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Forest floor bryophyte and lichen diversity in Scots pine and Norway spruce production forests

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ABSTRACT

Bryophytes and lichens are two main components of the forest floor vegetation. They provide essential ecosystem services, including nutrient recycling and water regulation. Here, we contrast the species richness, cover and community composition of forest floor bryophytes and lichens in Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) dominated production forests. The study sites were located in the hemiboreal zone of southern Sweden, and represented early-, mid- and late rotation stands. Our aim was to examine the potential consequences for forest floor biodiversity from the decreasing use of Scots pine production forests in this region.

Whereas Scots pine and Norway spruce stands did not differ in bryophyte cover, we found a higher cover of lichens in Scots pine stands, and highest in the intermediate aged stands. Also the species richness of lichens was higher in the Scots pine stands, while bryophyte species richness was higher in the Norway spruce stands. Differences in canopy cover and associated light transmittance to the forest floor appears to be important drivers for distinctive different forest floor communities in the Scots pine and Norway spruce stands, as revealed by Non-Metric Multidimensional Scaling (NMDS). Mean Ellenberg indicator values for bryophytes and lichens showed that species associated with Scots pine stands were characterized by their tolerance of brighter conditions, higher insolation, and better adaptation to a continental climate. Norway spruce stands instead had a comparably larger proportion of species tolerating lower light, but also indicators of higher available nutrient levels, humidity, and pH. The outcome of the Ellenberg indicator species analysis, as well as the larger cover of lichens,and adaptations to drought found among some mosses, revealed that forest floor communities are shaped by different environmental factors in Scots pine and Norway spruce production stands. These environmental differences, and the quantified shifts in forest floor communities identified in this study, indicate the large shifts in understory bryophyte and lichen species composition and abundance that is likely to occur if Scots pine stands are converted to Norway spruce.

1. Introduction

Bryophytes and lichens constitute an important part of the vegetation in a wide range of different ecosystems. In both temperate and boreal forests they play a key role in ecosystem functioning, due in part to their contribution to carbon and nitrogen fixation (Turetsky 2003; Zedda & Rambold 2015). The ability of bryophytes to quickly absorb water and release it slowly, contributes to the retention of a humid microclimate in many forest ecosystems, with resultant benefits to nutrient recycling (Brown & Bates 1990), and environmental water regulation (Hallingbäck et al. 2000). Hence, the loss of bryophytes in forest ecosystems may negatively influence decomposition rates, nitrogen availability and also soil carbon accumulation (Turetsky et al. 2012). Understory lichens also contribute to soil formation and stabilization, especially in early successions (Longton 1992). Since many species of lichens have evolved to live under nutrient- and water-limited conditions, they play an important role as pioneers, supporting early vegetation growth and succession (Zedda & Rambold 2015). For instance, dead lichen matter often provides the first source of organic matter for soil formation in primary succession (Ashman & Puri 2002).

Bryophytes and lichens are also excellent bio-indicators of environmental variables, such as soil nutrient content and pH (Stevens et al. 2012; Hodgetts et al. 2019). Moreover, both bryophytes and lichens are more sensitive to environmental changes than many other plant groups (Britton & Fisher 2010; Hallingbäck & Tan 2010). This is in part due to their relatively low competitive ability with vascular plants, as well as

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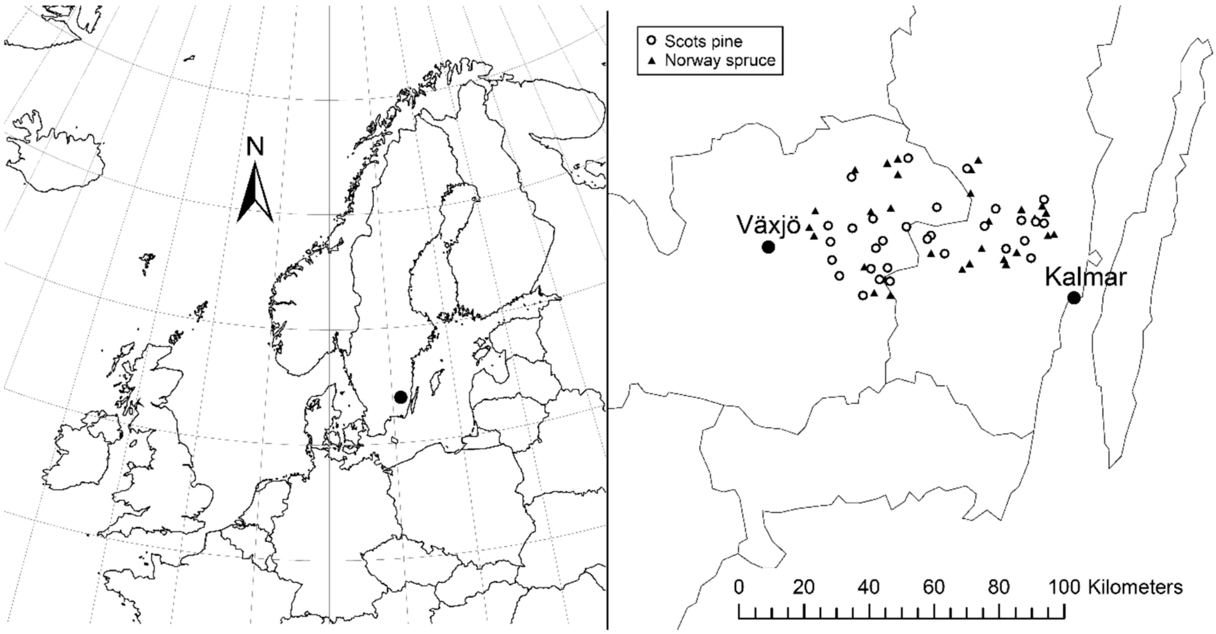

Fig. 1. The study area, including 30 Norway spruce and 30 Scots pine production stands is situated in the south-eastern part of Sweden.

their limited ability to regulate water uptake (Proctor 1990; Kranner et al. 2008). This sensitivity makes them strongly affected by the alteration and degradation of habitats. In this respect, the modification of natural systems, via e.g. the intensification of agriculture and forestry, and anthropogenic climate change, are now considered the most severe threats to European bryophytes (Hodgetts et al. 2019). Lichens also suffer from habitat loss and degradation, of which deforestation and the replacement of natural forests with plantations has severe implications for lichen communities (Scheidegger & Werth 2009).

In Sweden, intensive forest management, typically consisting of clear cutting, soil scarification, and planting of even-aged monocultures, which are regularly thinned, and in some regions coupled with the use of drainage ditches (Hallberg 2019), has reduced the populations of many bryophyte species associated with older forest conditions and limited disturbance (Hallingbäck 1996; Sandström et al. 2015). The majority of red listed bryophyte species in Swedish forests are dependent on late decomposition stages of dead wood, and these species are expected to experience further declines due to the lack of coarse dead wood in this decay class.

Sweden's forestry relies almost exclusively on two native conifer species, Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), which comprise 80% of standing volume (SFA, 2014). Scots pine and Norway spruce represent early- and late successional tree species respectively (Lundmark 1988). When it comes to competition between the two tree species, Scots pine has a bimodal distribution with respect to site fertility, as it occurs naturally on coarse, dry soils, but is also able to grow in relatively wet nutrient poor sites (Connolly & Kelly 2000), whereas Norway spruce generally outcompetes Scots pine on more fertile mesic sites (Engelmark & Hytteborn 1999). Under natural and semi-natural conditions in boreal Fennoscandia, disturbance-succession dynamics in forest systems range from even-aged dynamics driven by stand-replacing disturbances (e.g. fire, storms), to small-scale gap dynamics driven by local tree mortality (insects, fungi, senescence) (Kuuluvainen & Aakala 2011). Regeneration of Scots pine is generally favoured by large-scale disturbance processes, (e.g. fire storms; Kuuluvainen 2009) whereas the shade tolerant Norway spruce can often outcome Scots pine in later successional stages, especially on more fertile soils (Engelmark & Hytteborn 1999).

In forestry, these site associations and regeneration characteristics are normally taken into consideration when deciding which tree species to use during production stand establishment (Keskitalo et al. 2016). However, there are now concerns that sites traditionally regenerated with Scots pine in southern Sweden are being converted to production stands of Norway spruce (SFA, 2018). Norway spruce is the most commonly chosen tree species for regenerating sites in many southern Swedish regions, regardless of site conditions (SFA, 2019). A key motivator is that Norway spruce is thought to provide high timber production, good revenue, and has well-established management regimes (Felton et al. 2020), with the important additional benefit of being relatively unpalatable to browsing herbivores (Lodin et al. 2017; SFA 2017).

In this study, we assessed the implications of the use of two different conifer tree species in production forests, Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), on forest floor bryophyte and lichen cover, species richness and composition. The study was initiated to evaluate the biodiversity consequences of Scots pine production stands decline in southern Sweden (Lindbladh et al. 2019; Petersson et al. 2019). We also see our results as helping to fill a notable gap in our understanding of how tree species selection in intensively managed production forests can alter habitat availability for understory bryophyte and lichen communities. To do so, we addressed two primary issues in this study. First, we tested how bryophyte and lichen species richness, cover, and community composition, varied between Scots pine and Norway spruce stands at different stand ages. Second, we used the bryophyte species data in combination with Ellenberg indicator values, to estimate which aspects Scots pine and Norway spruce forest floor abiotic conditions differed from each other.

2. Materials and method

2.1. Study area

The studied sites are situated in the hemiboreal zone (Ahti et al. 1968) of southern Sweden, with the central point of the study area located at the coordinates 56°56′N, 15°34′E (Fig. 1.). The mean monthly temperature in this area ranges from 6 – 15 °C during the summer (June-August), down to −1°C during winter (December-February). The average growing season is 200–230 days, and precipitation ranges from 800 mm $year^{-1}$ in the west, to 600 mm $year^{-1}$ in the east of the study area (SMHI 2019).

Table 1
Stand structure variables from 60 stands of Scots pine and Norway spruce, 30, 55 and 80 years old, from ANOVA followed by Tukey post hoc test. The variables are presented as the mean and standard error (se) for each stand category consisting of tree species and stand age. Different letters indicate significant ($p < 0.05$) differences between the combination of tree species and stand age.

	Scots pine						Norway spruce						
	30		55		80		30		55		80		
	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	transf.
Basal area: total	15.5^{ab}	0.7	16.6^{ab}	0.9	22.6^{bd}	1.3	16.9^{ab}	1.5	25.4^{cd}	2.3	30.9^{c}	2.0	
Basal area: broadleaves	0.2^{ac}	0.1	0.1^{c}	0.0	0.2^{ac}	0.1	0.7^{ab}	0.1	0.2^{ac}	0.1	1.2^{b}	0.4	log + 1
Basal area: Scots pine	15.0^{a}	0.7	16.3^{a}	0.9	20.9^{b}	1.2	0.7^{c}	0.3	1.1^{c}	0.2	0.9^{c}	0.3	
Basal area: Norway spruce	0.3^{a}	0.1	0.3^{a}	0.0	1.5^{a}	0.4	15.5^{b}	1.5	24.1^{c}	2.3	28.8^{c}	2.2	
Stem density: total	1450^{a}	149	651^{b}	44	611^{b}	114	1558^{a}	255	811^{b}	89	913^{ab}	90	log + 1
Stem density: broadleaves	305^{a}	79	93^{ab}	28	34^{b}	14	341^{a}	91	37^{b}	15	162^{a}	35	log + 1
Stem density: Scots pine	1066^{a}	166	426^{a}	18	447^{a}	102	57^{b}	33	25^{b}	6	9^{b}	3	log + 1
Stem density: Norway spruce	80^{a}	23	132^{a}	32	130^{a}	29	1160^{b}	175	749^{b}	81	742^{b}	184	log + 1
Canopy openness	42.5^{a}	1.9	46.9^{a}	1.5	48^{a}	2.2	24.4^{b}	1.7	24.4^{b}	1.1	24.8^{b}	1.6	
Hard dead wood (m^3 ha^{-1})	1.9^{a}	0.6	2.9^{a}	0.7	4.2^{a}	1.1	1.0^{a}	0.3	3.9^{a}	1.2	14.5^{b}	3.4	
Soft dead wood (m^3 ha^{-1})	0.8^{a}	0.3	1.2^{a}	0.3	0.9^{a}	0.4	1.0^{a}	0.4	2.2^{a}	0.6	7.9^{b}	2.8	
Tree saplings ha^{-1}	1403^{a}	318	621^{a}	167	635^{a}	313	633^{a}	219	135^{b}	65	1107^{a}	166	log + 1
Vascular plant cover	75.2^{a}	8.1	77.3^{a}	8.7	70.1^{a}	8.5	26.3^{b}	3.6	19.2^{b}	2.4	25.4^{b}	5.5	
Humus layer thickness	4.4^{ac}	0.6	4.8^{abc}	0.5	6.6^{bc}	0.4	4.7^{a}	1.6	5.7^{abc}	0.5	7.8^{b}	0.4	
C:N ratio (humus layer)	33.3^{bc}	0.7	36.1^{b}	0.8	37.3^{b}	0.9	28.5^{a}	1.2	34.1^{b}	0.8	29.8^{ac}	1.3	
pH (B-horizon)	5.1^{a}	0.07	5.1^{a}	0.05	5.0^{a}	0.04	5.2^{a}	0.1	5.0^{a}	0.07	4.9^{a}	0.06	

2.2. Site selection

Sixty production forest stands with a standing volume of at least 80% of either Norway spruce (30 replicates) or Scots pine (30 replicates) were selected from two stand databases. To capture early, mid and late rotation stands, three different stand age classes, 30 years (±5), 55 years (±5) and 80 years (±5), were selected (i.e. 10 replicates of each tree species and age category). To minimize confounding sources of variability, all stands were selected based on their location on mesic soils of low-intermediate fertility, rather than either poor soils (may exclude Norway spruce) or fertile soils (may exclude Scots pine). To locate these types of stands with intermediate fertile soils, we used information about site index (SI). SI equates with a stand's projected dominant height (m) at 100 years age, and is a common tool for evaluating and comparing forest site productivity. The selected stands were restricted to SI 24–29 for Norway spruce. In order to enable comparisons of SI between tree species, Scots pine stand's SI was transformed into corresponding SI for Norway spruce according to Hägglund and Lundmark (2003). To further minimize between-site variation, all stands were situated on till soils possessing either rhyolite or granite bedrock (SGU, bedrock map, soil type map 1:25 000–1:100 000). In order to reduce historical differences between stands, the two younger age categories were restricted to those established on previously forested land (Swedish land survey: Ekonomiska kartan 1941–1949). This could not be done for the oldest stands, because the resolution of older maps was insufficient to determine land-use. Stands area averaged 7.9 ha ± 4.3 SD (range 2.8–31.7 ha) in size.

2.3. Stand structure

In southern Sweden, Scots pine and Norway spruce are the two dominating tree species, constituting 29% and 47% of standing volume respectively (SFA, 2014; SLU 2018). In silviculture, both Scots pine and Norway spruce are typically managed as even-aged monocultures with two or three commercial thinnings before final harvest. Strip roads, of approximately four meters width, are created at the first commercial thinning, with additional harvests made by stemwise selection within the forest left between strip roads (approximately 20 m in width). In subsequent thinnings only trees between strip roads are selected for harvest. Guidelines for how much basal area should be retained after thinning differ for the two conifer species, as does the recommended rotation length, which is usually longer for Scots pine than Norway spruce. Scots pine stands are traditionally thinned to a lower basal area relative to Norway spruce stands. Here most of the 30-year-old stands had a single commercial thinning, and the majority of 55-year-old stands had been thinned twice and two of the 80 years old Scots pine stands were recently thinned for a third time.

2.4. Field methods

We surveyed ten circular (5.64 m radius, 100 m^2) plots in each of the 60 stands, during June-October of 2016. To minimize edge effects, plots were placed in the interior parts of the stands, and no closer than 30 m from forest edges. Plots were randomly placed (>25 m apart) using pre defined coordinates in ArcGIS © ESRI. Forest floor bryophytes (incl. mosses and liverworts) and macrolichens (e.g. excluding small crustose and foliose species growing on boulders) were surveyed on all types of substrates, e.g. soil, rocks and dead wood. The total cover of vascular plants was recorded in the plots (for vascular plant results see Petersson et al. 2019). Species that could not be identified in the field were collected (one sample per plot) and later identified under microscope. The vegetation inventory was conducted by LP and SN. Nomenclature follows Hallingbäck et al. (2006) and Nordin et al. (2018). The two separate species *Polytrichum commune* and *P. uliginosum*, were registered together as *P. commune* coll. The tree sapling layer, as defined by the number of stems of 0.3–1.3 m tall, was measured in the same area. To quantify differences in species coverage, a 2 × 2 m squared central plot was established in the very centre of each of the larger circular plots, within which the percentage cover of bryophytes and lichens species, as well as the total cover of vascular plants, was recorded. However, the 2 × 2 m plots used for cover measurments were shifted to the closest suitable location if, a) > 50% of the plot consisted of boulder/bedrock surface, b) the plot contained living trees > 1.3 m tall, or c) it was unusually wet – as indicated by open water surface, or by > 20% cover of *Sphagnum* species (with the exception for *S. girgensohnii* and *S. capillifolium*).

Measurements of stand characteristics were conducted during the same time period as the species surveys, e.g. soil measurements were determined at stand level, while canopy openness and forest density (basal area m^2 ha^{-1}) and stem number (n ha^{-1}) were measured on plot level. Using the vegetation plot's centroid, diameter at breast height (1.3 m) was measured on each tree within a radius of 7 m for the 30 and 55-year-old stands, and within 10 m for the 80-year-old stands. In plots with < 5 tree stems, the radius was extended to 10 or 15 m. To quantify the amount of dead wood, all woody pieces, including wind throws, stumps and dead trees > 10 cm Ø, were measured within the 100 m^2 plots. All dead wood was divided into two decay classes of hard or soft dead wood. If the outer surface easily could be pierced by a knife, it was defined as soft. Canopy openness was calculated from hemispherical photographs taken from the central points of each plot, at 1 m above ground level. The pictures were analysed in Gap Light Analyser (Frazer et al. 2000), excluding the two outer rings of the circular grid to avoid the inclusion of ground vegetation in the calculations.

To further determine soil properties, four sub-samples of the humus layer and B-horizon were collected from the centre of four of the plots in each stand, and then merged into one sample. The humus layer was sampled down to 10 cm with a 4.4 cm Ø probe. In sites with shallow soil layers, more samples had to be taken to achieve the same amount of soil. At the same time as the soil was collected, the humus thickness was measured. The top 10 cm of the B-horizon was sampled the same way and was used for determining soil pH (SS-ISO 10390:2007). After drying and milling, the N (Dumas) content of the humus layer was analysed with a LECO FP-428 analyser, and carbon content was determined by loss of ignition. A conversion factor of 1.9 (Pribyl 2010) was used for converting loss of ignition into carbon. The content of carbon and nitrogen was then used for determining the C:N-ratio.

2.5. Statistical methods

All statistical analyses were performed at the stand level. Species cover was calculated as average cover of the ten 2 × 2 m plots within each stand and species richness was calculated as total number of species found in the ten 100 m^2 plots layed in each stand. The analyses were conducted in R version 3.5 (R Core Team 2018). The forest stand structural data (Table 1) was analysed by ANOVA, followed by Tukey post hoc test in R package Emmeans (Lenth 2018). Some variables were log(+1) transformed to normalize the data.

2.5.1. Species richness

Differences in species richness (defined as the number of species per stand) between Scots pine and Norway spruce dominated stands of different age classes, were analysed in a Generalized Linear Model with a Poisson error distribution in package glmmTMB (Magnusson et al. 2017). Using ANOVA, the differences in cover of the different organism groups were also analysed between tree species and stand age classes. Both the analyses of species richness and cover were conducted through backward model selection starting with a full model including tree species, stand age and the interaction between these. Non-significant terms were removed (as tested by type II ANOVA) but tree species was always kept in the final model. Mean species richness and comparisons between tree species and stand age was calculated with a Tukey post hoc test (Lenth 2018).

2.5.2. Community composition

To examine differences in forest floor species composition between different stands, the species matrix consisting of bryophytes and lichens of all stands was analysed together using Non-Metric Multidimensional Scaling (NMDS). The number of the 100 m^2 sample plots in which species were present in every stand (0–10) was used as a measurement of frequency. First, the species communities were analysed using the metaMDS function in Vegan package in R (Oksanen et al., 2013). As a second step, correlations between the community structure and environmental data were tested in permanova (999 permutations) with Vegan envfit function (Oksanen et al., 2013). The least significant environmental variables were removed one at a time until only significant variables were left. Bray-Curtis dissimilarity index was used for the NMDS and for fitting the environmental scores.

2.5.3. Forest floor differences

To examine whether aditional abiotic differences occurred, aside from those measured (canopy openness, humus layer nitrogen and B-horizon pH), we used Ellenberg indicator values for bryophytes, according to Bernhardt-Römermann et al. (2018) together with Ellenberg indicator values for lichens (Volkmar 2010) with competion of some missing indicator values from (Fabiszewski & Szczepańska 2010). Six different environmental indicators were analysed: moisture, light, reaction (environmental acidity), nitrogen, temperature and continentality. Previous research has demonstrated that the outcome of abundance-weighted species data differs little from presence-absence data (Diekmann 2003). For that reason we decided to use the presence absence data on stand level, as collected from the 100 m^2 plots in this analysis and computed unweighted community means of the Ellenberg values. Species with indifferent responses to certain environmental variables were excluded from each of these analyses. Calculating means of values from ordinal scale (such as indicator values) is a common approach, for instance in environmental monitoring. However, it's important to keep in mind that unequal sized scale intervals may cause errors to means and standard deviations (Stevens 1946). To identify differences in forest floor abiotic conditions between Scots pine and Norway spruce, the mean values were tested against tree species and stand age in a linear regression, in the same systematic order as described in the species richness section.

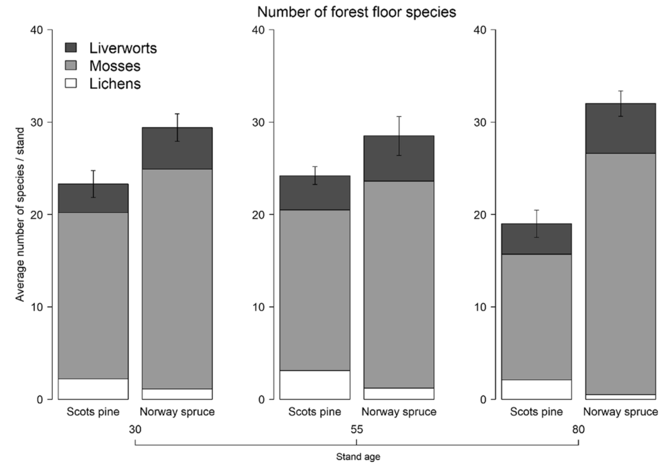

Fig. 2. Number of forest floor species found in Scots pine and Norway spruce stands. Forest floor species are divided into organism groups and presented as the average number of species per stand. The error bars show SE for total forest floor species richness for the combination of tree species and stand age, as tested by GLM (Appendix A: Table A1).

3. Results

3.1. Stand variables

The basal area of Norway spruce stands was higher than for Scots pine stands in the two oldest age categories (Table 1). Stem densities were higher in the younger stand categories. However, the 80-year-old Norway spruce stands were not significantly different from the youngest stands in terms of stem density. The most frequently encountered broadleaved tree species were birch (*Betula pendula*, *B. pubescens*), oak (*Quercus robur*, *Q. petraea*), rowan (*Sorbus aucuparia*) willow (mainly *Salix aurita*, *S. capraea*) and aspen (*Populus tremula*). Stem density of broadleaves was highest in the youngest stands and in the oldest Norway spruce stands. When it comes to basal area of broadleaves, it was highest in the old Norway spruce stands and lowest in the 55-year-old Scots pine stands. The amount of small tree saplings (0.3–1.3 m) varied considerably between different stands and was significantly lower in the 55-year-old stands. Canopy openness and vascular plant cover (primarily *Vaccinium myrtillus*; Petersson et al. 2019), was higher in the Scots pine stands throughout all stand age classes. With respect to soil properties, the humus layer was significantly thicker in the 80-year-old Norway spruce stands, compared to the 30-year-old stands for both Scots pine and Norway spruce. The C:N-ratio was lowest in the 30-year-old Norway spruce stands and highest in the 55-year-old Norway spruce and Scots pine stands. There was no significant difference in the pH of the B-horizon.

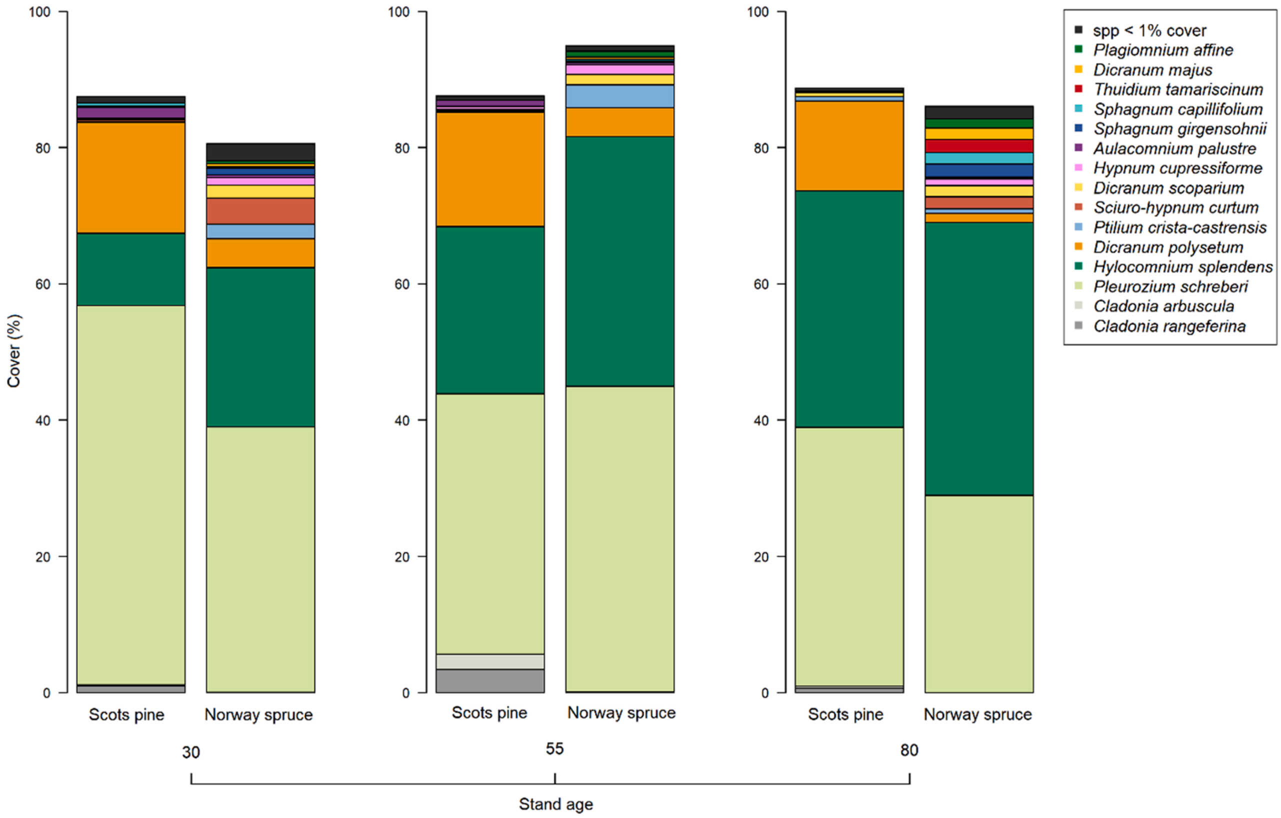

Fig. 3. Percentage cover of bryophytes and macrolichens in Scots pine and Norway spruce stands of different age. All species with > 1% cover in at least one of the tree species or stand age categories are presented separately, whereas species with a coverage below this threshold are grouped together.

3.2. Forest floor species richness

A total of 78 species of mosses and 19 species of liverworts were encountered during the surveys. Norway spruce stands supported a higher number of bryophyte species in total per stand (Fig. 2), and the highest average species richness (31.6 ± 1.8 SE) was found in the 80-year-old Norway spruce stands. In contrast, the lowest species richness (16.9 ± 1.3 SE) was found in the 80-year-old Scots pine category. For all surveyed stands, regardless of age, the number of bryophyte species was significantly higher in the Norway spruce stands, which had on average 29 species, compared to 20 species in the Scots pine stands (Appendix A: Table A1). There was also a larger number of bryophyte species (32) that were only found in the Norway spruce stands, in comparison Scots pine stands (11). Nine different species of bryophytes are on the list of species indicating high forest conservation values ('signalarter') according to the Swedish forest agency (Appendix B: Table B1) (Nitare & Hallingbäck 2000). In total 73 recordings of species indicating high forest values were made in the 600 plots, 20 in the Scots pine stands and 53 in the Norway spruce stands. None of the species found in the surveys are on the red list of threatened species in Sweden, but one species - *Splachnum ampullaceum* - is red listed (NT) in Europe (Hodgetts et al. 2019; Art-databanken 2020).

In total, 12 species of macrolichens were found during the survey. Species richness was on average higher in Scots pine stands, than in Norway spruce stands (Appendix A: Table A1). Species belonging to the genera of *Cladonia* (mainly reindeer lichens) were the most common in terms percentage cover (Fig. 3). The highest lichen species richness (7) was found in a 55 years old Scots pine stand, whereas understory macrolichens were completely absent in 14 Norway spruce stands across all age classes. Six lichen species were only found in Scots pine stands and three lichen species were only found in Norway spruce stands.

Table 2
Comparisons of the of forest floor vegetation between Scots pine and Norway spruce stands. The differences between the different taxa are tested against the interaction of tree species and age in a regression model (interaction is only included if significant). Predicted mean values are presented.

	mean	estimate	SE	df	t	p-value	sign
Total vegetation cover							
Scots pine	87.8	−0.8	4.2	58	−0.2	0.85	–
Norway spruce	87						
Bryophytes							
Scots pine	85.2	1.7	4.2	58	0.4	0.68	–
Norway spruce	86.9						
Lichens							
Scots pine	2.6	−2.6	0.8	54	−3.4	0.001	**
Norway spruce	0.04						
Scots pine × 30	1.4	−1.1	1.3	54	−0.8	0.40	–
Norway spruce × 30	0.003						
Scots pine × 55	5.6	−5.6	1.3	54	−4.2	<0.0001	***
Norway spruce × 55	0.08						
Scots pine × 80	1.0	−1.0	1.3	54	−0.7	0.46	–
Norway spruce × 80	< 0.01						
Liverworts							
Scots pine	0.2	0.09	0.09	58	1	0.30	–
Norway spruce	0.3						
Mosses							
Scots pine	85	1.7	4.2	58	0.4	0.69	–
Norway spruce	86.6						

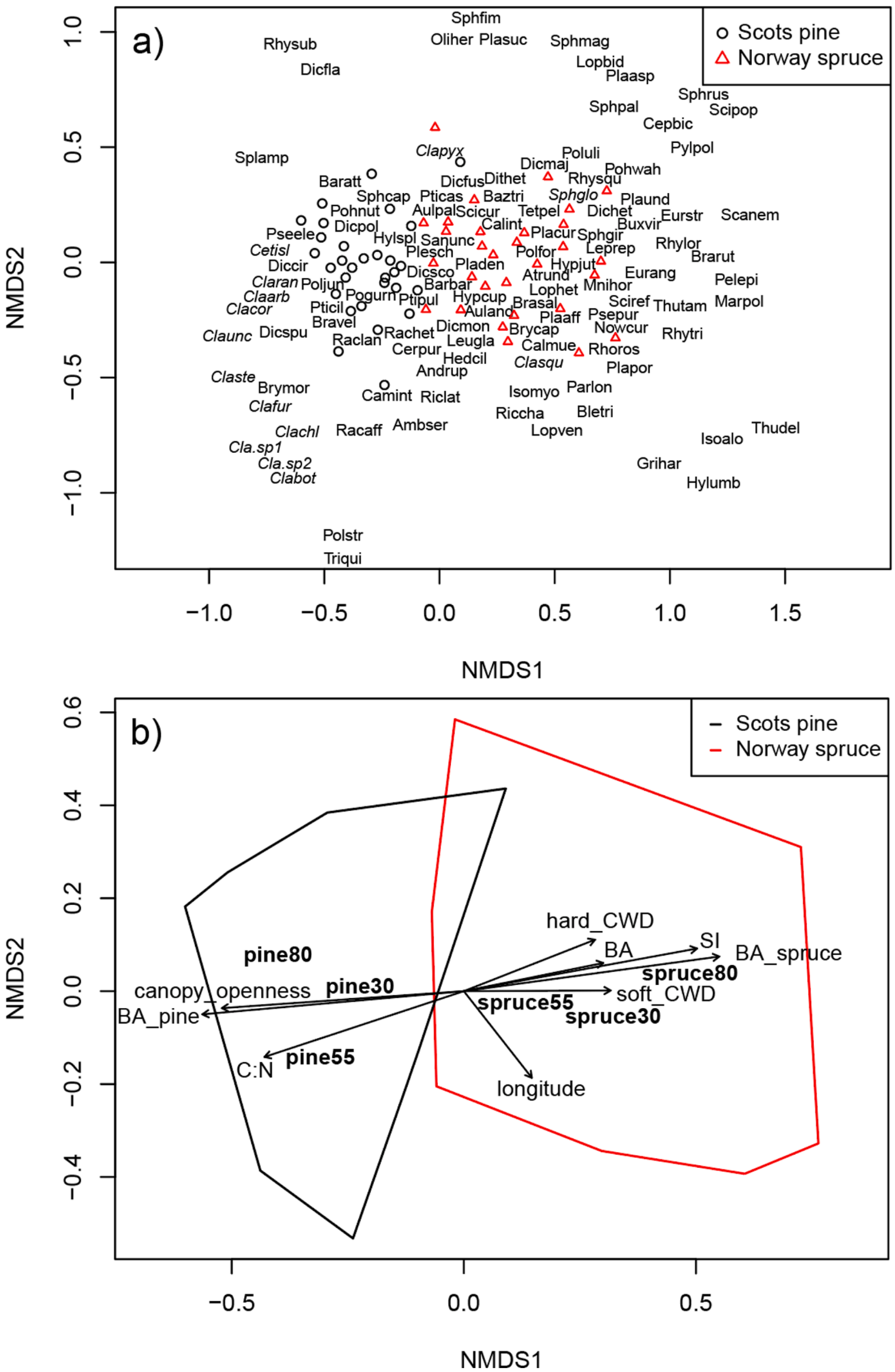

Fig. 4. NMDS plot of the the 111 species of bryophytes and lichens surveyed in Norway spruce and Scots pine dominated stands. In (a), the location of each stands is determined by the forest floor community composition of Norway spruce (triangles) and Scots pine (circles) forest stands. Lichen species are indicated by italic font and bryophyte species are written with regular font. Species name codes consist of the three first letters of the genus and the three first letters of the specific name (see Appendix B: Table B1). NMDS plot (b) shows the association of 9 different environmental variables and the six different stand categories (Table 3). The black and red hulls show the outer line of the location of the Scots pine and the Norway spruce stands in the ordination plot. Environmental variables were marked as bold if they consisted of factorial variables. The stress value was 16.3. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.3. Forest floor species cover

Total cover of forest floor vegetation (bryophytes and macrolichens together) did not significantly differ between Scots pine and Norway spruce stands (Table 2), and the total cover was on average 87.8% and 87% respectively. There was neither a difference in cover between stands of different age nor as an interaction between the dominant tree species and stand age. Mosses were the most abundant organism group, constituting 99.6 and 96.8% of the total forest floor vegetation in Norway spruce and Scots pine stands respectively.

Of the organism groups assessed, only lichen cover differed significantly between Scots pine and Norway spruce stands (Table 2). The abundance of lichens was significantly higher in the Scots pine stands, when comparing the two tree species stand types. However, when considering the interaction of tree species and stand age, cover was only significantly higher in the 55-year-old category of Scots pine stands (Table 2).

The most abundant bryophyte species in both Scots pine and Norway spruce stands was the mosses *Pleurozium schreberi* and *Hylocomnium splendens* (Fig. 3). In Scots pine stands, *Dicranum polysetum* constituted a considerable part of the cover of species remaining. The most common liverwort in both Scots pine and Norway spruce stands, was *Ptilidium pulcherrimum* and two most common species of lichens were *Cladonia rangeferina* and *C. arbuscula.*

3.4. Community composition

The multivariate analysis showed that the two different stand types,

Table 3
Environmental variables included in Fig. 4b, as a result of the backward selection of environmental variables, which only included significant ($p < 0.05$) variables.

Variable name	r2	Pr (>r)	sign.	Explanation
C:N	0.46	0.001	***	Carbon-to-nitrogen ratio
canopy_openness	0.62	0.001	***	Measured canopy openness from hemispherical photographs
hard_CWD	0.21	0.001	***	Volume of hard dead wood
soft_CWD	0.23	0.001	***	Volume of soft dead wood
BA	0.21	0.002	**	Total basal area
BA_pine	0.72	0.001	***	Basal area of Scots pine
BA_spruce	0.70	0.001	***	Basal area of Norway spruce
longitude	0.13	0.027	**	Longitude position of stand
SI	0.59	0.001	***	Site index
Stand category	0.61	0.001	***	Factors consisting interaction of tree species and stand age
pine30				Scots pine stands 30 years old
pine55				Scots pine stands 55 years old
pine80				Scots pine stands 80 years old
spruce30				Norway spruce stands 30 years old
spruce55				Norway spruce stands 55 years old
spruce80				Norway spruce stands 80 years old

dominated by Scots pine or Norway spruce were important determinants for the understory bryophyte and lichen communities (Fig. 4a-b). Among the 97 bryophyte species included in the analysis, there was a larger proportion associated with Norway spruce than with Scots pine (Fig. 4b). Examples included several species within the genera of *Hypnales*, e.g. *Brachythecium*, *Sciuro-hypnum*, *Plagiothecium* (most of the species), *Thuidium* and *Rhytidiadelphus*. The number of Scots pine associated taxa was lower, but included e.g. *Ptilidium ciliare*, *Dicranum spurium*, *S. ampullaceum*, *Plagiothecium succulentum* and species belonging to the genus of *Racomitrium*.

In contrast, most of the 14 lichens included in the analysis were more strongly associated with the Scots pine stands, including the two most commonly encountered lichen species *C. rangiferina* and *C. arbuscula*.

In the NMDS, 9 of the 14 environmental variables were significant ($p < 0.05$) (Table 3). Excluded environmental variables were latitude, abundance of the understory shrub layer, vascular plant cover, mineral soil pH and humus layer thickness. The Scots pine bryophyte communities were more associated with higher canopy openness and a larger C:N ratio than the communities of Norway spruce stands (Fig. 4b). The Norway spruce stands, instead had more species communities associated with both hard and soft dead wood, higher SI and basal area.

3.5. Different forest floor conditions of Scots pine and Norway spruce stands

The result from the analysis using Ellenberg indicator values, revealed significant differences (Fig. 5 a-f; Appendix A: Table A2) between Scots pine and Norway spruce stands for all the environmental variables tested. Norway spruce stands had a larger proportion of forest floor species indicating more humid and dark conditions, compared to Scots pine stands (Fig. 5b). There was also an effect of stand age, whereby the 80-year-old stands were associated with significantly more species requiring more humid conditions than the 55-year-old stands (Fig. 5a). The bryophyte and lichen flora also indicated a higher proportion of species tolerant of acidic conditions and with lower requirements for nitrogen in the Scots pine stands, compared to the Norway spruce stands (Fig. 5d). Ellenberg values indicated that the conditions were less acidic in the 80-year-old stands than in the 55-year-old stands (Fig. 5c), although our direct pH measurements in the B-horizon did not show this. Finally, a higher proportion of species indicating higher temperatures and more continental conditions were found in the Scots pine stands (Fig. 5e-f).

4. Discussion

Previous studies have emphasized the importance of site fertility and moisture for the understory community composition of boreal forests (Lahti & Väisänen 1987; Økland and Eilertsen, 1993). The importance of these gradients becomes especially distinct when comparing a wider ecoline (Whittaker 1967) of forest stands, e.g. when including vegetation types extending from xeric lichen-dominated Scots pine forests to moist and nutrient rich forests, which in this region are often dominated by Norway spruce (Cajander 1909). Furthermore, soil nutrient and moisture conditions become clear determinants of understory communities at the extremes ends of ecolines (Nihlgård 1970; Persson 1981). In contrast to these extremes, our study focused on an 'intermediate' band of the boreal forest ecoline, which could be planted with either of the two tree species considered. With respect to natural forest succession, these sites correspond to those in which Scots pine occurs as a pioneer species, followed by Norway spruce ingrowth and overshadowing in later successions. It was under these conditions that we found the tree species and associated openness of the canopy had a significant effect on the forest floor bryophyte and macrolichen communities.

4.1. Forest floor vegetation cover

Bryophytes associated with forest interiors tend to be dependent on stable environmental conditions, making their populations susceptible to disturbances associated with final harvesting, and subsequent soil scarification for stand regeneration (Schmalholz & Gustafsson 2016). For this reason, bryophyte coverage usually increases with stand age, partly as a result of the decline in competition with field layer vegetation when the canopy closes after clearcut stage, but also because of the time required for forest floor vegetation establishment (Schmalholz & Hylander 2009). Here, we did not find any significant increase in bryophyte cover between the youngest and oldest stands assessed (Fig. 3), indicating that the bryophyte cover had largely stabilized by the time 30 years at elapsed since regeneration disturbance. This conclusion is likewise supported by Schmalholz and Hylander (2009), who found that the cover of bryophytes stops increasing once stands reach 30 year of age in their study of a chronosequence of Norway spruce dominated stands in southern-central Sweden.

The higher cover of vascular plants in the Scots pine stands (Table 1), could have been expected to negatively impact on the forest floor vegetation of these stands (Carleton 1990). Nevertheless, our study did not detect any significant difference in the total forest floor coverage of bryophyte and lichens between Scots pines and Norway spruce stands (Table 2). This suggests, at least for the conditions assessed, that there is no significant trade-off between the upper-level coverage of the understory (e.g. ericaceous shrubs), and the underlying forest floor vegetation in these forest stands. In this regard, bryophytes appear to be using microhabitats that are not available to, or provided by, vascular plants (Qian et al. 1998).

Forest floor lichens, especially from the genera of *Cladonia*, often dominate the understory in dry and rocky sites, especially in northern boreal forests (Ahti & Oksanen 1990). However, in this study, lichens only constituted a small fraction of the vegetation, albeit making a slightly larger contribution to the 55-year-old Scots pine stands. Forest floor lichens can be sensitive to competition from feathermosses (Coxson & Marsh 2001), and tend to be outcompeted as favourable conditions for feathermosses increase, e.g. due to increased canopy cover (Sulyma 2009). Because of the sensitivity of lichens to competition with other flora, some studies have found that lichen cover can be favoured by disturbance. For instance, Bråkenhielm and Persson (1980) and Tonteri et al. (2016) found a temporary increase in reindeer lichens after commercial thinning, which was thought to result from increased light transmittance in combination with reduced competition from dwarf shrubs. In this study, the high canopy cover of the Norway spruce stands, and the competition from feather mosses and vascular plants in the Scots

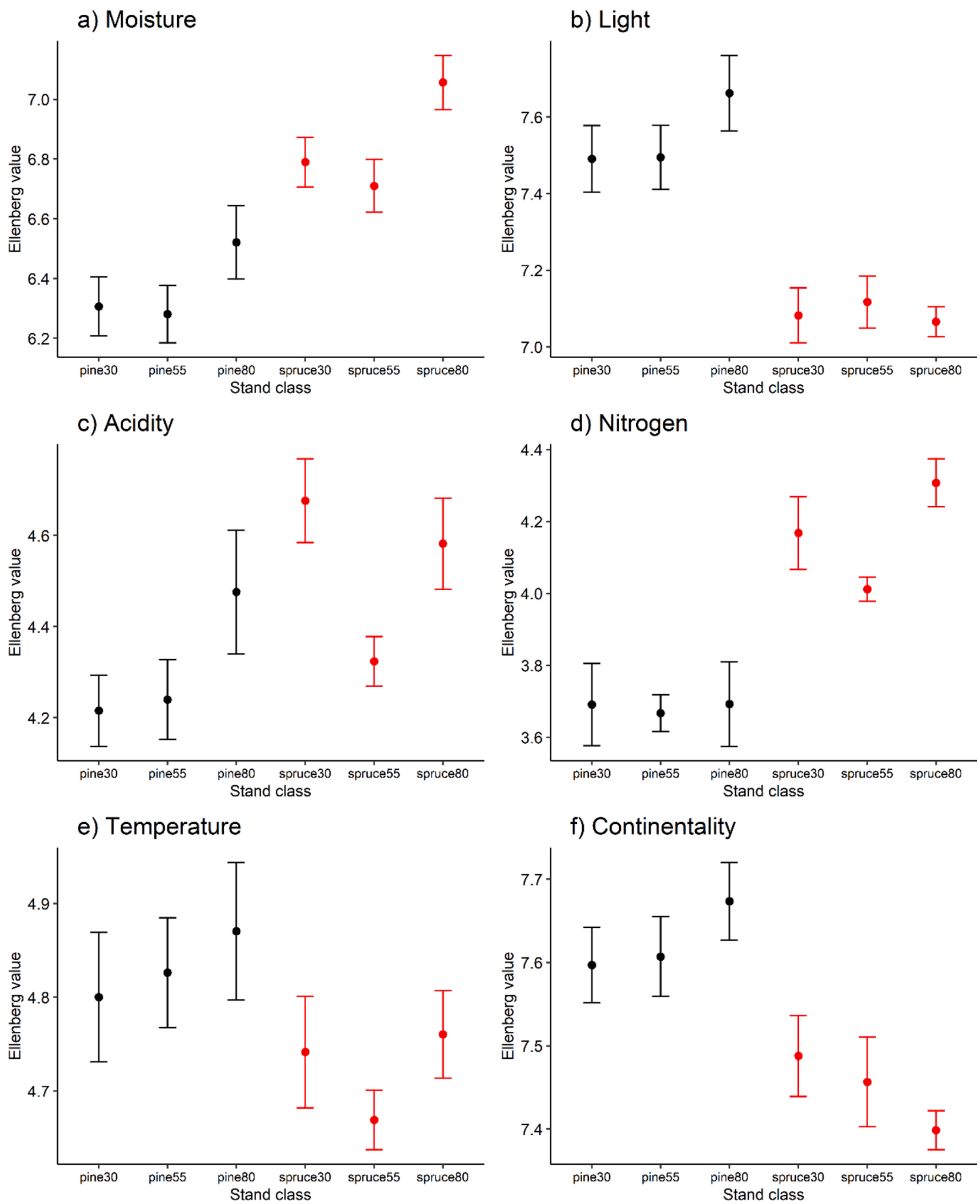

Fig. 5. a-f. Mean Ellenberg indicator values and SE for forest floor bryophytes and lichens at stand level, in Scots pine and Norway spruce production stands.

pine stands, likely limited the expansion of forest floor macrolichens.

4.2. Species richness and community composition

Scots pine and Norway spruce stands differed in terms of the community composition and species richness of bryophytes and lichens. With respect to community composition, the multivariate analysis highlighted the importance of the two different managed tree species in distinguishing between the different forest floor communities that developed. Bryophyte species richness was higher in Norway spruce stands for all stand ages (Fig. 2; Appendix A: Table A1). The highest mean species richness was found in 80-year-old Norway spruce stands, for which there was also a larger amount of both soft and hard dead wood compared to the other stand age classes. From the species associated with the Norway spruce stands, there was also a comparably larger variety of substrate-associations and life forms. This included species strongly associated with dead wood, such as *Lepidozia reptans*, *Dicranum fuscescens*, *Tetraphis pellucida*, *Blepharosroma trichophyllum*, and *Nowellia curvifolia* (Söderström 1988; Atherton et al. 2010). In comparison with younger Norway spruce stand categories, the bryophyte layer in the 80-year-old stands included the more frequent occurrence of additional 'mat' and 'turf forming' species (e.g. *Thuidium tamariscium*, *Dicranum majus*, *Plagimnium* affine, *Sphagnum capillifolium* and *S. girgensohnii*), which formed patches among more common species, such as *P. schreberi* and *H. splendens* (Fig. 3).

A comparably limited number of bryophytes were associated with the Scots pine stands. For example, there were no dead wood-associated species among the bryophytes primarily occurring or exclusive to Scots pine stands (Fig. 5b). Of the species that did occur within these stands, many are tolerant of silicate rich substrates, and can otherwise be found on boulders, rocks and soils in dry open forest land (Hallingbäck and Knorring, 2006; Longton, 1992). In comparison to the species found in

Norway spruce stands, Scots pine associated species are often specialized in dryer conditions. For example, the lichen species *Cetraria islandica*, *Cladonia rangiferina* and *C. arbuscula* were found more frequently in the Scots pine stands (Appendix B: Table B1). All of these lichen species can tolerate dehydration and are often found in xeric environments (Kuusipalo 1985; Hájek et al. 2001). Drought adaptations were also exhibited by some Scots pine associated bryophytes, such as the hair-pointed leaves of *Racomitrium heterostichum*, *R. lanuginosum*, and *Campylopus introflexus*, the infolding of the leaf margins in *Polytrichum juniperinum*, and the undulate leaves of *Dicranum spurium*, which form small water-retaining chambers (Hallingbäck and Knorring, 2006; Watson, 1914).

4.3. Forest floor microhabitat differences

Because of the range of structural differences that distinguished Scots pine and Norway spruce stands (Table 1), we also expected differences in the microhabitats provided, and abiotic habitat-associations of the forest floor species that occurred. Correspondingly, the results of the Ellenberg indicator analysis (Appendix A: Table A2) showed significant differences between Scots pine and Norway spruce stands, for all of the variables tested. The higher canopy openness found in the Scots pine stands (Table 1), correspondingly had a higher proportion of forest floor species indicative of higher light transmittance relative to Norway spruce stands. Also the higher cover of lichens found in the Scots pine stands, is consistent with what can be expected from more open forest conditions (Bäcklund et al. 2015; Boudreault et al. 2015).

Scots pine stands were also characterised by species tolerating higher temperatures and having better adaptations to continental climates. This might also be a consequence of the higher degree of canopy openness in these stands. Moreover, the usually thinner humus layer, characteristic for Scots pine stands, is a common cause of soil moisture deficiency (Økland and Eilertsen, 1993). This can in turn result in vascular plant withering, an has previously shown to be an important driver of both vascular species richness and understory composition in Scots pine forests (Økland and Eilertsen, 1993; Økland 1995), and might be a reason for lower the species richness of vascular plants that also can be found in Scots pine production stands (Petersson et al. 2019). Relatedly Scots pine stands supported a higher proportion of species indicative of continental conditions, whereas Norway spruce stands supported more oceanic condition species. Continental conditions are associated with warm dry summers and colder winters, conditions probably enhanced in Scots pine stands by their lower canopy cover and reduced protection from frost.

Over exposure to intense light can cause damage both to bryophytes and lichens (Heber & Lüttge 2011), and bryophytes sensitive to desiccation can be particularily sensitive to high exposure of UV-B light (Takács et al. 1999). At the same time, the insufficient levels of light as often found in dense Norway spruce stands planted on agricultural land, can even limit the cover of relatively shade tolerant species of weft forming mosses (Nihlgård 1970). In contrast to the comparably more bright and open environment found in the Scots pine stands, the micro climate of the Norway spruce stands was affected by higher canopy cover resulting in less light reaching to the forest floor (Table 1.). The reason for this is because of Norway spruce stands comparably larger leaf area (Goude et al. 2019), and possibly also the an effect of the lower thinning intensities generally applied in Norway spruce stands. In this study, the mean Ellenberg light value and the canopy openness, as measured from the hemispherical pictures, both showed significant differences between Norway spruce and Scots pine stands.

The higher canopy cover of Norway spruce stands, likely contributed to the occurrence of forest floor species associated with more humid cold microclimates. A gradient in humidity and moisture levels between open Scots pine and shady Norway spruce has been shown to be of importance for determining understory bryophyte composition (Dynesius et al. 2021). Substrate pH is also known to be of importance for many bryophyte species (Hydbom et al. 2012), and higher pH is often associated with higher species richness (Hylander & Dynesius 2006). Complicating this relationship, different species of bryophytes are often associated with different ranges of pH, with resultant impacts on bryophyte species composition (Hallingbäck 2016; Tyler & Olsson 2016). Because the bryophytes recorded in this study were found on all types of substrates, it's possible that the characteristics and availability of other growth substrates aside from the forest floor (e.g. different types and availability of dead wood) may be affecting our results. This caveat is especially relevant for the 80-year-old Norway spruce stands, in which there was more dead wood relative to the other stand categories (Table 1). For example, whereas the top soil pH is generally similar in Scots pine and Norway spruce stands (Augusto et al. 2003), and the pH of soft dead wood is relatively similar for both of the tree species assessed, debarked hard dead wood from Scots pine can be more acidic than that of Norway spruce (Wiklund 2003). Because of this, the results from the Ellenberg indicator analysis likely reflect the characteristics of the different microhabitats that are available within Scots pine and Norway spruce managed stands. Whereas nitrogen levels may also have influenced outcomes, and the Ellenberg value for nitrogen were on average higher in the oldest and youngest Norway spruce stands, interpretation of these results can be complicated by, for example, the capacity of some species e.g. *P. schreberi* and *H. splendens* to have symbiotic relationships with nitrogen fixing cyanobacteria (DeLuca et al. 2002; Stuiver et al. 2015). Furthermore, we cannot quantify the extent to which outcomes were influenced by *a priori* differences in site conditions, such as differences associated with historical land use.

4.4. Implications for species conservation and forest management

Although some of the 80-year-old stands of Norway spruce supported relatively large amounts of dead wood, and nine bryophyte species were encountered which are considered to be indicators of forests with high conservation value (Norén & Larsson 2014), no nationally red listed species occurred in our study (note that *Splachnum ampullaceum* - is red listed in Europe). In terms of the ecosystem services implications of our results, the similarity in bryophyte cover between Scots pine and Norway spruce stands could indicate that the ecological functions provided specifically by the bryophyte community (i.e. water regulation and nutrient recycling) overlapped between the two stand types. However, differences were observed between Norway spruce and Scots pine stands in the community composition of the forest floor bryophyte and lichen communities, as well as in the Ellenberg values for bryophytes. These results, in combination with the fact that production forests are the dominant source of forest area in Sweden, indicate that the conversion of Scots pine stands to Norway spruce will result in large scale shifts in forest floor conditions and associated bryophyte and lichen communities.

CRediT authorship contribution statement

Lisa Petersson: Conceptualization, Investigation, Methodology, Data curation, Formal analysis, Writing - original draft. **Staffan Nilsson:** Investigation, Methodology, Writing - review & editing. **Emma Holmström:** Conceptualization, Supervision, Methodology, Writing - review & editing. **Matts Lindbladh:** Supervision, Writing - review & editing, Conceptualization. **Adam Felton:** Conceptualization, Supervision, Methodology, Writing - review & editing, Funding acquisition.

Declaration of Competing Interest

The authors declared that there is no conflict of interest.

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Appendix A

See Tables A1 and A2

Table A1
Average species richness (species/stand) between the combination of tree species and stand age. Stand age is only included in the analysis if there are significant differences.

	mean	SE	df	t	p-value	sign.
All species						
Norway spruce	33.9	1.1	54	7.9	< 0.0001	***
Scots pine	23.0	0.9	54			
Norway spruce 30	32.8	1.8	54	3.6	0.0007	***
Scots pine 30	24.2	1.6	54			
Norway spruce 55	32.2	1.8	54	3.1	0.0032	**
Scots pine 55	24.8	1.6	54			
Norway spruce 80	36.9	1.9	54	6.9	< 0.0001	***
Scots pine 80	20.2	1.4	54			
Norway spruce 30/55	29.3	1.7	27	0.3	0.94	
Norway spruce 30/80	28.5	1.7	27	−1.0	0.55	
Norway spruce 55/80	31.9	1.8	27	−1.4	0.36	
Scots pine 30/55	23.1	1.5	27	0.5	0.89	
Scots pine 30/80	24.1	1.5	27	2.0	0.12	
Scots pine 55/80	18.9	1.4	27	2.5	0.047	*
Bryophytes						
Norway spruce	29.0	1.0	54	7.3	<0.0001	***
Scots pine	19.6	0.8				
Norway spruce 30	28.3	1.7	54	3.2	0.002	**
Scots pine 30	21.1	1.4				
Norway spruce 55	27.3	1.6		2.8	0.007	**
Scots pine 55	21.1	1.4				
Norway spruce 80	31.6	1.8		6.5	<0.0001	***
Scots pine 80	16.9	1.3				
Mosses						
Norway spruce	24.0	0.9	54	6.7	<0.0001	***
Scots pine	16.2	0.7	54			
Norway spruce 30	23.8	1.5	54	2.8	0.007	**
Scots pine 30	18.0	1.3	54			
Norway spruce 55	22.4	1.5	54	2.5	0.02	*
Scots pine 55	17.4	1.3	54			
Norway spruce 80	26.1	1.6	54	6.2	< 0.0001	***
Scots pine 80	13.6	1.2	54			
Liverworts						
Norway spruce	4.9	0.4	58	2.96	0.004	**
Scots pine	3.4	0.3	58			
Lichens	mean	SE	df	t	p-value	sign.
Norway spruce	0.9	0.2	58	−4.38	<0.0001	***
Scots pine	2.5	0.3	58			

Table A2
Differences in mean Ellenberg-values for bryophytes at stand level for Scots pine and Norway spruce stands.

	estimate	SE	df	t	p-value	sign.
Moisture						
Scots pine - Norway spruce	−0.48	−0.48	56	−6.1	<0.0001	***
30–55	0.05	0.10	56	0.5	0.85	
30–80	−0.24	0.10	56	−2.5	0.18	
55–80	−0.29	0.10	56	−3.0	0.009	**
Light						
Scots pine - Norway spruce	0.46	0.06	58	7.4	<0.0001	***
Reaction						
Scots pine - Norway spruce	−0.22	0.08	56	−2.7	0.008	**
30–55	0.16	0.10	56	1.7	0.22	
30–80	−0.08	0.10	56	−0.9	0.67	
55–80	−0.25	0.10	56	−2.5	0.04	*
Nitrogen						
Scots pine - Norway spruce	−0.48	0.07	58	−6.6	<0.0001	***
Temperature						
Scots pine - Norway spruce	0.11	0.05	58	2.3	0.02	*
Continentality						
Scots pine - Norway spruce	0.18	0.04	58	4.8	<0.0001	***

Appendix B

See Table B1

Table B1
Number of occurrences of all species of bryophytes and lichens found throughout the survey of 600 plots located in Scots pine and Norway spruce dominated production stands. Abbrevations are used in the ordination plot (Fig. 4b) Indicator species for forests of high conservation values are categorized acording to (Nitare & Hallingbäck 2000) and the information about the red listed species originates from (Hodgetts et al. 2019).

Bryophyte species	Scots pine	Norway spruce	Signal species	Abbrevation
Amblystegium serpens	1	1		Amber
Andreaea rupestris	2	4		Andrup
Atrichum undulatum	3	13		Atrund
Aulacomnium androgynum	54	128		Auland
Aulacomnium palustre	74	97		Aulpal
Barbilophozia attenuata	2	2		Baratt
Barbilophozia barbata	17	38		Barbar
Bazzania trilobata	1	2	high	Baztri
Blepharostoma trichophyllum	0	9		Bletri
Brachytheciastrum velutinum	1	0		Bravel
Brachythecium rutabulum	0	2		Brarut
Brachythecium salebrosum	1	10		Brasal

(continued on next page)

Table B1 (*continued*)

Bryophyte species	Scots pine	Norway spruce	Signal species	Abbrevation
Bryum capillare	0	1		Brycap
Bryum moravicum	1	0		Brycap
Buxbaumia viridis[1]	0	5	high	Buxvir
Calypogeia integristipula	3	3		Calint
Calypogeia muelleriana	1	6		Calmue
Campylopus introflexus[2]	2	0		Camint
Cephalozia bicuspidata	0	1		Cepbic
Ceratodon purpureus	5	3		Cerpur
Dicranella heteromalla	4	16		Dichet
Dicranoweisia cirrata	24	2		Diccir
Dicranum flagellare	1	0	high	Dicfla
Dicranum fuscescens	11	55		Dichet
Dicranum majus	4	136		Dicmaj
Dicranum montanum	90	124		Dicmon
Dicranum polysetum	300	233		Dicpol
Dicranum scoparium	271	292		Dicsco
Dicranum spurium	32	2		Dicspu
Ditrichum heteromallum	5	6		Dithet
Eurhynchium angustirete	0	4		Eurang
Eurhynchium striatum	0	1	high	Eurstri
Grimmia hartmanii	0	1		Grihar
Hedwigia ciliata	6	14		Hedcil
Hylocomiastrum umbratum	0	1	high	Hylumb
Hylocomium splendens	289	299		Hylspl
Hypnum cupressiforme	161	242		Hypcup
Hypnum jutlandicum	0	7		Hypjut
Isothecium alopecuroides	0	4		Isoalo
Isothecium myosuroides	1	5		Isomyo
Lepidozia reptans	5	56		Leprep
Leucobryum glaucum	19	19	intermediate	Leugla
Lophocolea bidentata	0	1		Lopbid
Lophocolea heterophylla	17	130		Lophet
Lophozia ventricosa	1	3		Lopven
Marchantia polymorpha subsp polymorpha	0	1		Marpol
Mnium hornum	4	37		Mnihor
Nowellia curvifolia	0	6	intermediate-high	Nowcur
Oligotrichum hercynicum	1	0		Oliher
Paraleucobryum longifolium	0	10		Parlon
Pellia epiphylla	0	2		Pelepi
Plagiochila asplenioides subsp asplenioides	0	2		Plaasp
Plagiochila asplenioides subsp porelloides	0	7		Plapor
Plagiomnium affine	1	107		Plaaff
Plagiothecium curvifolium	5	74		Placur
Plagiothecium denticulatum	46	217		Pladen
Plagiothecium succulentum	7	0		Plasuc
Plagiothecium undulatum	0	9	high	Plaund
Pleurozium schreberi	300	300		Plesch
Pogonatum urnigerum	1	2		Pogurn
Pohlia nutans	230	177		Pohnut
Pohlia wahlenbergii	0	1		Pohwah
Polytrichastrum formosum	75	213		Polfor
Polytrichum commune coll.	5	30		Polcom
Polytrichum juniperinum	35	28		Poljun
Polytrichum strictum	1	0		Polstr
Pseudoscleropodium purum	0	7		Psepur
Pseudotaxiphyllum elegans	1	0		Pseele
Ptilidium ciliare	47	14		Pticil
Ptilidium pulcherrimum	120	175		Ptipul
Ptilium crista-castrensis	21	127		Pticas
Pylaisia polyantha	0	1		Pylpol
Racomitrium affine	1	0		Racaff
Racomitrium heterostichum	80	36		Rachet
Racomitrium lanuginosum	44	13		Raclan

Table B1 (*continued*)

Bryophyte species	Scots pine	Norway spruce	Signal species	Abbrevation
Rhodobryum roseum	0	20		Rhoros
Rhytidiadelphus loreus	0	9	high	Rhylor
Rhytidiadelphus squarrosus	1	12		Rhysqu
Rhytidiadelphus triquetrus	0	20		Rhytri
Riccardia chamedryfolia	0	1		Riccha
Riccardia latifrons	1	1		Riclat
Sanionia uncinata	13	17		Sanunc
Scapania nemorea	0	7		Scanem
Sciuro-hypnum curtum	38	142		Scicur
Sciuro-hypnum populeum	0	1		Scipop
Sciuro-hypnum reflexum	0	21		Sciref
Sphagnum capillifolium	43	54		Sphcap
Sphagnum fimbriatum	1	0		Sphfim
Sphagnum girgensohnii	11	62		Sphgir
Sphagnum magellanicum coll.	1	1		Sphcol
Sphagnum palustre	2	9		Sphpal
Sphagnum russowii	0	2		Sphrus
Splachnum ampullaceum[3]	2	0		Splamp
Tetraphis pellucida	9	60		Tetpel
Thuidium delicatulum	0	3		Thudel
Thuidium tamariscinum	0	39		Thutam
Tritomaria quinquedentata	1	0		
Lichen species	Scots pine	Norway spruce	Signal species	Abbrevation
Cetraria islandica	7	0		Cetisl
Cladonia arbuscula	180	20		Claarb
Cladonia botrytes	1	0		Clabot
Cladonia chlorophaea	2	0		Clachl
Cladonia cornuta	1	0		Clacor
Cladonia furcata	2	2		Clafur
Cladonia pyxidata	0	1		Clapyx
Cladonia rangiferina	244	45		Claran
Cladonia sp 1	2	0		Cla.sp1
Cladonia sp 2	1	0		Cla.sp2
Cladonia squamosa	0	11		Clasqu
Cladonia stellaris	4	0		Claste
Cladonia uncialis	1	0		Clauni
Sphaerophorus globosus	0	1		Sphglo

[1]Listed in the European habitat directive Annex II and in the Bern convention Appendix I.
[2]Listed as NA (not applicable), on the European red list.
[3]Listed as NT (near threatened) within Europe, and VU (vulnerable) within the EU on the European red list.

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