Number of logs on which found		
				MF	NF	Total
<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-group</i> (clade 1)	Crustose	not known	not assessed	1	1	2
<i>Micarea nigella-group</i> (clade 2)	Crustose	not known	not assessed	2	0	2
<i>Micarea nigella-group</i> (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

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 60F-254 pre-coated glass plates with 75 mm/75 µL Haematocrit capillaries (Hirschmann Laborgeräten). Extracts were run in solvent systems A and B (Culberson and Kristinsson, 1970; Orange et al., 2010).

### 2.3.2. 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 and 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 95C followed by five cycles of 30 s at 95C (denaturation), 30 s at 58C (annealing), and 1 min at 72C (extension); for the remaining 40 cycles, the annealing temperature was decreased to 56C; and the PCR program ended with a final extension for 7 min at 72C. 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 95C followed by six cycles of 1 min at 95C (denaturation), 1 min at 62C (annealing), and 105 s at 72C (extension); for the remaining 35 cycles, the annealing temperature was decreased to 56C; and the PCR program ended with a final extension of 10 min at 72C. 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 (<https://www.macrogen.fi>).

## 2.4. Statistical analysis

We illustrated the effect of forest management on the number of species detected from the studied DWU by calculating species accumulation curves with a “specaccum” function of the “vegan” package (Oksanen et al., 2019) for macrolichens, crustose lichens and obligate lignicoles in different forest types (categorical, natural/ managed). We further investigated the stand level relationship between species richness and forest management 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. To account for the landscape level hierarchy of the study design we included the group identity of the stands as a nested random effect.

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 (categorical, natural/managed), decay stage (continuous, 2–5) and dead wood type (categorical, log/stump) as explanatory variables. To account for the landscape (the geographical grouping of stands) and stand-level (DWU within stand) hierarchy of the study design (DWU within stand) we included site identity within group identity as a nested random effect. We utilized the “glmmTMB” function of the package “glmmTMB” to perform both the generalized linear and mixed models (Brooks 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) as an environmental variable. 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 3). 19 species were obligate lignicoles. Of these, 17 were crustose lichens belonging to the genera *Absoconditella*, *Chaenotheca*, *Micarea*, *Thelocarpon* and *Xylographa*, and 2 were macrolichens belonging to the genus *Cladonia* (Table 3). 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), *Lepraria jacksonii* (n = 55) and a macrolichen *Vulpicida pinastri* (n = 49) (Table 3).

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 4). The accumulation curves indicate rather high number on undetected species of crustose lichens.

On DWU-level, forest type did not have significant relationship with any of the studied lichen groups (Table 5). 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 83 taxa on decay stage 2 (762 observations on 41 units), 74 taxa on decay stage 3 (782 observations on 35 units), 62 taxa on decay stage 4 (535 observations on 32 units), and 31 taxa on decay stage 5 (105 observations on 13 units) (Table 6 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 5).

### 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 3).

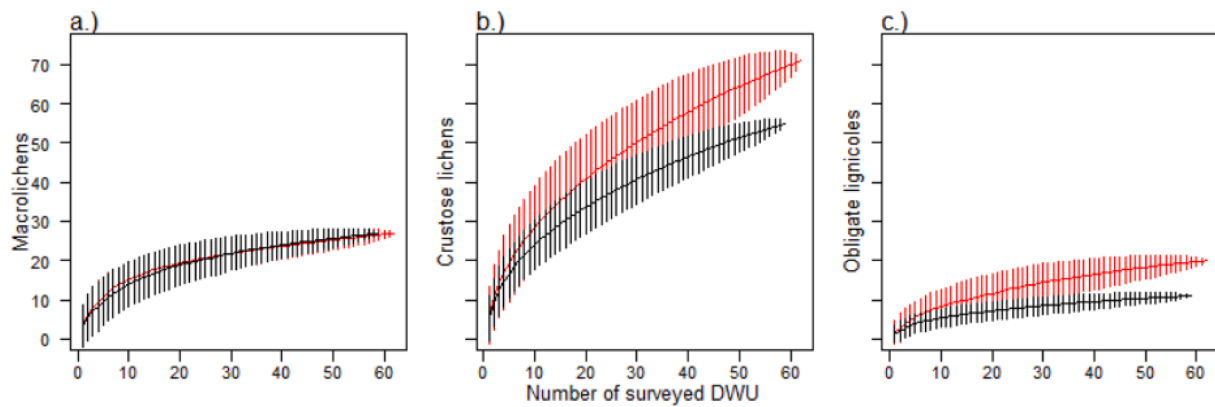
On site level, forest type explained best the community composition of crustose lichens whereas the macrolichen communities were similarly explained by forest management type and site. For obligate lignicoles, the site identity explained the community composition better than forest type (Fig. 3).

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 6, p. 41).

## 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



**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 4**

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)	2.372	0.120	11.88	<0.000***
Forest type (natural)	0.137	0.279	0.490	0.624
Crustose				
(Intercept)	2.929	0.111	26.317	<0.000***
Forest type (natural)	0.267	0.152	1.757	0.079•
Obligate				
(Intercept)	1.4553	0.1826	7.971	<0.000***
Forest type (natural)	0.449	0.234	1.921	0.055•

**Table 5**

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)	1.580	0.320	4.942	0.000***
Decay (2–5)	–0.136	0.057	–2.384	0.017*
Forest type (natural)	0.092	0.332	0.277	0.781
Dead wood type (stump)	–0.531	0.140	–3.797	0.000***
Crustose				
(Intercept)	2.237	0.187	11.980	<0.000***
Decay (2–5)	–0.176	0.053	–3.356	0.000***
Forest type (natural)	0.170	0.131	1.304	0.192
Dead wood type (stump)	–0.175	0.116	–1.508	0.131
Obligate				
(Intercept)	0.829	0.295	2.807	0.005**
Decay (2–5)	–0.177	0.083	–2.126	0.034*
Forest type (natural)	0.194	0.230	0.847	0.397
Dead wood type (stump)	–0.478	0.203	–2.357	0.018*

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 and 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 and 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 and 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; Rogers, 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 understorey 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 and 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



**Table 6**  
Lichen species on *Picea abies* decay stages 2–5.

Species	Decay stage			
	2	3	4	5
<i>Absconditella lignicola</i>	x	x	x	x
<i>Biatora cf. helvola</i>	x			
<i>Biatora chrysantha</i>	x	x	x	
<i>Biatora efflorescens</i>	x	x	x	
<i>Biatora fallax</i>	x		x	
<i>Biatora globulosa</i>	x	x		
<i>Biatora helvola</i>	x	x		
<i>Biatora meiocarpa</i>				
<i>Biatora ocelliformis</i>	x		x	
<i>Calicium viride</i>	x			
<i>Cetrariella delisei</i>	x			
<i>Chaenotheca brunneola</i>	x			
<i>Chaenotheca chlorella</i>		x		
<i>Chaenotheca chrysocephala</i>		x	x	
<i>Chaenotheca ferruginea</i>	x			
<i>Chaenotheca gracillima</i>		x		
<i>Chaenotheca laevigata</i>				
<i>Chaenotheca stemonea</i>				
<i>Chaenotheca trichialis</i>	x			
<i>Chaenothecopsis consociata</i>		x		
<i>Chaenothecopsis pusilla</i>				
<i>Chaenothecopsis savonica</i>		x	x	
<i>Chaenothecopsis sp.</i>	x			
<i>Chaenothecopsis viridireagens</i>			x	
<i>Cladonia arbuscula</i>	x	x	x	
<i>Cladonia bacilliformis</i>		x		
<i>Cladonia botrytes</i>	x	x	x	
<i>Cladonia carneola</i>	x	x		
<i>Cladonia cenotea</i>	x	x	x	
<i>Cladonia cf. chlorophaea</i>				
<i>Cladonia chlorophaea</i>		x	x	
<i>Cladonia coniocrea</i>	x	x	x	x
<i>Cladonia crispata</i>	x			
<i>Cladonia cyanipes</i>		x		
<i>Cladonia deformis</i>	x			x
<i>Cladonia digitata</i>	x	x	x	x
<i>Cladonia fimbriata</i>	x	x	x	
<i>Cladonia gracilis</i>		x	x	
<i>Cladonia grayi</i>	x	x	x	x
<i>Cladonia macilenta</i>	x	x	x	
<i>Cladonia norvegica</i>	x	x	x	x
<i>Cladonia ochrochlora</i>			x	
<i>Cladonia parasitica</i>	x			
<i>Cladonia pyxidata</i>		x	x	
<i>Cladonia rangiferina</i>				x
<i>Cladonia squamosa</i>	x	x	x	
<i>Cladonia sulphurina</i>	x	x	x	
<i>Cladonia symphyocarpa</i>				x
<i>Coenogonium pineti</i>	x	x	x	x
<i>Epigloea urosperma</i>	x	x	x	x
<i>Fellhanera subtilis</i>	x	x		
<i>Frutidella pullata</i>	x			
<i>Hypocnomyce scalaris</i>	x		x	x
<i>Hypogymnia physodes</i>	x	x	x	x
<i>Icmadophila ericetorum</i>	x			
<i>Lecania furfuracea</i>	x			
<i>Lecanora pulicaris</i>	x			
<i>Lecanora symmicta</i>		x		
<i>Lecidea albofuscescens s.lato</i>	x			
<i>Lecidea leprariooides</i>				
<i>Lecidea nylanderii</i>	x			
<i>Lecidea turgidula</i>	x	x		
<i>Lepraria caesioalba</i>		x	x	
<i>Lepraria elobata</i>	x	x	x	
<i>Lepraria finkii</i>		x		
<i>Lepraria incana</i>	x			
<i>Lepraria jackii</i>	x	x	x	x
<i>Lepraria sp 1</i>	x			
<i>Lepraria sp 2</i>	x	x		
<i>Lepraria sp 3</i>				
<i>Loxospora elatina</i>	x			
<i>Micarea anterior</i>	x	x	x	
<i>Micarea byssacea</i>	x	x	x	

**Table 6 (continued)**

Species	Decay stage			
	2	3	4	5
<i>Micarea contexta</i>	x	x	x	
<i>Micarea czarnotae</i>			x	
<i>Micarea denigrata</i>		x		x
<i>Micarea elachista</i>	x			
<i>Micarea fallax</i>	x	x	x	
<i>Micarea globulosella</i>	x	x	x	
<i>Micarea hedlundii</i>		x	x	x
<i>Micarea laeta</i>	x	x	x	
<i>Micarea melaena</i>	x	x	x	x
<i>Micarea melaeniza</i>				x
<i>Micarea microareolata</i>			x	
<i>Micarea micrococca</i>	x	x	x	x
<i>Micarea micrococca agg.</i>				
<i>Micarea misella</i>	x	x	x	x
<i>Micarea nigella s.str. (clade 3)</i>	x	x		x
<i>Micarea nigella-group (clade 1)</i>		x		
<i>Micarea nigella-group (clade 2)</i>	x	x	x	x
<i>Micarea nigella-group (clade 4)</i>	x	x		x
<i>Micarea nowakii</i>	x	x		
<i>Micarea peliocarpa</i>	x			
<i>Micarea prasina</i>	x	x	x	x
<i>Micarea pseudomicrococca</i>		x		
<i>Micarea pusilla</i>	x			
<i>Micarea sp 1</i>				x
<i>Micarea sp 2</i>	x			
<i>Micarea sp 3</i>			x	
<i>Micarea tomentosa</i>		x		x
<i>Mycoblastus affinis</i>	x			
<i>Mycoblastus sanguinarius</i>	x	x	x	
<i>Ochrolechia androgyna</i>			x	
<i>Ochrolechia microstictoides</i>				
<i>Opegrapha niveoatra</i>			x	
<i>Parmeliopsis ambigua</i>	x	x	x	
<i>Parmeliopsis hyperopta</i>	x	x	x	
<i>Peltigera degenii</i>			x	
<i>Peltigera praetextata</i>			x	
<i>Placynthiella dasae</i>	x	x	x	x
<i>Placynthiella icmalea</i>	x	x	x	x
<i>Platismatia glauca</i>	x	x	x	
<i>Puttea margaritella</i>		x		
<i>Steinia geophana</i>			x	
<i>Thelocarpon depressellum</i>	x			
<i>Thelocarpon intermediellum</i>	x	x	x	x
<i>Thelocarpon lichenicola</i>		x	x	
<i>Thelocarpon strasseri</i>	x	x	x	
<i>Trapeliopsis flexuosa</i>	x	x	x	x
<i>Trapeliopsis granulosa</i>		x		
<i>Vulpicida pinastri</i>	x	x	x	x
<i>Xylographa parallela</i>		x		
<i>Xylographa soralifera</i>	x	x	x	
<i>Xylographa trunciseda</i>	x	x		
<i>Xylographa vitiligo</i>	x	x	x	
<i>Xylopsora friesii</i>	x			
	83 taxa	74 taxa	62 taxa	31 taxa

added without replacing the old ones (Ulizcka and 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 highest 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 and LeBlanc, 1975; Jansová and Soldán, 2006).

The dead wood type (logs vs stumps), has also a significant effect on



**Fig. 3.** Site level non-metric multidimensional scaling (NMDS) for (a) macrolichens, (b) crustose lichens, and (c) obligate lignicoles. The site names indicate lichen community on each site, red being the natural and black managed sites. The  $r^2$  and p-values are reported for the variables assessed in the permutation test.

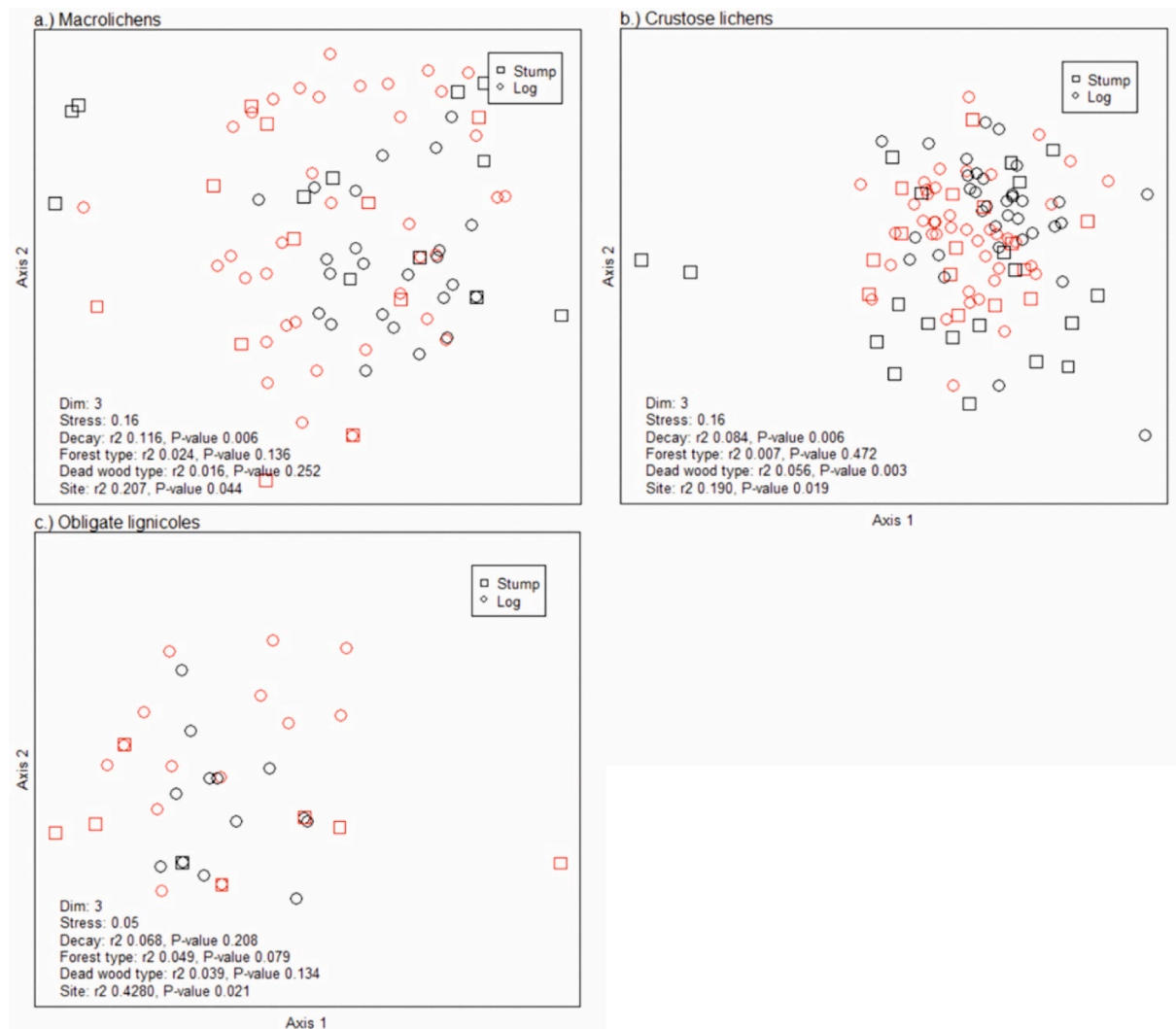
lichen species richness on DWU-level. This is especially evident for the macrolichens and obligate lignicoles, both for which species richness is higher on logs than on stumps. For macrolichens, this might simply be because logs are larger units than stumps and hence offer more space to grow on. For 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 7 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, the composition of lichen communities on dead wood were studied for two variables: site and forest management. From the studied groupcrustose lichen communities were most influenced by forest management and obligate lignicoles most by the site identity whereas for macrolichens both variables had intermediate effect. This shows that especially for 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. Crustose lichens, on the other hand, are affected by forest management on species richness and community levels. Possible reasons include aspects in their biology, such as their growth form, sensitivity to environmental changes and specialization to microhabitats (for further see Section 4.1).

On dead wood level, lichen communities are influenced mostly by decay stage, dead wood type (log vs stump), and site identity. Macrolichen communities are explained especially by decay stage, whereas crustose lichen communities are explained by 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



**Fig. 4.** Dead wood unit (DWU) level non-metric multidimensional scaling (NMDS) for (a) macrolichens, (b) crustose lichens, and (c) obligate lignicoles. Each symbol indicates the lichen community on a DWU on a natural (red) or managed (black) site.

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 influence crustose 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 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 later 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 and Myllys manuscript). Eleven taxa could not be identified with certainty; these specimens either represent groups that have taxonomic unclarity 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, 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. Influence of decay stage is supported by previous studies as well. By comparing how many records per species were made on logs and stumps, on the other hand, we found out that several lichen species on dead wood prefer either stumps or logs as their growing substratum. This result can be useful for conservation planning when aiming to increase species diversity in managed forests.

### CRedit authorship contribution statement

**Annina Kantelinen:** Conceptualization, Investigation, Visualization, Project administration, Funding acquisition, Writing – original draft, Writing – review & editing. **Jenna Purhonen:** Formal analysis, Visualization, Writing – original draft, Writing – review & editing. **Panu Halme:** Conceptualization, Formal analysis, Writing – review & editing. **Leena Myllys:** Conceptualization, Writing – review & editing, Supervision, Project administration, Funding acquisition.

### Declaration of Competing Interest

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

### Data availability

Data will be made available on request.

### 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 (personal grants for the first author), a postdoctoral grant from Alfred Kordelin Foundation (a personal grant for the second author), and the Academy of Finland (Grant 323711).

### Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2022.120529>.

### 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. *Ecol. Bull.* 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*. doi: 10.1371/journal.pone.0145808.
- Boch, S., Prati, D., Hesse, 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*. doi: 10.1371/journal.pone.0055461.
- Bäcklund, S., Jönsson, M., Strengbom, J., Frisch, A., Thor, G., 2016. A Pine Is a Pine and a Spruce Is a Spruce – The Effect of Tree Species and Stand Age on Epiphytic Lichen Communities. *PLOS ONE* 11(1): e0147004. <https://doi.org/10.1371/journal.pone.0147004>.
- 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. *R J.* 9, 378–400.
- Bunnell, F., Spribille, T., Houde, I., Goward, T., Björk, C., 2008. Lichens on down wood in logged and unlogged forest stands. *Can. J. For. Res.* 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, 47–55.
- Coppins, B.J., 1983. A taxonomic study of the lichen genus *Micarea* in Europe. *Bull. Br. Museum (Nat. Hist.) Bot. Ser.* 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. <https://doi.org/10.1139/cjb-76-4-641>.
- Culberson, C.F., Kristinsson, H.D., 1970. A standardized method for the identification of lichen products. *J. Chromatogr. A* 46, 85–93.
- Czarnota, P., 2007. The lichen genus *Micarea* (Lecanorales, Ascomycota) in Poland. *Pol. Bot. Stud.* 23, 190.
- Forsslund, A., Koffman, A., 1998. Species Diversity of Lichens on Decaying Wood: A Comparison between Old-growth and Managed Forest. *Botaniska Institutionen, Stockholms Universitet, Växt-ekologi*, pp. 1–40.
- Foucard, T., 2001. Svenska skorplavlar och svampar som växer på dem. *Stenströms Bokförlag*, p. 392.
- Fridman, J., Walheim, M., 2000. Amount, structure and dynamics of dead wood on managed forestland in Sweden. *For. Ecol. Manage.* 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. <https://doi.org/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. <https://doi.org/10.1007/s00442-005-0283-1>.
- Grime P, J., 1979. *Plant strategies and vegetational processes*. London Wiley.
- Guzow-Krzemińska, B., Czarnota, P., Lubek, A., Kukwa, M., 2016. *Micarea soralifera* sp. nov., a new sorediate species in the *M. prasina* group. *Lichenologist* 48, 161–169.
- Halonen, P., Hyvärinen, M., Kauppi, M., 1991. The Epiphytic Lichen Flora on conifers in relation to climate in the Finnish Middle Boreal Subzone. *Lichenologist* 23, 61–72. <https://doi.org/10.1017/S0024282991000117>.
- 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, p. 704.
- 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. *Biodivers. Conserv.* 12, 1587–1607. <https://doi.org/10.1023/A:1023645730446>.
- Kalela, A., 1961. Waldvegetationszonen Finnlands und ihre Klimatischen paralleltypen. *Archiv. Soc. Zool. Bot. Fenn. Vanamo* 16, 65–83.
- Kantvilas, G., Jarman, S.J., 2006. Recovery of lichens after logging: preliminary results from Tasmanian wet forests. *Lichenologist* 38, 383–394.
- Kantvilas, G., Minchin, P., 1989. An analysis of epiphytic lichen communities in Tasmanian cool temperate rainforest. *Vegetatio* 84, 99–112. <https://doi.org/10.1007/BF00036510>.
- Kruys, N., Jonsson, B.G., 1997. Insular patterns of Calicioid lichens in a boreal old-growth forest-wetland mosaic. *Ecography* 20, 605–613. <https://doi.org/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. <https://doi.org/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. <https://doi.org/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., Malicek, J., Svensson, M., Tsurykau, A., Sérusiaux, E., Myllys, L., 2019b. Sharpening species boundaries in the *Micarea prasina* group, with a new circumscription of the type species *M. prasina*. *Mycologia* 111, 574–592.
- Launis, A., Myllys, L., 2019. *Micarea fennica*, a new lignicolous lichen species from Finland. *Phytotaxa* 409, 179–188.
- Launis, A., Pykälä, J., van den Boom, P., Sérusiaux, E., Myllys, L., 2019a. Four new epiphytic species in the *Micarea prasina* group from Europe. *Lichenologist* 51, 7–25.
- Linder, P., Ostlund, L., 1998. Structural changes in three mid-boreal Swedish forest landscapes, 1885–1996. *Biol. Conserv.* 85, 9–19.
- Löhmus, P., Löhmus, A., 2001. Snags and their lichen flora in old Estonian peatland forests. *Ann. Bot. Fennici* 38, 265–280.

- Löhmus, A., Löhmus, P., 2011. Old-forest species: the importance of specific substrata vs. stand continuity in the case of calicioid fungi. *Silva Fenn.* 45, 1015–1039.
- 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. *For. Ecol. Manage.* 259, 883–892. <https://doi.org/10.1016/j.foreco.2009.11.028>.
- Maliček, J., Palice, Z., Vondrak, J., Kostovcik, M., Lenžová, V., Hofmeister, J., 2019. Lichens in old-growth and managed mountain spruce forests in the Czech Republic: assessment of biodiversity, functional traits and bioindicators. *Biodivers. Conserv.* 1–32 <https://doi.org/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. <https://doi.org/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., Launis, A., 2018. Additions to the diversity of lichens and lichenicolous fungi living on decaying wood in Finland. *Graph. Scr.* 30, 78–87.
- Myllys, L., Lohtander, K., Källersjö, M., Tehler, A., 1999. Sequence insertion and ITS data provide congruent information in *Roccella canariensis* and *R. tuberculata* (Arthoniales, Euascomycetes) phylogeny. *Mol. Phylogenet. Evol.* 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.
- 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. Available from: <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, pp. 44–45.
- Paillet, Y., Berges, L., Hjäältén, 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.
- Pykälä, J., Jääskeläinen, K., Rämä, H., Launis, A., Vitikainen, O., Puolasmaa, A., 2019. Lichens. In: Hyvärinen, E., Juslén, A., Kempainen, E., Uddström, A. & Liukko, U.-M. (Eds.), *The 2019 Red List of Finnish Species*. Ministry of the Environment & Finnish Environment Institute, Helsinki, pp. 263–312.
- R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. - <https://www.R-project.org/>.
- 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. <https://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 W, R., 1988. Succession and survival strategies in lichen populations on a palm trunk. *Journal of Ecology* (76), 759–776.
- Rogers, R.W., 1990. Ecological strategies of lichens. *Lichenologist* 22, 149–162.
- 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. *For. Ecol. Manage.* 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. <https://doi.org/10.2307/3243911>.
- Selva, S.B., 2003. Using calicioid 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. *Ecol. Bull.* 49, 11–41.
- Sillett, S.C., Antoine, M.E., 2004. Lichens and bryophytes in forest canopies. In: Lowman, M.D., Rinker, H.B. (Eds.), *Forest Canopies*, second ed. Elsevier Academic Press, Oxford, UK, pp. 151–174.
- Smith, C.W., Aptroot, A., Coppins, B.J., Fletcher, A., Gilbert, O.L., James, P.W., Wolsley, P.A. (Eds.), 2009. *The Lichens of Great Britain and Ireland*. British Lichen Society, pp. 1046.
- Spribille, 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.
- Spribille, 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, p. 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 Ecol.* 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.
- Vaahtera, E., Aarne, M., Ihalainen, A., Mäki-Simola, E., Peltola, A., Torvelainen, J., Uotila, E., Ylitalo, E. (Eds.), 2018. *Finnish Forest Statistics*. Natural Resources Institute Finland (Luke), Helsinki. 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. <https://doi.org/10.1098/rspb.2014.2004>.
- 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*. doi: 10.1371/journal.pone.0203540.
- Vondrák, J., Malíček, J., Šoun, J., Pouska, V., 2015. Epiphytic lichens of Stuzica (E Slovakia) in the context of Central European old-growth forests. *Herzogia* 28, 104–126.
- 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>.
- 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*. Academic Press, New York, NY, pp. 315–322.
- Wilhere, G.F., 2003. Simulations of snag dynamics in an industrial douglas-fir forest. *For. Ecol. Manage.* 174, 521–539.
- Yarranton, G.A., 1972. Distribution and succession of epiphytic lichens on Black Spruce near Cochrane, Ontario. *Bryologist* 75, 462–480.
- 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.