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

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A B S T R A C T

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 lichens 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 lichens 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 lichens 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 lichens 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 lichens, 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 Ostlund, 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 lichens not known from other substrata and 418 as facultative lichens 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; Malícek et al., 2019), and

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Lichens are considered to be one of the most reliable indicators of forest-continuity and forest quality (Johansson and Gustafsson, 2001; Paitel 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; Rudolph 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; Nasimbeni et al., 2010; Malíček et al., 2019; Nirthamo 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 and 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 and Löhmus, 2011). This exposure lichen 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 (Spiribille 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 micromelichens (Spiribille 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; Kruys and Jonsson, 1997; Crites and Dale, 1998; Forslund and Koffman, 1998; Kruys et al., 1999; Löhmus and Löhmus, 2001; Jüriado et al., 2003; Caruso et al., 2008; Spiribille et al., 2008; Löhmus and Löhmus, 2011; Svensson et al., 2016) and North America (Selva, 1994; Bunnell et al., 2008; Spiribille 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 (Forslund 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 (Renwall, 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-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

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 Taivastia 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 Ostrobottinia kajanensis 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)
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 possible. As previous studies have shown, the species richness of epiphytic lichens is not uniformly distributed but much greater in hotspots (Neitlich et al., 2019). Therefore, a comprehensive inventory of species diversity is sought dead wood to find some. This method prevents most of the plots from being 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 ≥ 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 unincoricated 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 <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).

2.2.3. 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 ≥ 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 unincoricated 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 <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 lichenicolous are crustose lichens (Table 3 on pages 23–25) that are not known from other substrata (Spribille 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; Spribille 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 (Pykalä et al.) and number of occurrences in managed (MF) and natural forests (NF).

| Species                      | Growth form | Ecology based on literature | Red List assessment | Number of logs on which found |
|------------------------------|-------------|------------------------------|---------------------|-------------------------------|
|                              |             |                              | MF      | NF      | Total |
| Abiesgrandiella lignicola    | Crustose    | Obligate                      | LC       | 20      | 19    | 39    |
| Biatora chrysantha           | Crustose    | Facultative                   | LC       | 3       | 0     | 3     |
| Biatora efforscens           | Crustose    | Facultative                   | LC       | 4       | 2     | 6     |
| Biatora fallax               | Crustose    | Facultative                   | VU       | 1       | 4     | 5     |
| Biatora globulosa            | Crustose    | Facultative                   | LC       | 2       | 1     | 3     |
| Biatora helvola              | Crustose    | Facultative                   | LC       | 5       | 1     | 6     |
| Biatora cf. helvola          | Crustose    | not known                     | not assessed | 1      | 2     | 3     |
| Biatora meiscarpia           | Crustose    | Facultative                   | LC       | 0       | 1     | 1     |
| Biatora ocelliformis         | Crustose    | Facultative                   | LC       | 1       | 1     | 2     |
| Calicium viride              | Crustose    | Facultative                   | LC       | 1       | 0     | 1     |
| Cetrariella delisei          | Macro: fruticose | Facultative                   | LC       | 1       | 0     | 1     |
| Chaenotheca brunnaneola      | Crustose    | Obligate                      | LC       | 0       | 2     | 2     |
| Chaenotheca chilorea         | Crustose    | Facultative                   | NT       | 0       | 1     | 1     |
| Chaenotheca chrysocarpa      | Crustose    | Facultative                   | LC       | 0       | 2     | 2     |
| Chaenotheca ferruginea       | Crustose    | Facultative                   | LC       | 2       | 1     | 3     |
| Chaenotheca gracillina       | Crustose    | Facultative                   | NT       | 0       | 1     | 1     |
| Chaenotheca laevigata        | Crustose    | Facultative                   | VU       | 0       | 1     | 1     |
| Chaenotheca stemorea         | Crustose    | Facultative                   | VU       | 0       | 1     | 1     |
| Chaenotheca trichtialis      | Crustose    | Facultative                   | LC       | 1       | 0     | 1     |
| Chaenothecopsis consociata   | Crustose    | Lichenicolous                  | LC       | 0       | 1     | 1     |
| Chaenothecopsis pusilla      | Crustose    | Facultative/lichenicolous     | LC       | 0       | 1     | 1     |
| Chaenothecopsis savonica     | Crustose    | Lichenicolous/facultative     | LC       | 0       | 2     | 2     |
| Chaenothecopsis sp.          | Crustose    | Not known                     | not assessed | 1      | 0     | 1     |
| Chaenothecopsis viridireagens| Crustose    | Lichenicolous/ Facultative    | NT       | 1       | 1     | 2     |
| Cladonia arbuscula           | Macro: fruticose | Facultative                   | LC       | 7       | 6     | 13    |
| Cladonia bacilliformis       | Macro: foliose | Obligate                      | LC       | 1       | 1     | 2     |
| Cladonia botrytes            | Macro: foliose | Facultative                   | LC       | 12      | 4     | 16    |
| Cladonia carneola            | Macro: foliose | Facultative                   | LC       | 3       | 0     | 3     |
| Cladonia cuneata             | Macro: foliose | Facultative                   | LC       | 4       | 8     | 12    |
| Cladonia chlorophaea         | Macro: foliose | Facultative                   | LC       | 0       | 4     | 4     |
| Cladonia cf. chlorophaea     | Macro: foliose | Not known                     | not assessed | 0      | 2     | 2     |
| Cladonia connicrea           | Macro: foliose | Facultative                   | LC       | 38      | 45    | 83    |
| Cladonia crispata            | Macro: foliose | Facultative                   | LC       | 1       | 0     | 1     |
| Cladonia cyanipes            | Macro: foliose | Facultative                   | LC       | 1       | 0     | 1     |
| Cladonia deformis            | Macro: foliose | Facultative                   | LC       | 2       | 0     | 2     |
| Cladonia digitata            | Macro: foliose | Facultative                   | LC       | 15      | 17    | 32    |
| Cladonia fimbriata           | Macro: foliose | Facultative                   | LC       | 14      | 10    | 24    |
| Cladonia gracilis            | Macro: foliose | Facultative                   | LC       | 3       | 0     | 3     |
| Cladonia grayi               | Macro: foliose | Facultative                   | LC       | 10      | 6     | 16    |
| Cladonia macilenta           | Macro: foliose | Facultative                   | LC       | 2       | 1     | 3     |
| Cladonia norvegica           | Macro: foliose | Facultative                   | NT       | 8       | 13    | 23    |
| Cladonia ochrochlorella      | Macro: foliose | Facultative                   | LC       | 0       | 1     | 1     |
| Cladonia parasitica          | Macro: foliose | Obligate                      | VU       | 1       | 1     | 2     |
| Cladonia pyxidata            | Macro: foliose | Facultative                   | LC       | 1       | 1     | 2     |
| Cladonia rangiferina         | Macro: fruticose | Facultative                   | LC       | 1       | 0     | 1     |
| Cladonia squamulosa          | Macro: foliose | Facultative                   | LC       | 2       | 8     | 10    |
| Cladonia subulina            | Macro: foliose | Facultative                   | LC       | 2       | 7     | 9     |
| Cladonia symphycarpa         | Macro: foliose | Facultative                   | LC       | 0       | 1     | 1     |
| Coenogonium pineti           | Crustose    | Facultative                   | LC       | 14      | 11    | 25    |
| Epigloea aaroperma           | Macro: fruticose | Facultative                   | LC       | 9       | 10    | 19    |
| Fulhazana subtilis           | Crustose    | Facultative                   | LC       | 1       | 2     | 3     |
| Frutidella pullata           | Crustose    | Facultative                   | LC       | 1       | 1     | 2     |
| Hypocnemomyce scalaris       | Crustose    | Facultative                   | LC       | 1       | 3     | 4     |
| Hypogymnia physodes          | Macro: fruticose | Facultative                   | LC       | 6       | 16    | 22    |
| Icmadophila ericetorum       | Crustose    | Facultative                   | LC       | 0       | 1     | 1     |
| Leccaria farfurae            | Crustose    | Facultative                   | not assessed | 0      | 1     | 1     |
| Lecanora pulicaris           | Crustose    | Facultative                   | LC       | 1       | 0     | 1     |
| Lecanora symmica             | Crustose    | Facultative                   | LC       | 1       | 0     | 1     |
| Lecidea albouccescens s.lato | Crustose    | Facultative                   | NT       | 0       | 1     | 1     |
| Lecidea lepratoides          | Crustose    | Facultative                   | LC       | 0       | 1     | 1     |
| Lecidea nylanderi            | Crustose    | Facultative                   | LC       | 1       | 1     | 2     |
| Lecidea turgidula            | Crustose    | Facultative                   | LC       | 1       | 1     | 2     |
| Lepraria caesioalba           | Crustose    | Facultative                   | LC       | 0       | 4     | 4     |
| Lepraria elobata             | Crustose    | Facultative                   | LC       | 6       | 0     | 6     |
| Lepraria finkii              | Crustose    | Facultative                   | LC       | 0       | 2     | 2     |
| Lepraria incana              | Crustose    | Facultative                   | LC       | 0       | 2     | 2     |
| Lepraria jackii              | Crustose    | Facultative                   | LC       | 20      | 35    | 55    |
| Lepraria sp 3                | Crustose    | not known                     | not assessed | 1      | 0     | 1     |
| Lepraria sp 1                | Crustose    | not known                     | not assessed | 0      | 2     | 2     |
| Lepraria sp 2                | Crustose    | not known                     | not assessed | 0      | 4     | 4     |
| Luxxpora claina              | Crustose    | Facultative                   | LC       | 0       | 2     | 2     |
| Micaeares anterior           | Crustose    | Obligate                      | NT       | 9       | 13    | 22    |

(continued on next page)
we used 10% potassium hydroxide (K) and sodium hypochlorite (C). 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 the plate for chemical spot tests and thin-layer chromatography (TLC). For spot tests, the samples were run in solvent systems A and B (Culberson and Kristinsson, 1970; Orange et al., 2010).

### Table 3 (continued)

| Species | Growth form | Ecology based on literature | Red List assessment | Number of logs on which found |
|---------|-------------|-----------------------------|---------------------|--------------------------------|
|         |             |                             | MF                  | NF                            | Total |
| Micarea byssacea | Crustose | Facultative | LC | 2 | 10 | 12 |
| Micarea contexta | Crustose | Obligate | NT | 7 | 19 | 26 |
| Micarea denuigera | Crustose | Obligate | LC | 3 | 2 | 5 |
| Micarea elachista | Crustose | Facultative | VU | 2 | 2 | 4 |
| Micarea globulosaella | Crustose | Facultative | NT | 2 | 6 | 8 |
| Micarea helandii | Crustose | Obligate | VU | 2 | 2 | 4 |
| Micarea melaena | Crustose | Facultative | LC | 6 | 10 | 16 |
| Micarea melaeniza | Crustose | Obligate | DD | 0 | 1 | 1 |
| Micarea micrococcca | Crustose | Facultative | LC | 13 | 8 | 21 |
| Micarea micrococcca agg. | Crustose | Facultative | not assessed | 1 | 0 | 1 |
| Micarea misella | Crustose | Obligate | LC | 24 | 17 | 41 |
| Micarea nigella s.str. (clade 3) | Crustose | Obligate | DD | 2 | 3 | 5 |
| Micarea nigella-group (clade 1) | Crustose | not known | not assessed | 1 | 1 | 2 |
| Micarea nigella-group (clade 2) | Crustose | not known | not assessed | 2 | 0 | 2 |
| Micarea nigella-group (clade 4) | Crustose | not known | not assessed | 5 | 4 | 9 |
| Micarea nowaki | Crustose | Obligate | DD | 1 | 1 | 2 |
| Micarea pelicarpa | Crustose | Facultative | LC | 0 | 1 | 1 |
| Micarea praunia | Crustose | Facultative | LC | 32 | 42 | 74 |
| Micarea puillia | Crustose | Facultative | not assessed | 2 | 0 | 2 |
| Micarea fallax | Crustose | Facultative | not assessed | 3 | 5 | 8 |
| Micarea microaerolata | Crustose | not assessed | 0 | 1 | 1 |
| Micarea laeta | Crustose | Facultative | not assessed | 4 | 1 | 5 |
| Micarea pseudomicrococcca | Crustose | Facultative | not assessed | 0 | 1 | 1 |
| Micarea cernotae | Crustose | Facultative | not assessed | 1 | 0 | 1 |
| Micarea sp 1 | Crustose | not known | not assessed | 1 | 0 | 1 |
| Micarea sp 2 | Crustose | not known | not assessed | 1 | 0 | 1 |
| Micarea sp 3 | Crustose | not known | not assessed | 0 | 1 | 1 |
| Micarea tomentosa | Crustose | Obligate | VU | 0 | 2 | 2 |
| Mycoblastus affinis | Crustose | Facultative | LC | 1 | 0 | 1 |
| Mycoblastus sanguinarius | Crustose | Facultative | LC | 0 | 0 | 1 |
| Ochrolechia androgyna | Crustose | Facultative | LC | 0 | 4 | 4 |
| Ochrolechia microtomentosa | Crustose | Facultative | LC | 0 | 1 | 1 |
| Opegrapha niveopes | Crustose | Facultative | NT | 0 | 1 | 1 |
| Parmeliopsis ambigua | Macro: foliose | Facultative | LC | 13 | 13 | 26 |
| Parmeliopsis hyperopta | Macro: foliose | Facultative | LC | 4 | 16 | 20 |
| Peligera degeni | Macro: foliose | Facultative | LC | 0 | 1 | 1 |
| Peligera praeestata | Macro: foliose | Facultative | LC | 0 | 1 | 1 |
| Placynthiella daue | Crustose | Facultative | LC | 27 | 33 | 60 |
| Placynthiella icmata | Crustose | Facultative | LC | 27 | 30 | 57 |
| Plactinatia glauca | Macro: foliose | Facultative | LC | 4 | 9 | 13 |
| Pustesia margarithella | Crustose | Facultative | NT | 1 | 3 | 4 |
| Steinia geophana | Crustose | Facultative | LC | 0 | 1 | 1 |
| Thelocarpon depressellum | Crustose | Obligate | VU | 0 | 1 | 1 |
| Thelocarpon intermediellum | Crustose | Facultative | NT | 10 | 2 | 12 |
| Thelocarpon lichenicola | Crustose | Facultative | LC | 2 | 0 | 2 |
| Thelocarpon straesseri | Crustose | Obligate | VU | 1 | 4 | 5 |
| Trapedilopsis flexuosa | Crustose | Facultative | LC | 14 | 17 | 31 |
| Trapedilopsis granulosa | Crustose | Facultative | LC | 1 | 0 | 1 |
| Vulpicida pinastri | Macro: foliose | Facultative | LC | 28 | 21 | 49 |
| Xylographa paralitea | Crustose | Obligate | VU | 0 | 1 | 1 |
| Xylographa sororifera | Crustose | Facultative | LC | 11 | 18 | 29 |
| Xylographa truncicida | Crustose | Obligate | VU | 0 | 2 | 2 |
| Xylographa vitiligo | Crustose | Obligate | LC | 0 | 7 | 7 |
| Xylourea frictii | Crustose | Obligate | LC | 0 | 1 | 1 |

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 (https://www.macrogen.fi).

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 the plate for chemical spot tests and thin-layer chromatography (TLC). For spot tests, the samples 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).
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 “speccum” function of the “vegan” package (Oksanen et al., 2019) for macrolichens, crustose lichens and obligate lichines 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 further investigated 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 we included site identity within group identity as a nested random effect. We utilized the “glimmTMB” function of the package “glimmTMB” 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 lichines. We performed the analysis on two levels, at standlevel 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 non-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 lichines. Of these, 17 were crustose lichens belonging to the genera Absconditella, Chenuotheca, Micarea, Thelocarpus 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 lichines (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 icmala (n = 57), Lepraria jackii (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 lichines are more species rich in natural than managed forests. Macrollichs, 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 lichines, 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 lichines. 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 lichines have higher species richness in natural forests than in managed forests. Macrollichs, 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 lichines are mostly crustose). Also, previous
be more shade tolerant than macrolichens (L macrolichens differ in some of their responses: crustose lichens seem to ecological studies in boreal forests have shown that crustose lichens and -

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: \( * * * = P \leq 0.000, * * = 0.000 < P \leq 0.01, * = 0.01 < P \leq 0.05, \ast = 0.05 < P \leq 0.1 \).  

| Macro                  | Estimate | Std. Error | z value | \( P(>|z|) \) |
|------------------------|----------|------------|---------|----------------|
| (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 | \( P(>|z|) \) |
|------------------------|----------|------------|---------|----------------|
| (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 (Hyvarinen 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 (Bunnel 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 and Angelstam, 1999; Hilmo et al., 2009; Lommi et al., 2010; Nascimbene et al., 2010; Malícek 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 |
| *Aurantiacladina* lichenocloca | x | x | x | x |
| *Biatora* cf. helvola | x | | | |
| *Biatora* chrysanth | x | x | | |
| *Biatora* efforescens | x | x | | |
| *Biatora* fallax | x | | | |
| *Biatora* globulosa | x | x | | |
| *Biatora* helvola | x | x | | |
| *Biatora* mesicarpa | | | | |
| *Biatora* ocelliformis | x | x | | |
| *Calcium* viride | x | | | |
| *Cetraria* delaei | x | | | |
| *Chaenotheca* brunnela | x | | | |
| *Chaenotheca* chryseochlora | | | | |
| *Chaenotheca* chrysochyna | | x | x | |
| *Chaenotheca* ferruginea | x | | | |
| *Chaenotheca* gracillima | | x | | |
| *Chaenotheca* laevigata | | | | |
| *Chaenotheca* stenomea | | | | |
| *Chaenotheca* trichialis | x | | | |
| *Chaenothecopsis* consocia | x | | | |
| *Chaenothecopsis* pusilla | x | | | |
| *Chaenothecopsis* savonica | x | x | | |
| *Chaenothecopsis* sp. | x | | | |
| *Chaenothecopsis* viridireogens | | | | |
| *Cladonia* arbuscula | x | x | x | |
| *Cladonia* bacciformis | x | x | x | |
| *Cladonia* borytis | x | x | | |
| *Cladonia* carnea | x | | | |
| *Cladonia* cenotea | x | x | x | |
| *Cladonia* cf. chlorophaea | | | | |
| *Cladonia* chlorophaea | x | | | |
| *Cladonia* coniocrea | x | x | x | x |
| *Cladonia* crispata | x | | | |
| *Cladonia* cyanipes | | x | | |
| *Cladonia* deformis | | x | x | |
| *Cladonia* digitata | x | x | x | |
| *Cladonia* fimbriata | | | | |
| *Cladonia* gracilis | x | x | | |
| *Cladonia* grays | x | x | x | x |
| *Cladonia* macilentia | x | x | x | |
| *Cladonia* norvegica | x | x | | |
| *Cladonia* ochroclara | x | | | |
| *Cladonia* parasitica | x | | | |
| *Cladonia* pyxidata | x | x | x | |
| *Cladonia* rangiferina | | x | | |
| *Cladonia* squamosa | x | x | x | |
| *Cladonia* subulata | x | x | x | |
| *Puttella* fallax | x | | | |
| *Hypogymnia* psophodes | x | x | x | x |
| *Lecanora* furfuracea | x | | | |
| *Lecanora* pulicaris | x | | | |
| *Lecanora* symmica | x | | | |
| *Lecidea* albofuscascens s.lato | x | | | |
| *Lecidea* leprariaoides | x | | | |
| *Lecidea* nylanderi | x | | | |
| *Lecidea* turdula | x | x | | |
| *Lepraria* caesiola | x | x | x | |
| *Lepraria* ebolata | x | x | x | |
| *Lepraria* finkii | x | | | |
| *Lepraria* incana | x | | | |
| *Lepraria* jackii | x | x | x | x |
| *Lepraria* sp 1 | x | | | |
| *Lepraria* sp 2 | x | | | |
| *Lepraria* sp 3 | x | | | |
| *Lecanora* elataina | x | | | |
| *Micarea* anterior | x | x | x | |
| *Micarea* byssacea | x | x | x | |

Table 6 (continued)

| Species | Decay stage |
|---------|-------------|
|         | 2 | 3 | 4 | 5 |
| *Micarea* contexta | x | x | x | |
| *Micarea* csernoret | x | x | | |
| *Micarea* denigrata | x | x | x | |
| *Micarea* elachista | x | | | |
| *Micarea* fallax | x | x | x | |
| *Micarea* globalibella | x | x | x | |
| *Micarea* heidlandii | x | x | x | x |
| *Micarea* lanta | x | x | x | x |
| *Micarea* melandra | x | x | x | x |
| *Micarea* melanorica | x | | | |
| *Micarea* microcorbicola | x | x | x | |
| *Micarea* micrococcus | x | x | x | x |
| *Micarea* micrococcus agg. | x | x | x | x |
| *Micarea* misella | x | x | x | x |
| *Micarea* nigella s.str. (clade 3) | x | x | x | x |
| *Micarea* nigella-group (clade 1) | x | | | |
| *Micarea* nigella-group (clade 2) | x | x | x | x |
| *Micarea* nigella-group (clade 4) | x | x | x | x |
| *Micarea* nowakii | x | x | x | x |
| *Micarea* pelocarpa | x | x | x | x |
| *Micarea* prasina | x | x | x | x |
| *Micarea* pseudomicrococcus | x | x | x | x |
| *Micarea* pusilla | x | x | x | x |
| *Micarea* sp 1 | x | | | |
| *Micarea* sp 2 | x | | | |
| *Micarea* sp 3 | x | | | |
| *Micarea* tomentosa | x | x | | |
| *Mycoblastus* affinis | x | | | |
| *Mycoblastus* sanguinarius | x | x | | |
| *Ochrolycchia* androgyna | x | | | |
| *Ochrolycchia* microsclerotides | x | | | |
| *Opogona* nivosa | x | x | | |
| *Parmeliopsis* ambiguus | x | x | x | |
| *Parmeliopsis* hyperbota | x | x | x | |
| *Peligeria* degeni | x | | | |
| *Peligeria* preussiana | x | | | |
| *Placynthiella* daase | x | x | x | x |
| *Placynthiella* icmolea | x | x | x | x |
| *Platismata* glauca | x | x | x | x |
| *Puttella* margariella | x | | | |
| *Stainia* geophana | x | | | |
| *Thelecoron* depressulm | x | | | |
| *Thelecoron* intermedium | x | x | x | x |
| *Thelecoron* lichenicola | x | x | x | x |
| *Thelecoron* strasser | x | x | x | x |
| *Tropilopha* flexuosa | x | x | | x |
| *Tropilopha* granulosa | x | | | |
| *Vulpicida* pinastri | x | x | x | x |
| *Xylographa* paralella | x | | | |
| *Xylographa* sorafera | x | x | | x |
| *Xylographa* trancisida | x | x | x | x |
| *Xylographa* vitiglo | x | x | x | x |
| *Xylographa* frisi | x | | | |

83 taxa 74 taxa 62 taxa 31 taxa

added without replacing the old ones (Uliiaka and Angelstam, 1999; Helio 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...
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). Absconditella lignicola, Micarea anterior, Micarea contexta, Micarea misella, Placynthiella dasae, P. icmalea, Thelocarpon intermediellum, Trachelopis 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 groups crustose 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. Macro- lichen 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
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., 2019a, 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 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 macrolichens 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

Anna 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.

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Appendix A. Supplementary material

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

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