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ORIGINAL PAPER

Large proportion of wood dependent lichens in boreal pine forest are confined to old hard wood

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Abstract Intensive forest management has led to a population decline in many species, including those dependent on dead wood. Many lichens are known to depend on dead wood, but their habitat requirements have been little studied. In this study we investigated the habitat requirements of wood dependent lichens on coarse dead wood (diameter >10 cm) of Scots pine *Pinus sylvestris* in managed boreal forests in central Sweden. Twenty-one wood dependent lichen species were recorded, of which eleven were confined to old (estimated to be >120 years old) and hard dead wood. Almost all of this wood has emanated from kelo trees, i.e. decorticated and resin-impregnated standing pine trees that died long time ago. We found four red-listed species, of which two were exclusive and two highly associated with old and hard wood. Lichen species composition differed significantly among dead wood types (low stumps, snags, logs), wood hardness, wood age and occurrence of fire scars. Snags had higher number of species per dead wood area than logs and low stumps, and old snags had higher number of species per dead wood area than young ones. Since wood from kelo trees harbours a specialized lichen flora, conservation of wood dependent lichens requires management strategies ensuring the future presence of this wood type. Besides preserving available kelo wood, the formation of this substratum should be supported by setting aside *P. sylvestris* forests and subject these to prescribed burnings as well as to allow wild fires in some of these forests.

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Introduction

The boreal forest has an extension of 14.3 million km^2 (Kasischke et al. 1995) and is one of the largest biomes on the planet. Forestry has profoundly modified forest habitats in this biome, especially in Northern Europe and Eastern Northern America (Esseen et al. 1997; Cyr et al. 2009). Intensive forest management has led to a decrease of structural diversity (Östlund et al. 1997), including a decrease in the amount of dead wood (Green and Peterken 1997). For instance, the volume of standing dead wood has been estimated to decrease with 90% in a region in Sweden during the past century (Linder and Östlund 1998). In old-growth boreal forests, dead wood is mainly created by self-thinning, pathogens and disturbances such as storms, fire, and insect outbreaks (Esseen et al. 1997; Niklasson and Granström 2000; Stokland et al. 2012). On the contrary, in managed forests trees are harvested before natural processes creating larger quantities of dead wood take effect. Furthermore, in today's managed forest landscapes in Fennoscandia, fire is usually suppressed and sanitation measures (such as salvage logging) after large disturbances prevent the accumulation of dead wood. As a result, the volume of coarse woody debris (CWD, i.e. wood with a diameter >10 cm) in managed boreal forests has been estimated to be only 2–10% of the amount in natural forests (Siitonen 2001). For certain dead wood types the decrease may have been even stronger. In managed forests, CWD of deciduous species, of large dimension and from late decay stages, are particularly rare (Jonsson et al. 2016). A large proportion of forest-dwelling species requires dead wood (Jonsson et al. 2005). The loss of habitat has led to population declines in many of these species (Siitonen 2001). Thus, the formation and maintenance of CWD are crucial factors for successful biodiversity management in forests (Botting and De Long 2009; Lassauce et al. 2011; Seibold et al. 2015). Which dead wood types that individual species are utilizing has been well explored in some regions, especially for macrofungi (Junninen and Komonen 2011) and beetles (Grove 2002), but less for other wood dependent species groups, such as lichens.

Lichens are a species rich group in boreal forests, being found on bark (corticolous lichens), soil (terricolous lichens), rocks (saxicolous lichens), and decorticated dead wood (lignicolous lichens) (Boch et al. 2013). The loss of a tree's bark results in a major shift in lichen species composition (Lõhmus and Lõhmus 2001). Ecological studies on lichens in forests have mainly focused on species growing on bark, even though dead wood has been recognized as an important substrate (e.g., Spribille et al. 2008). In Fennoscandia, 378 species have been reported from decorticated dead wood, of which 97 are restricted to this substrate (henceforth "wood dependent lichens"; Spribille et al. 2008). Wood dependent lichens may be more affected by a decreased amount of dead wood than generalist species and are therefore of higher conservation concern. Many species of wood dependent lichens occur in high abundances on stumps, snags, and to some extent logs, while dead branches are colonized by only a few species (Svensson et al. 2016). In several cases, snags have been found to be more species rich than logs (Kuusinen and Siitonen 1998; Humphrey et al. 2002; Runnel et al. 2013), but both these habitats host unique species (Hämäläinen et al. 2014). The age and decay stage of dead wood generally affect lichen species richness and composition (Nascimbene et al. 2008; Botting and De Long 2009; Caruso and Rudolphi 2009; Svensson et al. 2013). In boreal forests, fire has been found to decrease species richness of lichens (Hämäläinen et al. 2014). However, a few lichens, such as *Carbonicola anthracophila*, *C. myrmecina* (Bendiksby and Timdal 2013) and *Hertelidea botryosa* (Esseen et al. 1997; Lõhmus and Kruustük 2010) are fire-dependent and occur predominately on dead pine snags or stumps with charred wood (Grossmann 2014; Källén 2015).

In the European boreal region, Scots pine *Pinus sylvestris* is one of the dominant tree species. Under certain conditions, which probably include repeated wild fires, dead wood of *P. sylvestris* become hard and resin-impregnated and is then very long lasting. In Finland, such old, hard, resin-impregnated, silver-grey and decorticated trunks of *P. sylvestris* are called kelo trees (Niemelä et al. 2002). Several fungal species, mainly basidiomycetes (such as polypores and corticiaceous fungi) are confined to kelo substrates (Niemelä et al. 2002). Formation and decay of kelo trees are very slow processes. *P. sylvestris* can become up to 800 years old, and its transformation into kelo trees takes about 40 years after tree death (Sirén 1961; Leikola 1969). Kelo trees can remain standing for over 700 years (Niemelä et al. 2002), and final decay of the fallen stem may take another 200 years (Tarasov and Birdsey 2001). When a kelo tree breaks, the stump and log is quite resistant to further decay as the heartwood is resin-impregnated. As a result, the heartwood remains intact and the surface hard. Formation of kelo trees is not likely to occur in commercially managed forests with fast growing trees and short rotation cycles. Scientific studies on wood dependent lichens on kelo wood are currently lacking.

The aim of this study was to investigate the habitat requirements of wood dependent lichens on *P. sylvestris* wood. We analyzed to what extent wood type (low stumps, snags, logs), wood hardness, wood age, and occurrence of fire scars affect lichen species density (number of species per dead wood area) and composition. We hypothesized that species density and composition would differ between wood types and that especially old and hard wood would host different lichen species than younger and softer dead wood.

Materials and methods

Study area

Effaråsen, the study area, is located in the province of Dalarna in the southern boreal vegetation zone (Ahti and Jalas 1968) of Sweden (approximate central point 60°58′29″N, 14°01′55″E). Its c. 140 ha of forest land is dominated (i.e. >95%) by *P. sylvestris* (one of the two dominating tree species in Sweden), about 120–140 years of age, including some older trees. Other less abundant tree species in the area are Norway spruce *Picea abies* and birch (*Betula pendula* and *B. pubescens*). The ground vegetation is dominated by dwarf shrubs (*Vaccinium vitis-idaea* and *V. myrtillus*) and lichens (among fruticose species mainly *Cladonia* spp.). The study area is representative for old pine forests in central and northern Sweden which are close to being logged by clearcutting. The forest has never been clear-felled but traces of historical high-grading can be seen. In more recent time the forest is managed for wood production, including operations of thinning and a main part has been fertilized in 1982 and 2000. In the 1888 the area was hit by a severe fire (Hedberg et al. 1998). Remnants from this fire include fire-scarred *P. sylvestris* trees and large diameter snags, logs and stumps. Even though the studied forest is intensively managed today, it harbours old and hard wood (low stumps, snags, logs) as a legacy of more natural forest conditions.

Effaråsen is now hosting a large research project, in which trees and dead wood, old and newly created, are retained in different amounts (see Santaniello et al. 2016 for further details). The research treatments were applied 12 months before the lichen sampling took place, and we assume only a negligible effect on lichen species during this short time. Therefore, the studied forest stands represent old pine forests that are close to being logged by clearcutting. Fifteen stands, with a total area corresponding to about 70% of the area of the study landscape, were randomly allotted and homogenously distributed in the landscape, with the aim to cover the whole study area. In some occasions the stands are separated to each other by small forest patches not included in the experiment. Mean size of the inventoried stands was 6 ha (range 4–14.2 ha), mean altitude was 384 meters above sea level (range 370–400 m), mean number of stems per ha was 526 (range 290–640), mean tree height was 17 m (range 17–19 m), mean tree diameter at breast height (DBH) was 25 cm (range 20–30 cm), mean volume of coarse woody debris was 1.5 m^3 (range 0.95–3.45 m^3) (Table 1). The mean site productivity was 3.1 m^3 ha^{-1} $year^{-1}$ (range 2.4–4.3 m^3 ha^{-1} $year^{-1}$) (data from a database provided by the forest company Stora Enso Skog AB).

Study design

All sampling was conducted in plots along transects laid out across the longest possible distance in each of the 15 study stands. Ten 100 m^2 circular plots (radius 5.64 m) were established along each transect with 15–35 m distance between their mid-points depending on the length of the transect. In some stands there was not enough space for 10 plots along

Table 1 Characteristics of the 15 stands of study

Stand	Altitude (m)	Stand area (ha)	No. of stems (ha^{-1})	Mean tree height[a] (m)	Mean tree DBH[a] (cm)	Pine stems (%)	CWD volume (m^3 ha^{-1})
1	380	4.1	450	17	24	100	1.10
2	400	7.0	580	19	30	78	1.29
3	375	14.2	600	18	27	75	1.58
4	400	6.9	610	17	24	96	1.13
5	380	5.9	290	18	27	93	1.49
6	390	7.2	580	17	26	86	3.45
7	380	4.0	640	17	24	86	1.68
8	390	3.9	520	18	26	100	0.95
9	375	8.9	570	18	25	95	2.01
10	390	5.7	400	18	26	98	2.02
11	390	5.5	500	17	25	100	1.14
12	370	3.8	570	17	24	96	0.83
13	380	4.0	510	17	21	94	0.63
14	390	4.9	500	18	25	100	1.40
15	370	5.0	570	17	20	96	1.72

CWD coarse woody debris (diameter >10 cm)

[a] Tree height and diameter at breast height (DBH) are weighted by tree basal area

the transect. Then we laid out an additional transect covering the second longest distance for the remaining plots. Due to an error, only nine plots were established in one of the stands.

The amount of dead wood in terms of total area available for lichen colonization on different types of substrates was recorded in July–September 2013 (Santaniello et al. 2016). The coverage of wood dependent lichens and the amount and quality of dead wood was surveyed in September 2014. We surveyed only wood of *P. sylvestris*, which constitute >95% of the total dead wood available.

Dead wood inventory

In both the inventories carried out in this study, the dead wood characteristics were recorded as follows. All coarse woody debris (diameter >10 cm) within the circular plots was surveyed in order to assess the quality and quantity of dead wood. We divided the dead wood objects into groups according to their characteristics: (1) wood type (low stump, snag and log), (2) wood hardness (five categories), (3) occurrence of fire scars, and (4) wood age (long or short time since tree death). We divided standing dead wood into two height categories, low stumps are ≤50 cm tall (mostly stumps from harvested trees) and snags are >50 cm (stumps from harvested trees and naturally formed snags). Wood hardness was estimated using the method of Siitonen and Saaristo (2000), which is based on the depth a knife can be pushed into the wood. The scale is from 1 to 5, where 1 is very hard wood, 2 is hard wood, 3 is mid-hard wood, 4 is soft wood and 5 is very soft and highly decayed wood. Wood age was assessed by dividing dead wood into two distinct categories: (1) dead wood from trees judged to have died before or during the large forest fire in 1888 (hereafter termed ">120 years old"), with a characteristic furrowed surface and resin-impregnated wood) and (2) wood created from trees that had died more recently, probably mostly during the last 50 years (hereafter termed "<120 years old"). Diameter (at breast height, 130 cm above the ground) and height or length was measured, and the area of dead wood covered by bark and bryophytes was estimated. For the studied lichens, only dead wood without bark and bryophytes are available for colonization. Therefore, the area of dead wood that was available for lichens was calculated by first estimating its total surface area, assuming that every object was cylindrical, and then reducing the area by the estimated proportion of bark and bryophyte cover. The cut surfaces on stumps and logs were included in the calculations. For snags taller than 2 m the cut surface was not included since lichens were not inventoried there. Dead wood created at the experimental cutting in 2012–2013 was excluded, as we assumed that this wood was not colonised by any visible dead wood dependent lichens until the inventory. Old snags fallen after November 2012 were treated as standing as it is unlikely that wood dependent lichens had already reacted to this.

Lichen inventory

All lichen species classified as wood dependent by Spribille et al. (2008) were surveyed by G. Thor including *Cladonia botrytes*, which later has been shown to be only facultatively lignicolous (Bogomazova 2012). In Effaråsen, *C. botrytes* was searched for on the ground along all transects, but was only found lignicolous. Only dead wood objects with an overall area of exposed wood ≥25 cm^2 were inventoried. For objects partly outside the plot area, only the part inside the plot was inventoried. Standing objects were inventoried up to 2 m above the ground. The area covered by each lichen species was measured in cm^2 for each object. For every dead wood object with lichen occurrence, their characteristics were measured as described above. *Micarea denigrata* and *M. nowakii* are difficult to separate in the field and noted as *M. denigrata/nowakii*. The presence of *M. denigrata* was confirmed in the collected material, but not *M. nowakii*. The taxonomy of the genus *Xylographa* follow Spribille et al. (2015). Small specimens of *Xylographa parallela* and *X. pallens* can be difficult to separate in the field and, as small specimens were common in our study, these species were treated as *X. parallela/pallens*. The presence of both species in the area was confirmed in collections. *Trapeliopsis* sp. might represent an undescribed species. Reference material of lichens will be deposited in herbarium UPS (Museum of Evolution, Uppsala University).

Data analysis

In the statistical analyses, we considered each dead wood category in each stand as a replicate. From the dead wood inventory, we estimated the total surface area of dead wood. Furthermore, we calculated the area covered by each lichen species (Table 2).

Non-metric multidimensional scaling

Species composition was analysed for different dead wood categories (according to wood type, wood hardness, wood age and occurrence of fire scars) with non-metric multidimensional scaling (NMDS), using the Jaccard similarity coefficients (Jaccard distance) (Jaccard 1908; Pielou 1984) in a 2-dimensional space. The NMDS is an ordination method based on ranked Euclidean distances between samples. The data from the circular plots were pooled for each of the 15 forest stands. All ordination analyses were performed using R (version 3.2.1 and the packages Vegan, MASS and BiodiversityR) (R Core Team 2014; Oksanen et al. 2007). We calculated the stress and performed a permutational multivariate analysis of variance using a distance matrix to statistically compare the samples using the function "adonis" (Anderson 2001).

Rarefaction curves

In order to compare the species density on dead wood with different characteristics, we used sample-based rarefaction curves (Gotelli and Colwell 2001). The analysis was based on the following comparisons: (1) wood type, (2) wood hardness, (3) wood age, (4) wood hardness and age, (5) wood type and age. We used one hundred random re-samplings among sample units (i.e. each plot) and 95% confidence intervals (CI) for the statistical evaluations. The rarefaction curves were computed using the software EstimateS, version 9.1.0 (Colwell 2013). In order to compare the number of lichen species on equal amounts of available wood area, the x-axis was rescaled to represent the cumulative surface area. Calculations were made using the total bark and bryophytes free surface area of dead wood per plot.

Results

Among a total number of 523 dead wood objects inventoried, 242 (46%) were colonized by dead wood dependent lichens. The total number of lichen observations was 422. The total area of dead wood inventoried was 306.3 m^2 (low stumps: 27.3 m^2; snags: 44.4 m^2; logs:

Table 2 Observed dead wood-dependent lichens in an inventory of 523 dead wood objects of Scots pine

Species	Area occupied (cm^2)	No. of observations	Observed frequency wood type			Observed frequency wood age	
			Snags 146 obs.[a], 34%[b]	Low stumps 147 obs.[a], 35%[b]	Logs 129 obs.[a], 31%[b]	<120 years 148 obs.[a], 35%[b]	>120 years 274 obs.[a], 65%[b]
Mycocalicium subtile	73,071	37	1	0	0	0	1
Xylographa parallela/pallens	3229	55	0.21	0.12	0.67	0.31	0.69
Hertelidea botryosa (NT)	2584	37	0.56	0.26	0.18	0	1
Xylographa vitiligo	1674	80	0.25	0.36	0.39	0.30	0.70
Micarea denigrata/nowakii	1266	46	0.12	0.47	0.41	0.54	0.46
Xylopsora friesii	1166	13	0.79	0.07	0.14	0	1
Calicium trabinellum	1111	16	0.50	0.45	0.05	0.37	0.63
Cladonia parasitica (NT)	919	31	0.27	0.52	0.21	0.03	0.97
Carbonicola anthracophila (NT)	628	6	1	0	0	0	1
Trapeliopsis sp.	490	2	1	0	0	0	1
Micarea misella	487	18	0.19	0.46	0.35	0.67	0.33
Lecanora hypopta	343	10	0.75	0.17	0.08	0	1
Xylographa rubescens	213	4	0.25	0	0.75	0	1
Carbonicola myrmecina (NT)	180	1	1	0	0	0	1
Cladonia botrytes	156	53	0.03	0.87	0.10	0.96	0.04
Chaenotheca xyloxena	142	4	0.33	0.67	0	0.50	0.50
Chaenotheca brunneola	93	4	0.50	0	0.50	0	1
Puttea caesia	60	1	0	0	1	0	1
Calicium denigratum	15	1	1	0	0	0	1
Pycnora sorophora	7	2	0	0.50	0.50	0	1
Thelocarpon depressulum	4	1	0	0	1	0	1

Table 2 continued

Species	Observed frequency fire scars		Observed frequency wood hardness				
	With fire scars 67 obs.[a], 16%[b]	Without fire scars 355 obs.[a], 84%[b]	1 245 obs.[a], 58%[b]	2 71 obs.[a], 17%[b]	3 49 obs.[a], 11%[b]	4 54 obs.[a], 13%[b]	5 3 obs.[a], 1%[b]
Mycocalicium subtile	1	0	1	0	0	0	0
Xylographa parallela/pallens	0.10	0.90	0.54	0.13	0.20	0.11	0.02
Hertelidea botryosa (NT)	0.49	0.51	0.91	0.03	0.03	0.03	0
Xylographa vitiligo	0.13	0.87	0.61	0.13	0.10	0.16	0
Micarea denigrata/nowakii	0	1	0.37	0.30	0.09	0.22	0.02
Xylopsora friesii	0.62	0.38	0.85	0.15	0	0	0
Calicium trabinellum	0.13	0.87	0.62	0.19	0.06	0.13	0
Cladonia parasitica (NT)	0.26	0.74	0.71	0.16	0.13	0	0
Carbonicola anthracophila (NT)	0.83	0.17	1	0	0	0	0
Trapeliopsis sp.	1	0	0	1	0	0	0
Micarea misella	0	1	0.33	0.17	0.22	0.28	0
Lecanora hypopta	0.50	0.50	0.90	0.10	0	0	0
Xylographa rubescens	0.25	0.75	1	0	0	0	0
Carbonicola myrmecina (NT)	1	0	1	0	0	0	0
Cladonia botrytes	0	1	0.06	0.34	0.28	0.30	0.02
Chaenotheca xyloxena	0.25	0.75	0.50	0.25	0	0.25	0
Chaenotheca brunneola	0.25	0.75	0.50	0.50	0	0	0
Puttea caesia	0	1	1	0	0	0	0

Table 2 continued

Species	Observed frequency fire scars		Observed frequency wood hardness				
	With fire scars 67 obs.[a], 16%[b]	Without fire scars 355 obs.[a], 84%[b]	1 245 obs.[a], 58%[b]	2 71 obs.[a], 17%[b]	3 49 obs.[a], 11%[b]	4 54 obs.[a], 13%[b]	5 3 obs.[a], 1%[b]
Calicium denigratum	1	0	1	0	0	0	0
Pycnora sorophora	0	1	0.50	0.50	0	0	0
Thelocarpon depressulum	0	1	0	1	0	0	0

NT near threatened (red list category according to Swedish Species Information Centre 2015)

[a] Number of lichen observations

[b] Percentage of the lichen observations in relation to observations on all dead wood categories

234.6 m^2). The area covered by wood dependent lichens was c. 8.8 m^2 (low stumps: 0.2 m^2; snags: 7.1 m^2; logs: 1.5 m^2). Among the 21 wood dependent lichen species, four were red-listed (Swedish Species Information Centre 2015) (Table 2).

Wood age

The species density was about three times higher for old (>120 years old) dead wood than for young dead wood (Fig. 1a), a significant difference according to the 95% CI. Also species composition was clearly affected by wood age; the adonis test showed a significant difference in species composition between old and young dead wood (Fig. 2a). Thirteen species were only found on old dead wood, including three red-listed species (Table 2).

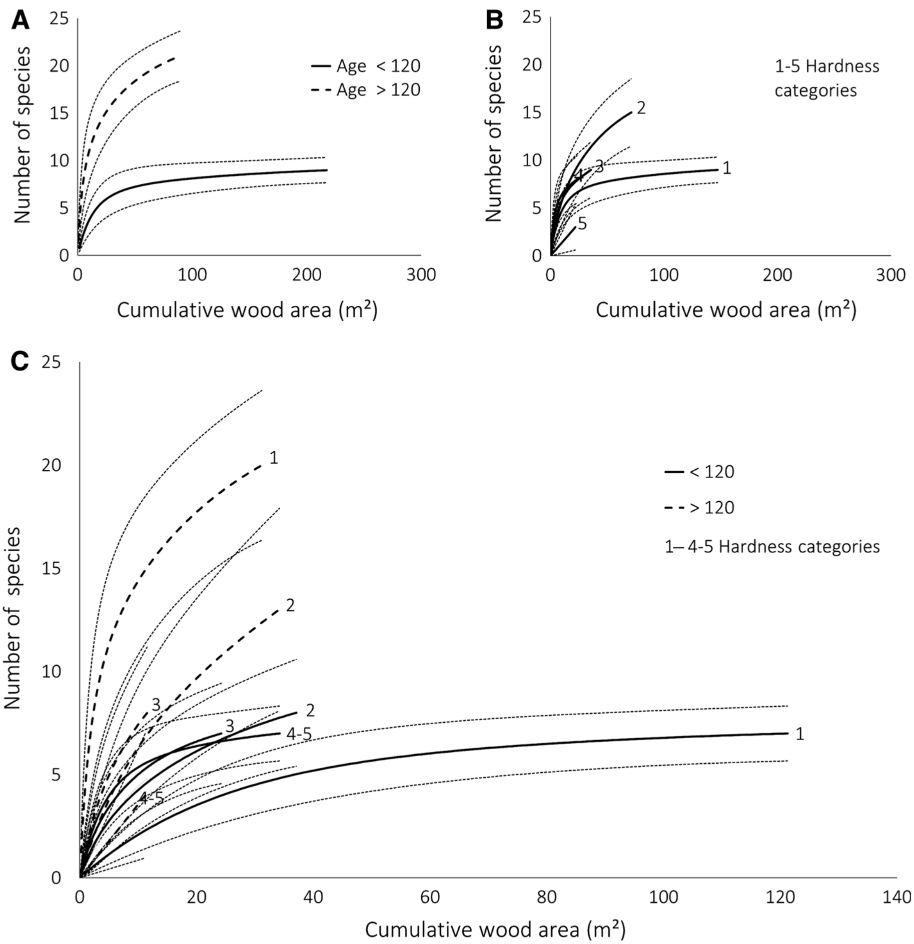

Fig. 1 Sample based rarefaction curves with 95% confidence intervals (*dashed lines*). Comparison of lichen species density between categories of dead wood with number of species on the *y*-axis and cumulative surveyed area on the *x*-axis for **a** age classes (>120, <120 years old), **b** dead wood hardness categories (from 1 to 5, where 5 is highly decayed and soft), and **c** age and hardness class. In **c** we merged hardness classes 4 and 5 due to data limitations

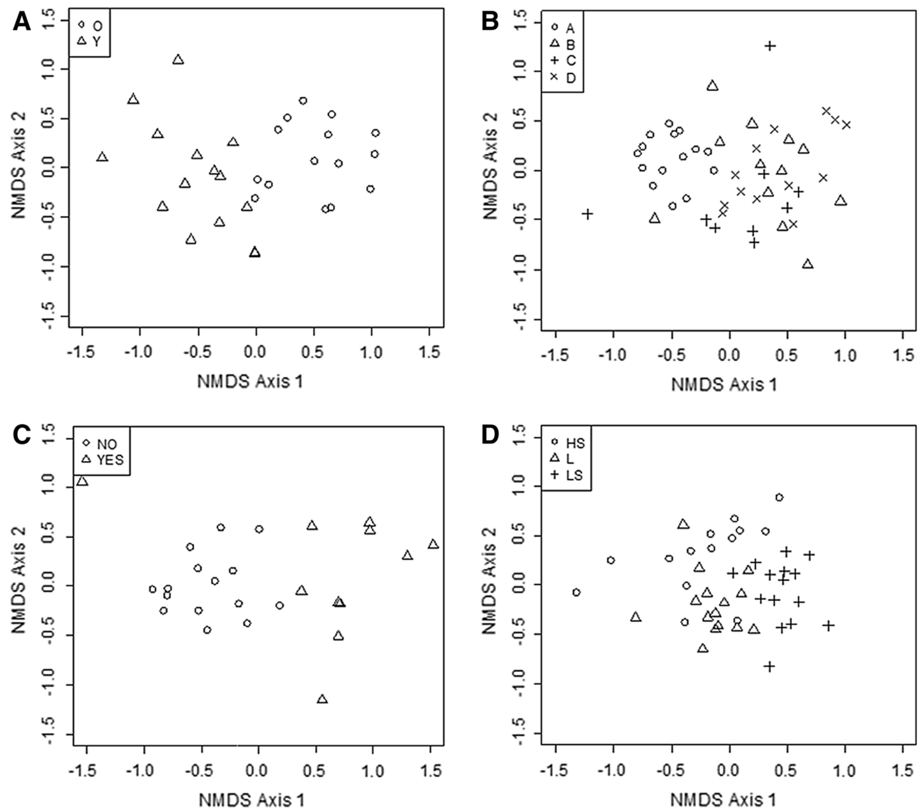

Fig. 2 Non-metric multidimensional scaling in a 2-D space. Comparison of lichen species composition between different substrates: **a** age, <120 and >120 years old, **b** hardness, from hard to soft (from 1 to 4–5; category 4 and 5 were merged due to data limitations in category 5), **c** occurrence of fire scars, **d** wood types (*Ls* low stumps, *Sn* snags, *Lo* logs). For the analysis of age, the NMDS solution was found after 9 iterations with a final stress value of 0.19 (Adonis test: $p = 0.001$, $p = 6.56$, with 1 degree of freedom). For the analysis of hardness the NMDS solution was found after 36 iterations, with a final stress value of 0.16 (Adonis test: $p = 0.001$, $F = 3.26$, with 3 degrees of freedom). For the analysis of occurrence of fire scars the NMDS solution was found after 56 iterations with a final stress value of 0.19 (Adonis test: $p = 0.001$, $F = 7.85$, with 1 degree of freedom). For the analysis of dead wood types the NMDS solution was found after 6 iterations, with a final stress value of 0.21 (Adonis test: $p = 0.001$, $F = 4.04$, with 2 and 42 degrees of freedom)

Wood hardness

Wood from hardness category 2 (the second hardest on a 5-level scale) had higher species density than both harder and softer wood (Fig. 1b). NMDS analyses revealed a significant difference in species composition between the hardness categories (Fig. 2b). This was especially the case for the hardest dead wood (category 1), which was clearly separated from the others. Fourteen species were only or almost only found on wood from hardness 1 and 2, including all four red-listed species (Table 2).

Wood type

Snags had the highest species density (Fig. 3a) of studied wood types. Snags >120 years old had a species density that was more than twice as high as that of the younger snags (Fig. 3b). The NMDS analyses revealed a significant difference in species composition between the three wood types (low stumps, snags, logs) (Fig. 2d).

Occurrence of fire scars

Fourteen species were found on burnt wood of which three were found only here (Table 2). Rarefaction analyses were not possible in this case, due to the low number of observations on burnt wood. The NMDS analyses revealed a significant difference in species composition (Fig. 2c), underlined by the graphical clear division between presence and absence of fire scars.

Old and hard wood

All the 21 species observed in this study occurred on old and hard wood (with age >120, hardness category 1 and 2). Eleven species were exclusive and two highly associated with such wood (Table 2). Of the four red-listed species, two were exclusive to old and hard wood and two almost only occurred here (Table 2). For dead wood >120 years old, there were most species in hardness category 1, followed by hardness category 2 (Fig. 1c).

Discussion

Wood age

The highest number of wood dependent species was found on old dead wood (>120 years). Also previous studies have shown that abundance of lichen species varies with the age of the wood (Humphrey et al. 2002). This may be because old dead wood has certain characteristics, such as less cellulose and lignin content (Stokland et al. 2012) and higher nitrogen content due to fungal mycelia, which are rich in nitrogen (Cowling and Merrill

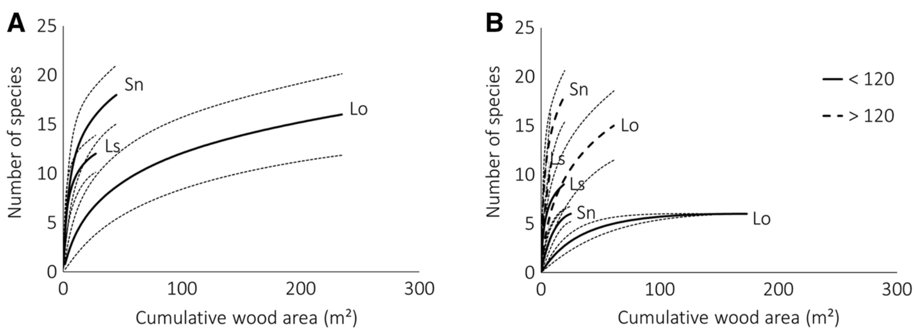

Fig. 3 Sample based rarefaction curves with 95% confidence intervals (*dashed lines*). Comparison between number of lichen species between different dead wood types with number of species on the *y*-axis and cumulative dead wood surface area on the *x*-axis, for **a** wood types (*Ls* low stumps, *Sn* Snags, *Lo* Logs), **b** age classes. Every curve represents one wood type

1966). Higher frequency of occurrences on older substrate may also be because lichens have had a longer time for colonization than on more recently formed substrate (Johansson et al. 2012). Our result highlights the importance of old dead wood for lichen occurrence.

Wood hardness

Species density was highest for hardness wood categories 2 and 3 (Fig. 1b). This can be due to that intermediate decomposition stages often show a wider range of microhabitats than earlier or later decay stages (Caruso and Rudolphi 2009; Kruys and Jonsson 1999; Wagner et al. 2014). Moreover, the progressive decrease of substratum stability over time is probably negative to lichens (Nascimbene et al. 2008).

Wood type

Species density was highest for old snags. This may be due to microclimatic and structural differences between dead wood types. Also previously, snags have been found to host more lichen species than e.g. logs (Humphrey et al. 2002; Lõhmus and Lõhmus 2001; Nascimbene et al. 2008; Svensson et al. 2016). Snags are considerably drier and more exposed to light. This is because logs are to a higher degree shaded by vegetation and covered by snow. Light exposition seems to be a very important variable for lichens (Rudolphi and Gustafsson 2011). For instance, Svensson et al. (2005) have found that the lichen species richness differs between the northern and southern side of snags.

Fire scar presence

The results indicate that many species occur on wood with fire scars (Table 2). *Carbonicola anthracophila* and *C. myrmecina* have been found to grow on burned wood even 300 years after fire (Esseen et al. 1997) indicating that species occurring on this substratum can survive for a long time on individual dead wood objects.

Old and hard wood

Our field experience is that almost all old (>120 years old) and hard (hardness category 1 and 2) wood has emanated from kelo trees. Though only rather few remaining standing kelo trees were found, logs, stumps and tops remaining from historical high-grading in the 19th century or earlier are scattered in the area. Our study shows that kelo wood had the highest species density, and a high proportion of wood dependent lichens depend on kelo wood. All the species found during the inventory occurred on such wood, and 11 species were confined to kelo wood. Of the four red-listed species, two were exclusive to kelo wood and two almost only occurred here, indicating the importance of this substrate to red-listed lichens. To fully understand lichens' habitat requirements, it is important to also consider the interactions between environmental variables, in this case age and hardness of the substratum.

Conservation and management implications

Of the 21 wood dependent lichen species found eleven species were confined to kelo wood (wood >120 years old and with wood hardness 1 and 2) and two almost only occurred here

(Table 2). Of the four red-listed species, two were exclusive to old and hard wood and two almost only occurred here (Table 2). This shows that kelo wood is an important substrate for dead wood dependent lichens in boreal *P. sylvestris* forests. Also in the agricultural landscape, kelo wood is important to wood dependent lichens (cf. Svensson et al. 2005). Special care should therefore be dedicated to such wood. Fire history data indicate that most past fires in boreal forests in Fennoscandia have not been stand replacing and many of the older *Pinus sylvestris* survived several fires (Kuuluvainen and Aakala 2011). These trees potentially could become kelo trees. Periodic occurrence of fire is important for the maintenance of the *Pinus*-dominated landscape as fire prevents the invasion of *Picea* and deciduous trees, while at the same time enhancing conditions for *Pinus* regeneration, facilitated by the continuous presence of large fire-tolerant *Pinus* trees (Kuuluvainen et al. 2002). During forest management operations, preserving what is already available of kelo wood is important. For instance, soil scarification practices should be avoided in stands where kelo wood is abundant. Moreover, the formation of this wood type should be supported by setting aside *P. sylvestris* forests as reserves in which prescribed burnings are carried out and where wild fires are accepted. Even though fire may promote the creation of kelo trees, it may also eliminate existing kelo wood. Therefore, in forests with high conservation values associated to dead wood, prescribed burning may be avoided. Probably it is difficult to create and conserve kelo trees in forests harvested by clearfelling and thinning in the long term, since there is a risk that future forestry operations will destroy future and currently available kelo wood. In general, it is valuable to maintain or develop old-growth forest structural attributes in managed forest landscapes (Bauhus et al. 2009). However, to our knowledge it has not been tested in Sweden if it is possible to create kelo trees in managed boreal landscapes. More knowledge is needed on how to sustain the formation of kelo trees.

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