Tree species impact on understory vegetation: Vascular plant communities of Scots pine and Norway spruce managed stands in northern Europe

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ABSTRACT

The tree species used in production forests can have direct implications for the understory vegetation, due to species-specific differences in the environmental conditions provided, and silviculture applied. In southern Sweden, there is an ongoing shift from even-aged managed stands of Scots pine (*Pinus sylvestris*) to even-aged Norway spruce (*Picea abies*). Here we evaluate the potential ecological consequences of these conversions by surveying the understory vascular plants, stand structural characteristics, and associated understory light levels in three age categories of Scots pine and Norway spruce stands. We quantify the extent of difference in light transmittance between the two stand types, and find large differences in understory abundance, especially among the dwarf shrubs species. Whereas bilberry (*Vaccinium myrtillus*) generally dominated Scots pine stand understory, the understory of Norway spruce stands was comparably sparse. Differences in vascular plant community composition indicate associated differences between the two stand types in the conditions prior to stand establishment, and subsequent understory development. In Scots pine stands the high abundance of dwarf shrubs may be outcompeting other species of vascular plants, causing a decline in species richness. In Norway spruce stands, species richness and abundance was instead apparently inhibited by limited light transmittance. In these stands generalist ruderal species and remnants from previous land use constituted a considerable part of plant species composition. Our findings suggest that the regional replacement of Scots pine with Norway spruce will lead to a noticeable loss of understory diversity, for which the decline in *Vaccinium* species will be the most prominent. We discuss the associated implications of our results for forest ecosystem services, and how shortened rotation lengths in Norway spruce stands would compound these impacts.

1. Introduction

Understory plants account for the majority of floristic diversity in northern conifer forests (Halpern and Spies, 1995), and further contribute to biodiversity by providing essential food and habitat resources for many wild species, including insects (Szujecki, 2012), birds (Storch, 1993) and deer (Felton et al., 2018). In addition, understory plants provide important ecosystem services by supporting tree-seedling regeneration, soil nutrient cycling (Busse et al., 1996, Nilsson and Wardle, 2005, Zhao et al., 2014, Chen and Chen, 2019), and non-wood forest products (e.g. bilberry *Vaccinium myrtillus*) for harvest and recreational enjoyment (Lindhagen and Bladh, 2013). The composition and abundance of understory plant communities that develop in forest ecosystems, are primarily thought to result from competitive interactions between different understory species, within the constraints of available soil resources and light transmittance as governed by the overstory (Kuusipalo, 1985). The tree species composition, proportions, and density of overstory trees is an important determinant of these interactions, due to its influence on light transmittance, soil insolation, moisture content, and nutrient cycling (Barbier et al., 2008, Felton et al., 2010). The diversity of understory plant communities can likewise be expected to change over time as the overstory develops, due to associated changes to light levels, litter-fall, nutrient cycling (Kumar et al., 2018), and disturbance regimes (Widenfalk and Weslien, 2009). Because of the direct and indirect contribution of understory vegetation to forest biodiversity, and the wide range of ecosystem services understory plants provide, it's important to understand the implications of different production forest management practices on this ecological community.

In Sweden, the majority of forest area is intensively used for biomass production. The Swedish forestry is defined by the rotational clearfelling of even-aged stands, and is extensively reliant on two native conifer species, Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), which together comprise 80% of standing volume (SFA, 2014). Their

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division of use is defined to some extent by their distinct ecological characteristics. Scots pine is a pioneer tree species that under natural conditions often establishes shortly after disturbances, such as fire or wind throw (Nilsson et al., 2012), on coarse, well drained and often nutrient poor soils (Engelmark and Hytteborn, 1999). In contrast, Norway spruce is a late successional shade-tolerant tree species which is a stronger competitor on mesic intermediate to nutrient-rich soils. Due in part to their distinctive ecologies, Scots pine is traditionally used in forestry to regenerate areas ranging from intermediate to poor site quality, whereas Norway spruce plantings are generally restricted to more fertile areas. However, in southern Sweden high browsing pressure on Scots pine saplings (Wallgren et al., 2013), together with Norway spruces' easier management and potentially better profits (Lodin et al., 2017), has led to an increase in Norway spruce regeneration on sites traditionally planted with Scots pine (Claesson et al., 2015, Skogsstyrelsen, 2017). This is occurring in a region where Norway spruce already comprises almost 50% of standing volume (SFA, 2014). As a result Norway spruce regeneration is no longer restricted to fertile sites in southern Sweden and is instead the most commonly chosen tree species for regeneration regardless of whether the site is of low, medium and high soil fertility (SFA, 2018). Hence, the proportion of Norway spruce in this region is projected to further increase, primarily at the expense of Scots pine (Claesson et al., 2015).

In this study we assess the potential implications for understory vegetation by studying differences in understory community composition and abundance within three age categories of Norway spruce and Scots pine stands in southern Sweden. The main purpose of this study was to examine the potential consequences for understory vegetation derived from a shift in the production crop tree species. As the rotation lengths used for Scots pine stands are generally longer than those of Norway spruce, and rotation lengths may further reduce in Norway spruce stands (Felton et al., 2017a), we also consider the potential implications of differences in these silvicultural practices for understory vegetation. We see this study as part of larger efforts to reduce knowledge gaps regarding the influence of production forest tree species choice on understory vegetation.

2. Method

2.1. Study area description

The study area (3200 km^2) is situated in the hemiboreal zone (Fig. 1.), of southern Sweden within the adjacent counties of Kalmar and Kronoberg. Annual mean temperature is 6 °C, ranging from 15 °C during the summer (June-August) to −1 °C in the winter (December-February), with a growing season of 200–230 days. Mean annual precipitation ranges from 800 mm/ year in the west, to 600 mm/year in the east (SMHI, 2019). The bedrock consists primarily of silicate rich granite and rhyolite, intermixed with patches of mafic rock. Soil texture is typically medium grained till and degraded sediment, but there are also areas with exposed basement rock, and peat (Wastenson and Fredén, 1994).

2.2. Site selection

Stands were selected from the land ownership databases of Sveaskog (state-owned forest company) and the Södra private forest owners association based on dominant tree species, age and site index classification, all according to the forest plans. The dominant tree species should be either monoculture (> 80% of basal area) of Norway spruce or Scots pine, and the stand age one of three distinct age classes, being either 30 (± 5 years), 55 (± 5 years) or 80 (± 5 years) years. Thereafter, a stratified random sample, based on the dominant tree species and age classes was made with 10 stands in each strata (further on referred to as stand types), in total 60 stands.

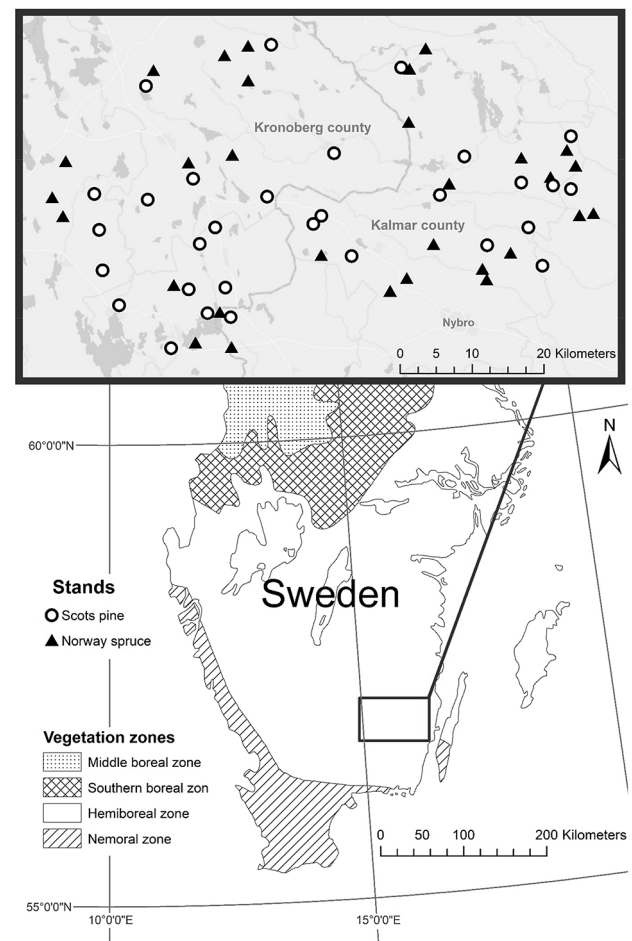The three age classes represented early, mid and late rotation stands

Fig. 1. The location of sixty Norway spruce and Scots pine study sites in the south eastern part of Sweden used to quantify differences in understory vegetation. Biogeographic zones according to (Wastenson et al., 1996). ESRI, HERE, Garmin, © OpenStreetMap contributors, and the GIS user community.

respectively. Most of the 30 year old stands had a single commercial thinning, and the majority of 55 year old stands had been thinned twice. Two of the 80 years old Scots pine stands were recently thinned for a third time. To minimize edaphic variability, all selected stands were located on till soils with either rhyolite or granite bedrock (SGU, bedrock map, soil type map 1:25 000–1:100 000), and at least 500 m away from any open water shoreline. To reduce site history differences, the two younger age categories were restricted to those established on previously forested lands (Swedish land survey: Economic map 1941–1949). This could not be done for the oldest stands because the necessary information was not available. Stands were further restricted to increase overlap in their site index (SI), a number equivalent to a stand's projected dominant height in meters after 100 years. Information about assumed stand SI was taken from forest management plans but corrected to a measured SI based on dominant height in the inventories described below.

2.3. Field methods

The vegetation survey, and most forest structure measurements, were conducted during June – October 2016. Soil samples, sapling layer and increment cores were collected during the same period of 2017. Stands averaged 7.9 ha ± 4.3 SD (range 2.8–31.7 ha) in size, and 10 plots of 2 × 2 m were randomly placed within each stand, no closer than 30 m from the forest age, and at least 25 m apart from each other, using GIS Collector © ESRI. Upon perusal, plot locations 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 too wet – as indicated by open water surface, or > 20% cover of *Sphagnum* species (with the exception for *S. girgensohnii* and *S. capillifolium*). Within each of the 600 plots, the percentage cover of terricoulus lichens, bryophytes (more details will come in an additional article) and vascular plants was recorded. To capture as much of the ground vegetation taxonomic diversity as possible, we also surveyed the presence of these taxonomic groups within a 100 m² plot surrounding each of the 2 × 2 m central plots. The layer of tree saplings was measured in the same area, as the number of stems of 0.3–1.3 m tall shrubs and tree saplings. The proportion of exposed soil, due to animal rooting or forest operations, and exposed stone surface, was also recorded.

Basal area was assessed using the vegetation plot's centroid and the diameter at breast height (DBH) 1.3 m above the root collar, of 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 surveyed circle was extended to 10 or 15 m radius. Stand age was primarily estimated from the average of four increment cores, but if permission for coring was denied from the forest owner, the number of branch whorls was counted instead. Stand site index was calculated from the average height and age (as estimated from increment cores and branch whorls) of the two trees with the largest DBH from each plot (Elfving and Kiviste 1997, Elfving 2010). Light transmittance was measured using circular hemispherical digital photos, taken with a Nikon D5300 and Sigma 4.5 mm f/2.8 fisheye lens. The photos were taken from the central point of each plot at 1 m above ground level. Pictures were analysed in Gap light analyser (GLA) (version 2.0), with the two outer rings excluded.

To examine eventual differences in soil properties and chemistry in the different sites, soil samples were taken and analysed. Within four plots, humus layer was sampled down to 10 cm with a 4.4c Ø tube. In plots with a shallow humus layer, several samples had to be taken to achieve the same volume. The amount of organic material was determined by loss of ignition (KLK 1965:1 mod) and transformed into carbon volumes (Sparks, 1996) by a conversion factor of 1.9 (Pribyl, 2010). Since many forest plants have the capacity to take up organic N, in addition to nitrate and ammonium (Lipson and Näsholm, 2001), N (Dumas) was also determined using a LECO FP-428 analyser. The top 10 cm of the B-horizon was sampled the same way, and its pH was analysed (SS-ISO 10390:2007). The thickness of the humus and iron pan layer (when present) was measured in cm. Soil moisture, water bodies, and soil layer thickness was classified according to Hägglund and Lundmark (2003).

2.4. Statistical methods

Our primary focus was to assess relationships between the dominant tree species, and the abundance and composition of understory vascular plant communities. After evaluating the influence of stand age, and controlling for edaphic factors, our focus turned to understanding the potential underlying processes that may be driving these patterns, with light transmittance a key consideration.

Statistical analyses were conducted in R (R Core Team, 2018). Before all statistical testing, an intra-class correlation coefficient test (ICC) (Cicchetti, 1994) was made, to control for cluster effects between plots located closer to each other within the stand. No correlation was detected (corr. coef. < 0.36). The following understory vegetation characteristics were tested in the study: Understory richness, ground cover and composition of functional groups and sapling abundance. The analyses were conducted at the stand level, using the six combinations of tree species and stand age. To compare forest structure between the different stand types, the evaluated aspects of forest structure were tested against the interaction of tree species and stand age in ANOVA, followed by a post hoc test (Tukey HSD). Light transmittance in relation to basal area, understory composition and community composition, and

their relation to stand type, was analysed at the sample plot level in a mixed model with the interaction of tree species and stand age used as explanatory variables, and the individual stands set as a random variable.

All species in the understory vegetation were classified and sorted to seven functional species groups, which was further on used in all analysis of understory vegetation response to stand types. The seven categories were: (1) dwarf shrubs (including the genus *Calluna*, *Empetrum* and *Vaccinium*), (2) grasses (also including *Cyperaceae* and *Luzula*), (3) herbs (also including *Lycopodiaceae*), (4) tree saplings (also including *Juniperus communis*), (5) ferns, (6) bryophytes and (7) terricoulus lichens.

In order to evaluate the understory vegetation response to stand types, the abundance of the functional species groups were tested against the interaction of tree species and stand age in ANOVA, followed by a post hoc test (Tukey HSD). General differences due to the tree species overstory were tested with a Welch two sample *t*-test.

2.4.1. Regression analysis

To further test the effect of tree species, stand age, and light transmittance on vascular plant abundance and the number of saplings ha^{-1}, linear regression was performed using stand averaged data. To trace out the more direct impact of light transmittance on understory vegetation, an additional analysis was made at the plot level with mixed model from R package lmerTest (Kuznetsova, 2017). In the first test, the total understory abundance was set as a response variable depending on sample plot estimates, where stand origin of the sample plots was nested as a random variable. Because of the initially skewed residual distribution from the Norway spruce model, the understory data was log (y + 1) transformed prior to further testing. No such transformation was needed for the Scots pine abundance data, but to assure that transformation didn't affect the outcome, models where Scots pine abundance were included were tested with the log(y + 1) response variable in addition to the original data. In the second test, the number of saplings ha^{-1} was tested after being transformed using log(y + 0.5). Here Scots pine and Norway spruce could be tested in the same model without violating the assumptions of normally distributed residuals. Finally, the species richness of vascular plants was tested in generalized mixed models (GLMM) (Bates et al., 2015), with Poisson log-normal link and stand set as random variable. Light transmittance was scaled before set as explanatory variable. All logistic tests were controlled for dispersion.

2.4.2. Multivariate analysis

Before analysing the community composition, all understory species recorded < 5 times across all stands were removed. Within each stand, the frequency of all plants present were calculated as the number of sample plots in which the species was present (0–10). Nonmetric Multidimensional Scaling ordination (NMDS) (Oksanen et al., 2013) was run with 999 permutations. To fit the assumption of species data having a Gaussian distribution, Bray-Curtis distance was used. As a second step, species scores were tested against 24 different environmental variables (Appendix: Table 7) considered to be of importance for community composition variation. The maximum correlation of all environmental gradients, and the average of factor levels were calculated by envfit function (Oksanen et al., 2013). The least significant variables were removed one at a time by systematic backward selection, until only significant variables were left.

3. Results

3.1. Stand structure and site characteristics

The measured site index (SI) was significantly higher (p < 0.001) in the Norway spruce stands (30.5 ± 2 SD) than in the Scots pine stands (25.9 ± 2.1 SD). The youngest stands had a significantly higher
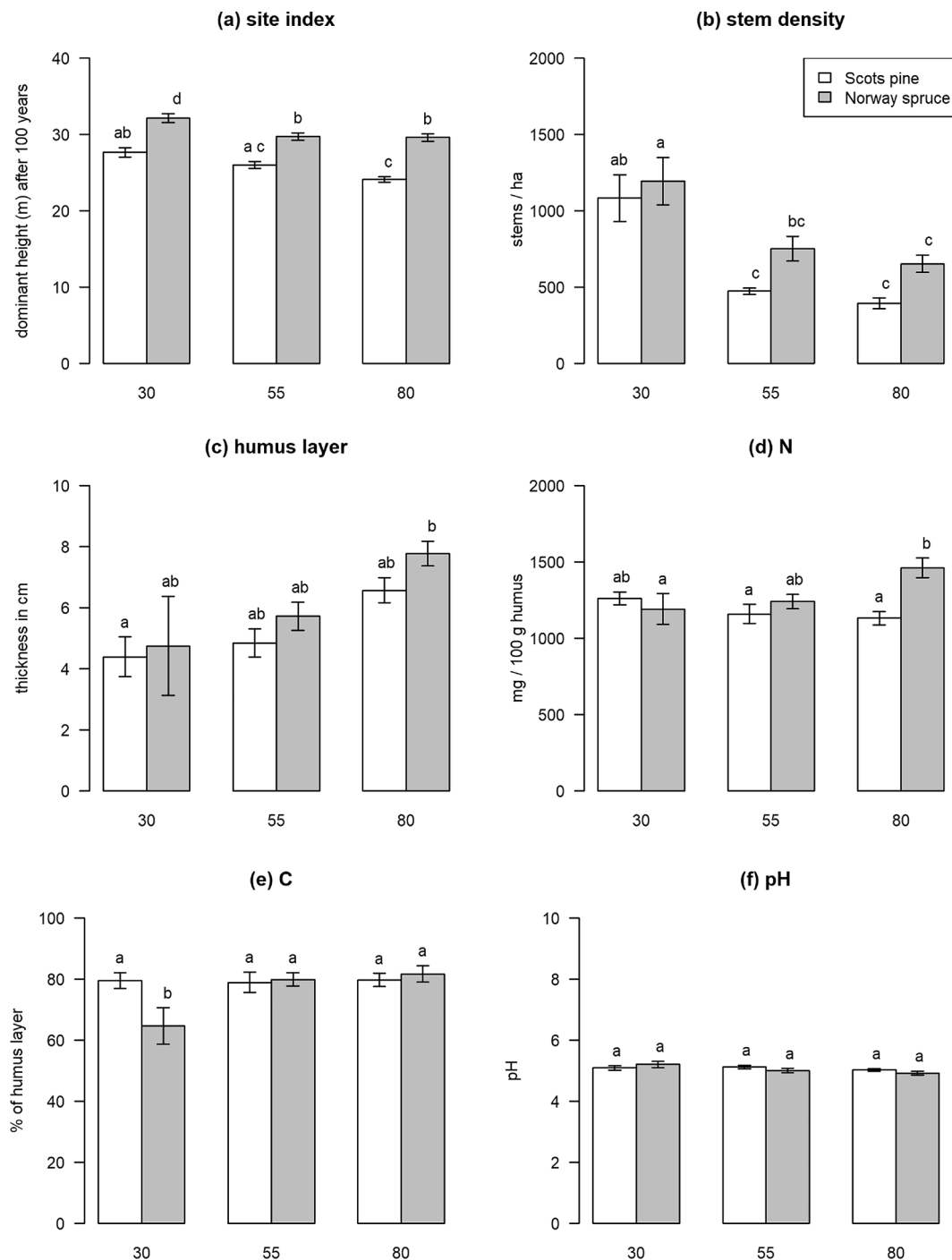
(a) site index

(b) stem density

(c) humus layer

(d) N

(e) C

(f) pH

Fig. 2. Scots pine and Norway spruce different stand characteristics of 30, 55 and 80 years old stands. Tree species and stand age is presented on the x-axis. The different units on the y-axis are presented together with ± SE. Significant differences between the interaction of tree species and stand age (Tukey's test; $p < 0.05$) are indicated by different letters "a", "b" and "c".

SI compared to the oldest stands of corresponding tree species Fig. 2a). Stem density was highest among the youngest stands, and decreased with stand age (Fig. 2b).

Humus layer thickness varied among stands. The only significant difference found here, was a thicker humus layer in oldest Norway spruce stands, compared to the youngest Scots pine stands (Fig. 2c). The result from the soil samples showed a significant higher content of nitrogen in the humus of old Norway spruce stands compared to the young stands (Fig. 2d). Carbon content only differed significantly in the youngest Norway spruce stands (Fig. 2e). B-horizon pH was however similar throughout all stand classes (Fig. 2f).

Light transmittance was significantly ($p < 0.001$) higher in the Scots pine stands (μ 45.8% ± 6.3 SD) than in the Norway spruce stands (μ 24.6% ± 4.6 SD) (appendix: Table 6.). Basal area was lower in the Scots pine stands (μ 18.3 ± 4.4 SD) than in the Norway spruce stands (μ 24.4 ± 8.5 SD) (appendix: Table 6.). The level of lights was associated with stand age, and increased in the older stands (Fig. 3). There is also a negative association with light transmittance and increasing basal area (Fig. 3).
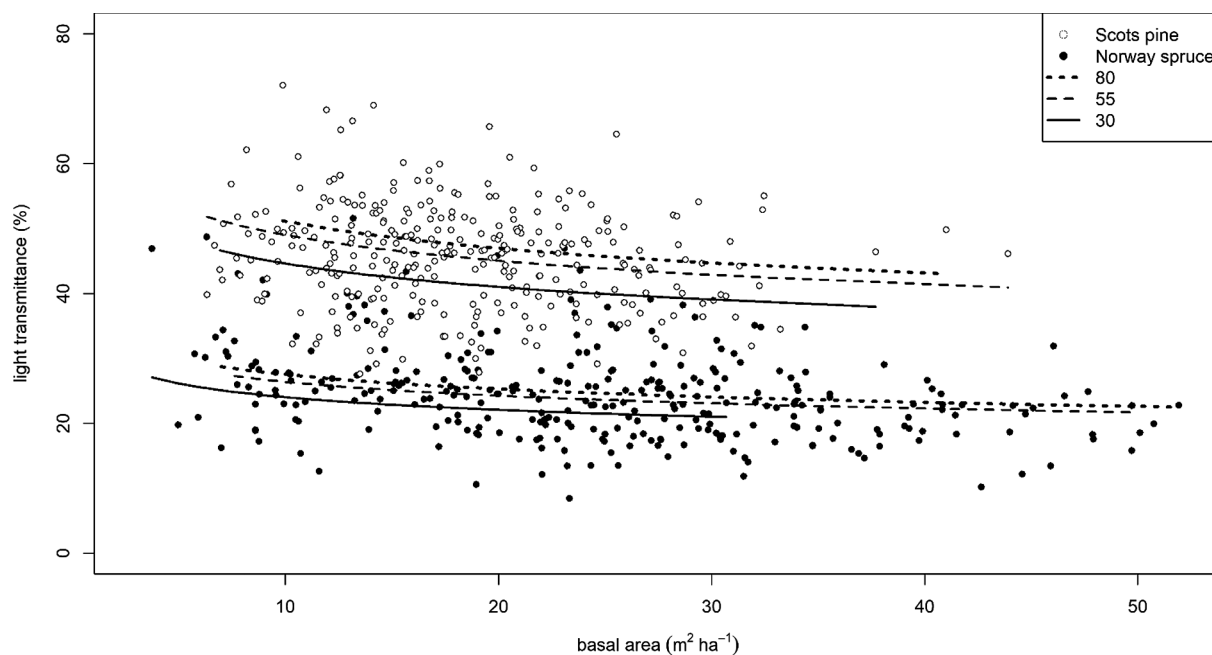
Fig. 3. Basal area (x-axis) plotted against light transmittance (y-axis) in 600 sites, representing 60 stands of Scots pine and Norway spruce. Trend lines show the predicted light transmittance as the average for each combination of tree species and stand age (30, 55 and 80 years). Stand was set as random variable in the model (appendix: Table 6).

3.2. Understory species richness

In total, 136 species of vascular plants were found in the understory (appendix: Table 8). Species richness was significantly higher (p < 0.001) in the Norway spruce stands (29 species per stand), compared to Scots pine stands (18 species per stand). Vascular species from all functional groups, i.e. tree saplings, dwarf shrubs, ferns, herbs,

grasses and sedges were present in all stand types (Fig. 4). In the Scots pine stands there was a significant decrease in species richness between the oldest and youngest stands (p = 0.005), with on average 10 more species in the young stands compared to the oldest stands. Norway spruce stand species richness however didn't vary significantly between different stand ages (p > 0.2).

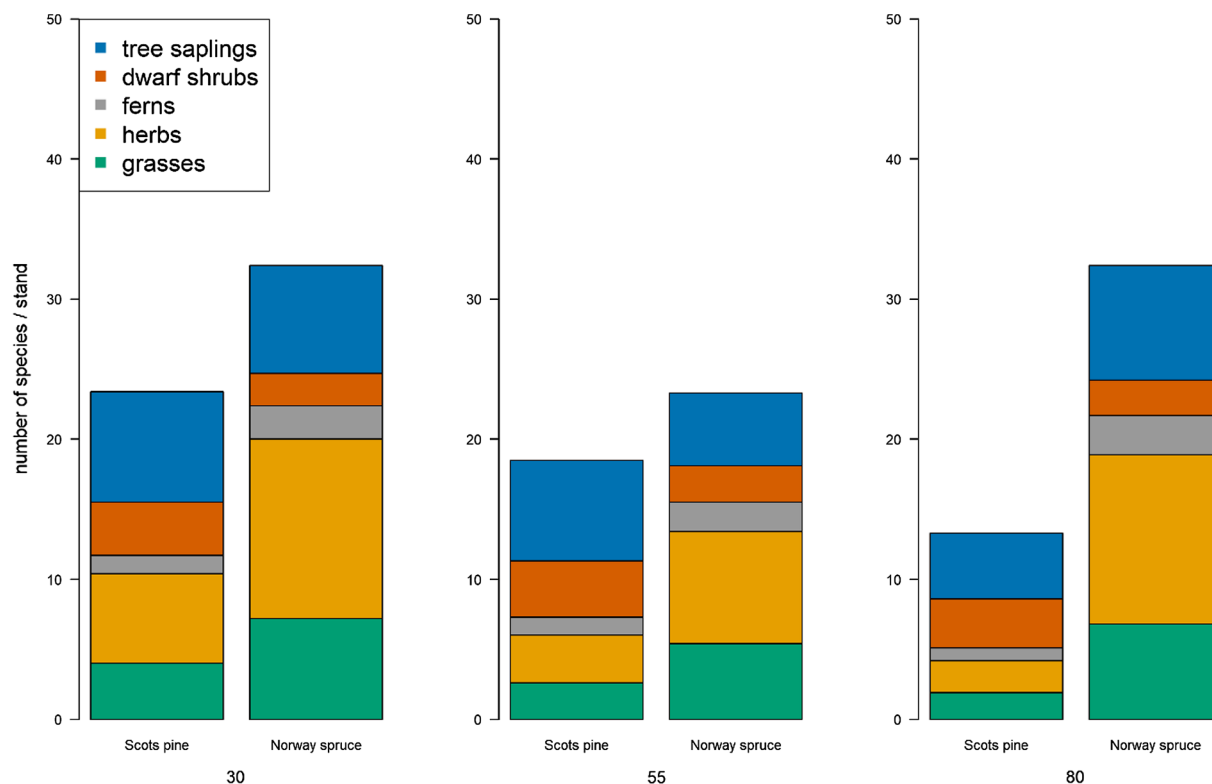
Fig. 4. Average number of species/stand, divided into different functional groups of understory vegetation. Dominant tree species; Scots pine and Norway spruce are presented on the x-axis together with stand age.
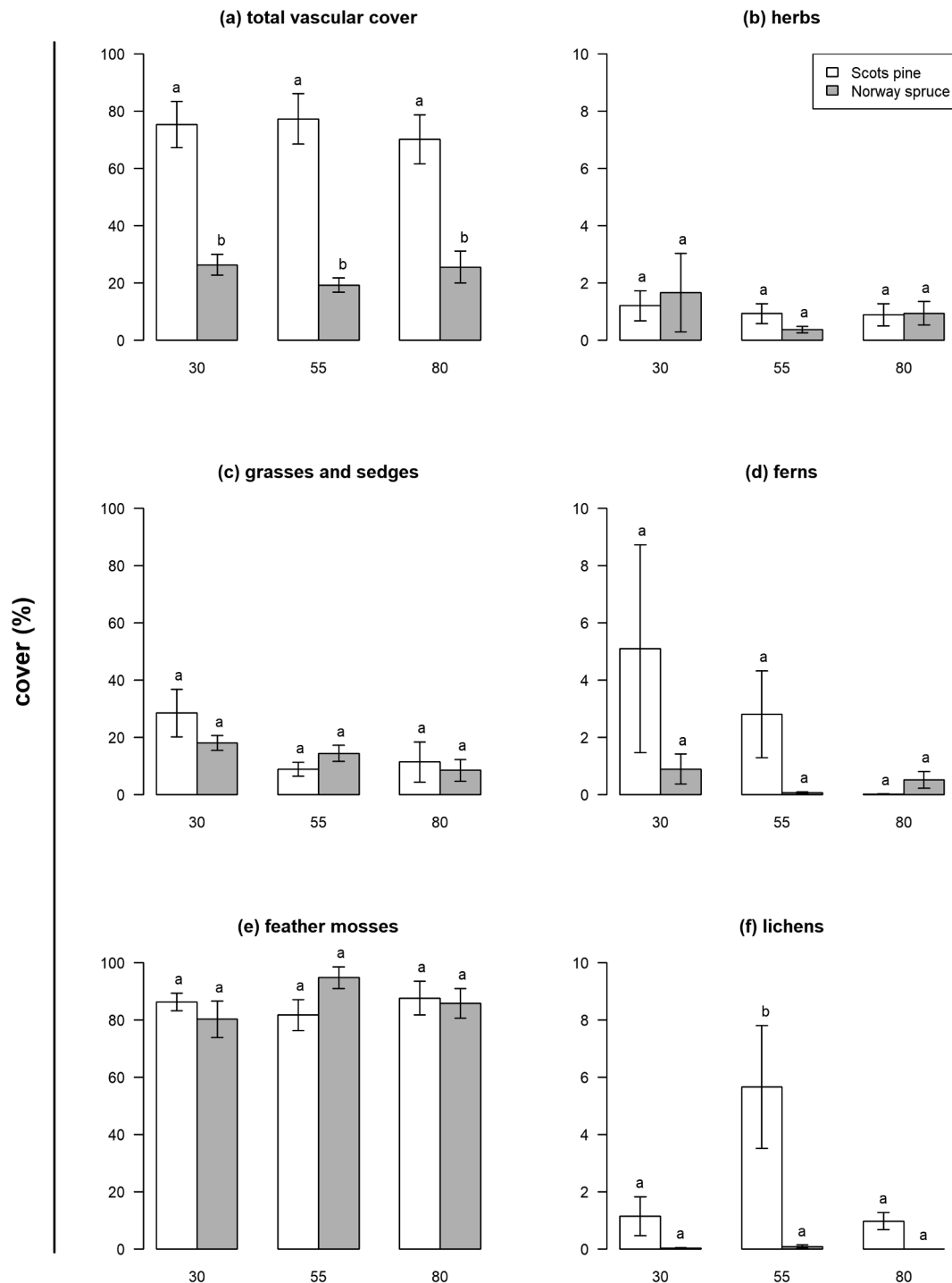
Fig. 5. Mean cover (%) ± SE of seven different functional species groups in 60 Scots pine and Norway spruce stands. Tree species and stand age is presented on the x-axis and percentage cover (%) ± SE is presented on the y-axis. Different letters "a" and "b" indicates a significant difference between the interaction of tree species and stand age (Tukey's test; $p < 0.05$). Note that y-axis scale varies in the different plots.

3.3. Composition of functional groups

Total ground vegetation cover and the composition of functional groups was significantly related to tree species and stand age (Fig. 5a). Dwarf shrub cover was significantly higher ($p < 0.001$) in Scots pine stands, throughout all maturity classes (Fig. 6). The increasing abundance of dwarf shrubs was negatively associated with the combined cover of herbs and grasses in the Scots pine stands (corr: −0.5, $p = 0.005$), but not in the Norway spruce stands (corr: −0.2, $p = 0.2$).

The most abundant species was *Vaccinium myrthillus*, followed by *V. vitis-idaea* and *Calluna vulgaris* (Fig. 6). The cover of terricoulus lichens was also significantly ($p = 0.005$) higher in Scots pine stands (Fig. 5f). When comparing the interaction between stand age and tree species, only the 55 year old Scots pine stands were significantly different from the other stand types (Fig. 5f). In contrast, the cover of herbs, ferns, feather mosses, grasses and sedges didn't vary significantly between the different stand types (Fig. 5b-e).
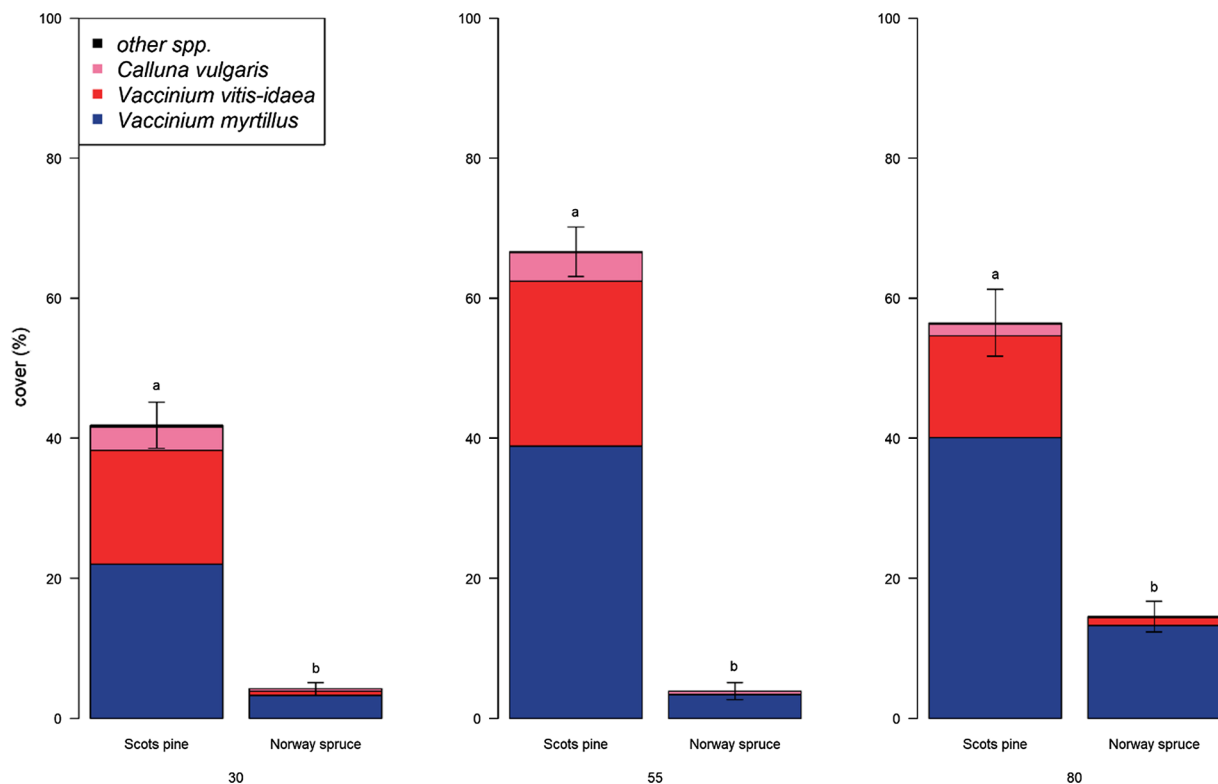
Fig. 6. Abundance of dwarf shrubs in 60 Scots pine and Norway spruce stands. Tree species and stand age is presented on the x-axis, and the abundance is presented as stand average percentage cover ± SE on the y-axis. The use of the letters "a" and "b" indicates a significant difference between the interaction of tree species and stand age (Tukey's test; $p < 0.05$).

3.4. Sapling abundance

Altogether, 22 different species of saplings, (0.3–1.3 m; including *Juniperus communis*) were recorded throughout the survey. The highest abundance of saplings was found in the young Scots pine stands and in the oldest Norway spruce stands (Fig. 7).

3.5. Understory total abundance

The regression analysis of tree species impact on the understory, showed a significantly higher abundance of understory vegetation in the Scots pine stands, compared to Norway spruce stands (Table 1a). Adding stand age as an explanatory variable for understory cover did not improve the model. Hence the large difference in light transmittance between stands of Scots pine and Norway spruce (Fig. 3), we also tested the relationship between light transmittance and the understory cover. When testing the two tree species in the same model, we found an increase in understory abundance at higher light levels (Table 1b). Meanwhile, when testing the interaction between tree species and light transmittance (Table 2a), we found that understory abundance only increased with higher light transmittance in the Norway spruce stands, whereas there was no significant effect in the Scots pine stands (Table 2b).

The impact from light transmittance on the number of saplings ha^{-1} was also tested (Table 3). Here the interaction of tree species and age was significant, and hence included in the model, together with light transmittance (Table 3). Number of saplings was significantly lower in plots located in 80 year old Scots pine stands, and also in the 55 year old Norway spruce stands (Table 3). Increasing light transmittance had a positive effect on the number of saplings (Table 3), but there was no interaction between light transmittance, tree species and stand age.

The understory species richness of Norway spruce stands was positively associated with increasing light transmittance (Table 4a),

whereas the species richness of Scots pine stands was not affected by light transmittance (Table 4b).

3.6. Community composition

The NMDS ordination of the understory for both Scots pine and Norway spruce (Fig. 8) reveals a distinct cluster of Scots pine stands, indicating similarities in community composition among these stands. In contrast, Norway spruce stands were more widely distributed, indicating larger variation in community composition between the Norway spruce stands. Although several commonly encountered species helped to define Scots pine stands (i.e. *Melampyrum pratense, Calluna vulgaris* and *Juniperus communis)*, Norway spruce community composition was primarily distinguished by the net contribution of a number of relatively uncommon species (see discussion below).

3.7. Environmental variables

Different environmental drivers accounted for the understory community composition of Norway spruce (Fig. 9) and Scots pine (Fig. 10). The most important gradient for Norway spruce understory communities was soil water level (Table 5). Soil water level was also correlated with other gradients for moisture, i.e. soil moisture and lateral soil water movement (Fig. 9). The vector also correlates with increasing basal area of broad leaves. Here we also have most of the sedges, together with other species favoured by moist site conditions i.e. *Juncus effusum, Lysmachia vulgaris* and *Molina caerulea*.

A number of species are associated with the area of disturbed soil, which is the second strongest explanatory vector. Most of these species following the increasing gradient of disturbance are ruderal species or species typical for semi-natural grass lands i.e. *Hypericum maculatum, Dactylus glomerata, Lathyrus linifolius, L. pratense* and Fragaria vesca (Tyler et al. 2014). In addition, a few of the less abundant core forest
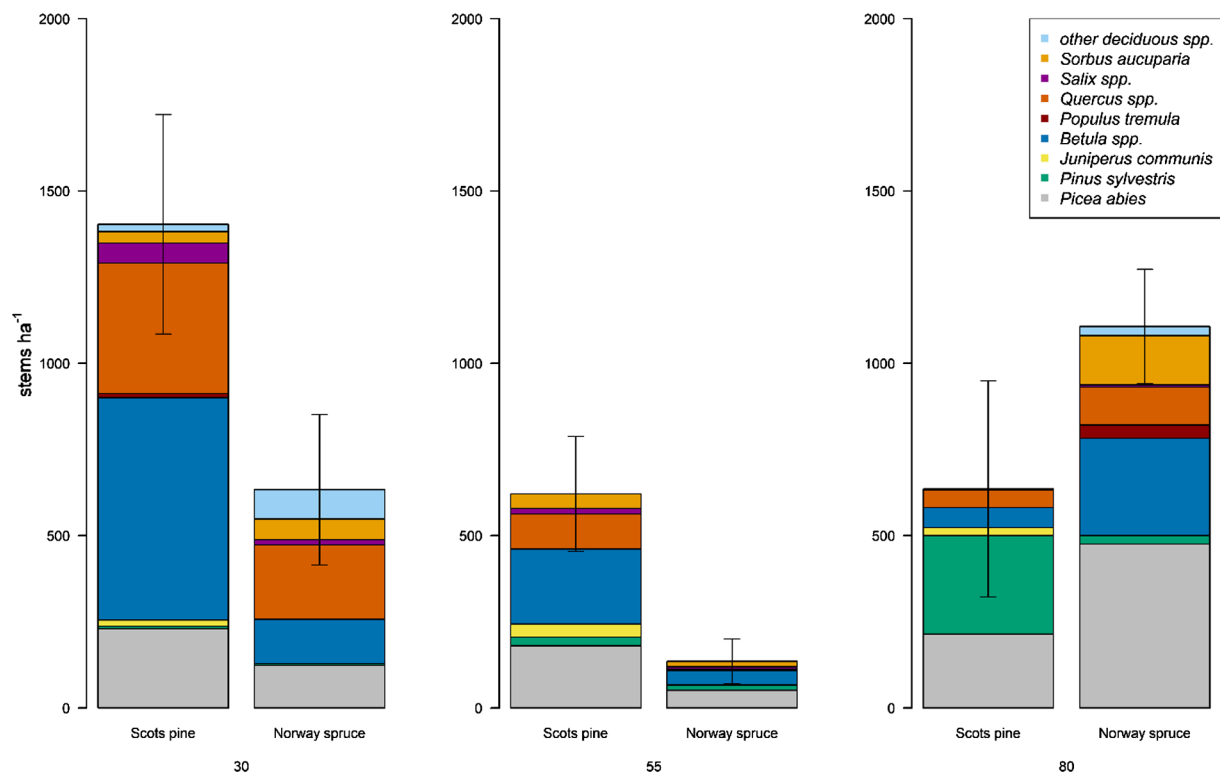
Fig. 7. Number of saplings ± SE found in Scots pine and Norway spruce stands. Tree species and stand age is presented on the x-axis and the stand average number of stems ha^{-1} is presented on the y-axis.

Table 1
Result of the linear regression, for which total understory abundance is tested against (a) dominant tree species and (b) light transmittance. Stand averages for 60 stands of Norway spruce and Scots pine are used in the models.

(a)

Variable Tree species	Estimate	SE	Transf.	Pr(> |t|)
Scots pine	50.6	3.8		< 0.001
Norway spruce	23.6	5.3		< 0.001

(b)

Variable Light transmittance	Estimate	SE	Transf.	Pr(> |t|)
Light transmittance	4.2 e^{-2}	5.8^{-3}	log(y + 1)	< 0.001

Table 2
Mixed model regression, for which understory abundance is tested against light transmittance in two separate models for (a) Norway spruce and (b) Scots pine. The analyses includes 300 plots each divided on 30 stands (random variable) of either Norway spruce or Scots pine.

(a)

Variable Norway spruce	Estimate	SE	Transf.	Pr(> |t|)
light transmittance	0.03	0.01	log(y + 1)	0.005

(b)

Variable Scots pine	Estimate	SE	Transf.	Pr(> |t|)
light transmittance	0.1	0.4		0.7

Table 3
The number of saplings log(y + 0.5) ha^{-1} analysed in a mixed model (n = 600) with stand was set as random variable.

Variable	Estimate	SE	p-value
Scots pine 30	0.6	0.4	0.2
Scots pine 55	0.4	0.5	0.5
Scots pine 80	−1.8	0.6	< 0.001
Norway spruce 30	0.2	0.3	0.6
Norway spruce 55	−1.2	0.4	0.004
Norway spruce 80	0.8	0.4	0.06
light transmittance	0.03	0.008	< 0.001

Table 4
Vascular plant species richness, and the association with light transmittance was tested separately for (a) Norway spruce and (b) Scots pine stands in generalized linear mixed models (GLMM), and with stands set as random variable. For each model, 30 stands containing 300 plots (100 m^2) were used.

(a)

Variable Norway spruce	Estimate	Distribution	SE	Pr(> |t|)
light transmittance	0.06	Poisson (log-link)	0.003	0.008

(b)

Variable Scots pine	Estimate	Distribution	SE	Pr(> |t|)
light transmittance	0.008	Poisson (log-link)	0.003	0.6

species are also found here, such as *Ribes alpinum*, *Hepatica nobilis* and *Convallaria majalis*.

In Scots pine stands, stem density of broadleaves was the environmental variable that best fit the ordination (Table 6, Fig. 10).

Consequently, tree saplings of *Populus tremula*, *Quercus* spp. and *Salix caprea* were associated with this axis. Both SI and stand age were significant and followed the same direction (i.e. SI increases with lower stand age). *Betula pubescens* and the fern *Pteridium aquilinum* were associated with these younger stands with higher SI (Fig. 10). In addition, Scots pine understory composition also altered with basal area, and the
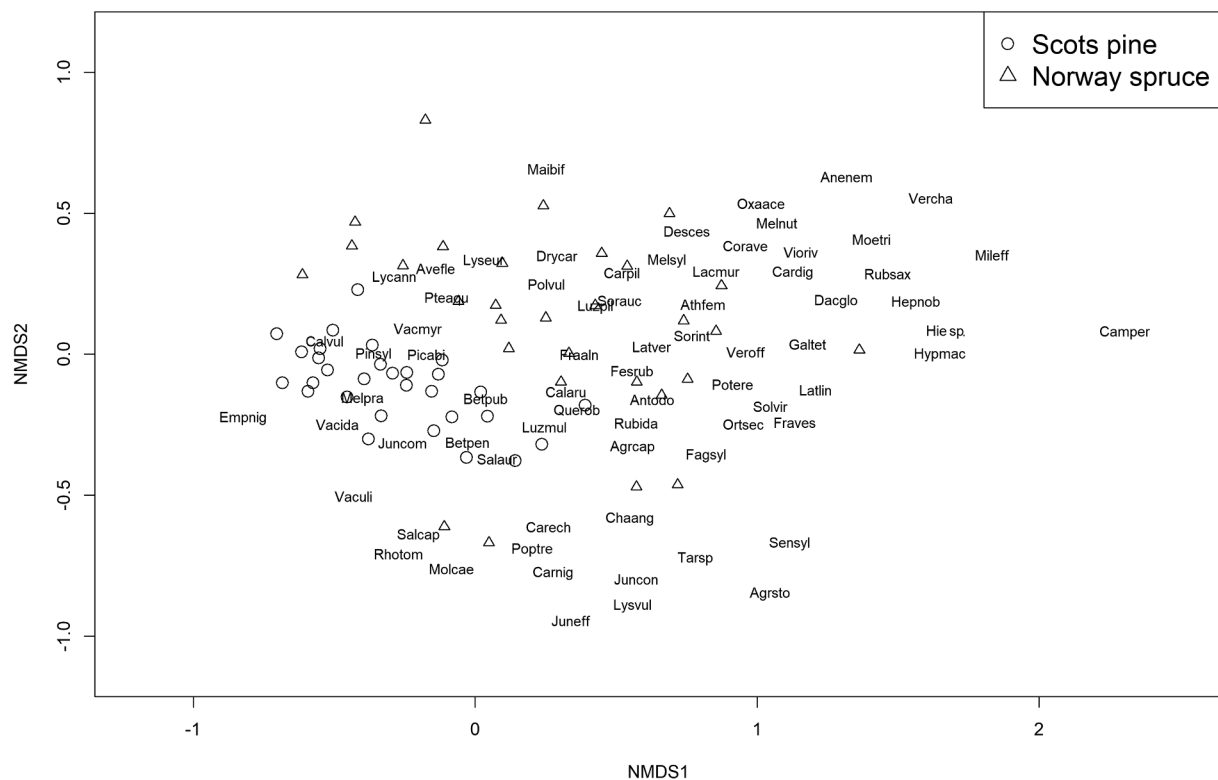
Fig. 8. Two dimensional NMDS of understory species composition in 30 Scots pine and 30 Norway spruce stands. The markers (circle = Scots pine and triangle = Norway spruce) represent the centre of each stand respectively. Hence, stands near each other in the ordination plot have more similar floristic assemblage. Codes consist of the three first letters if the genus and three first letters of the species names (see appendix: Table 8). Stress value = 15.3.

Gini-coefficient of basal area (Fig. 10). Finally, stand age and longitude explained the variation in species composition for both Scots pine and Norway spruce stands (Fig. 10, Fig. 9).

4. Discussion

Our study quantified the extent of differences in understory abundance and composition between stands dominated by different overstory tree species. Overall, the species richness of understory vascular plants was significantly higher in the Norway spruce stands than in Scots pine stands (Fig. 4), but Scots pine stands supported a higher coverage of vascular plants. Differences were also observed in the community composition of Scots pine and Norway spruce stands, and in the community variability of vascular plants supported by these two stand types (Figs. 8–10). These differences were particularly pronounced with respect to the dwarf shrubs, which on average covered 55% of the ground in Scots pine stands, and only 7.5% of the ground of Norway spruce stands (Fig. 6). For saplings, substantial differences in abundance were also observed between stand types, both in terms of the dominant tree species and stand age (Table 3). A number of potential drivers are likely to be underlying these observed patterns. Scots pine stands were characterised by relatively high understory light levels and a well-developed understory vascular plant community. In contrast, Norway spruce stands were characterised as being consistently darker than their Scots pine counterparts, with a sparser understory plant layer (Fig. 3, Fig. 5). There was however larger variation in the community composition of vascular plants found in Norway spruce than in Scots pine stands (Figs. 9 and 10). These observed differences in vascular plant community composition were in turn associated with distinct

apparent drivers (Table 4). Here we discuss these issues focusing on vascular plant coverage, species richness, and the potential underlying ecological drivers operating in these two production stand types, and briefly address their relevance to management decisions and ecosystem services.

4.1. Potential drivers

4.1.1. Light

According to Tonteri et al. (1990), light illumination dictates understory development in Norway spruce stands. Our study results are consistent with this view, as light appears to be limiting understory development in Norway spruce dominated stands (Table 1). Within Norway spruce stands, increasing light transmittance had a positive effect on understory vascular plant species richness and abundance. Furthermore, tree sapling abundance also increased with higher light transmittance. In contrast, no effect of light was found in the Scots pine stands. Available light was consistently higher in Scots pine stands, as was total vascular plant cover for all age classes. As the abundance of understory vascular plants in Scots pine stands didn't respond to differences in light illumination, this may suggests that light levels are sufficiently high in even the densest of Scots pine stands surveyed. Eldegard et al. (2019) found that bilberry cover peaked at a basal area of 30–40 m^2 ha^{-1}, and thereafter it started to decrease. Since we only had two plots of Scots pine with densities > 40 m^2 ha^{-1}, we weren't able to test for such patterns.

4.1.2. The additional roles of competition and disturbance

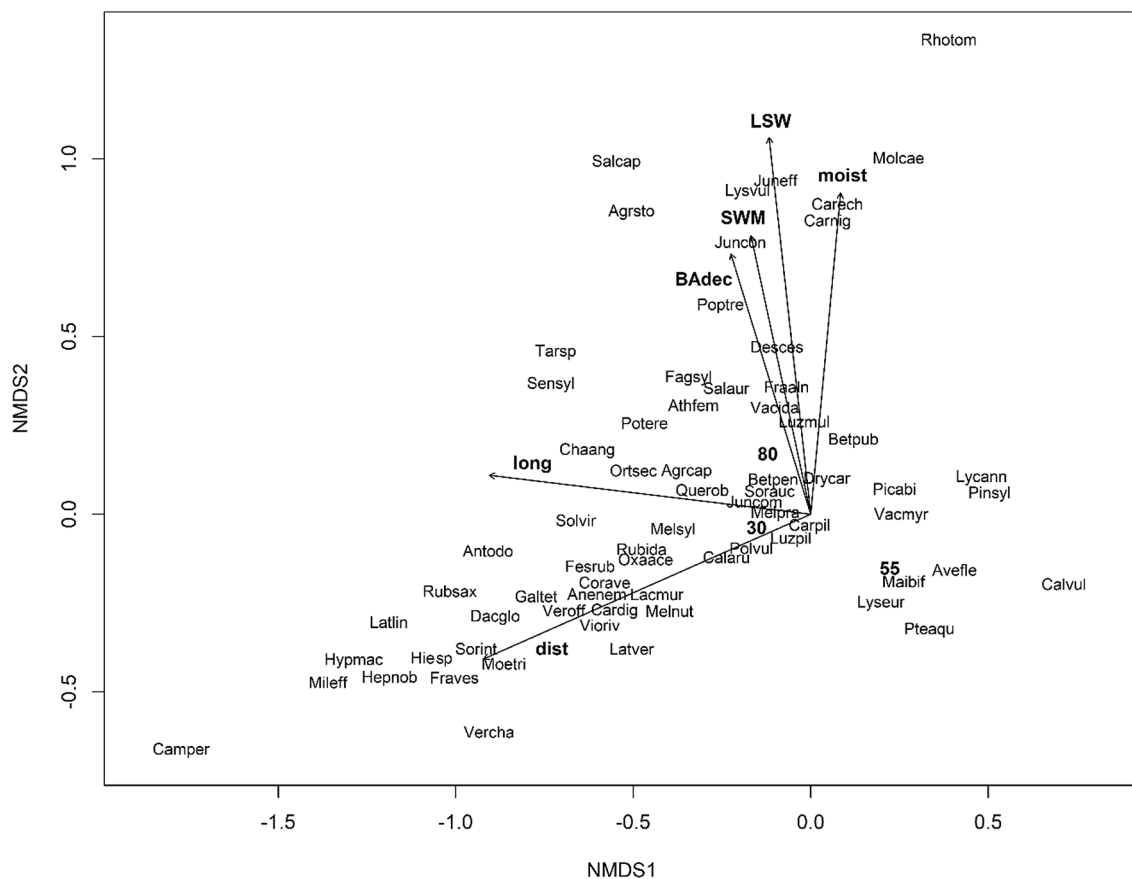In Scots pine stands, understory species richness reduced with stand

Fig. 9. Two dimensional NMDS of understory species composition of 30 Norway spruce stands, with arrows showing unconstrained explanatory variables positions in the ordination space. Arrow length is scaled by square root of their correlation. Species name codes consist of the three first letters if the genus and three first letters of the species names (see appendix, Table 8). stress value = 15.7.

age. This pattern of decreasing species richness has likewise been ob- served in a number of previous studies of Scots pine stands (Økland, 1995a, Widenfalk and Weslien, 2009). This pattern may result from the gradual competitive exclusion of early succession species, as the com- bined cover of herbs and grasses was negatively correlated with the increasing abundance of dwarf shrubs in the plots of Scots pine stands. Specifically, Vaccinium-species and bryophytes may prevent additional species from establishing. An alternative hypothesis is that Scots pine stands support low numbers of understory vascular plants because the environment provided is comparably harsh, as indicated in part by larger fluctuations in understory temperature (Økland, 1995b; Barbier et al., 2008). This variability may be of particular relevance to those understory species that are sensitive to thermal stress during seedling establishment, in comparison to perennial plants with extensive below ground rhizomes (Økland, 1995b).

We therefore suggest that the observed differences in the understory communities of Scots pine and Norway spruce stands are likely driven by distinct ecological drivers. Scots pine stands offer a bright environ- ment in which sufficient light for understory development does not seem to be a limiting resource. In these stands vascular plant diversity may instead be limited by competition from dwarf shrubs and feather mosses, which appears to be preventing less competitive understory species from establishing. Other studies have shown that natural dis- turbances, such as fires (Zackrisson, 1977), and to some extent artificial disturbances from forest management (Widenfalk and Weslien, 2009),

can enhance species richness and alter community composition in Scots pine dominated forests. Since the ecological strategy of Scots pine is to rapidly colonize areas following disturbance, it's not unlikely that un- derstory species associated with Scots pine may have developed the same strategy. In contrast, Norway spruce is a shade adapted late suc- cession tree species which can out compete other tree species under lower light conditions. Understory species in such environments may consequently be competing less against each other, than against the environmental constraints imposed by the overstory itself. This ex- planation is more in accordance with the resource quantity concept, which, in this case involves light being the most limiting resource for understory plant communities (Stevens and Carson, 2002). In addition, it's important to note that browsing by large herbivores is a dominant influence on understory vegetation and regenerating trees in Sweden's forests. In this study we did not quantify browsing intensity, but ac- knowledge its likely contribution to the outcomes observed (Felton et al., 2017b; Petersson et al., 2019).

4.1.3. Previous land use

Previous land-use also appears to be contributing to some of the observed differences in community composition between Norway spruce and Scots pine stands. The wider variation in community com- position found in Norway spruce stands (Figs. 8 and 9) may derive from a larger diversity of previous land use history in these stands. Even though the youngest and middle aged stands used in this study were
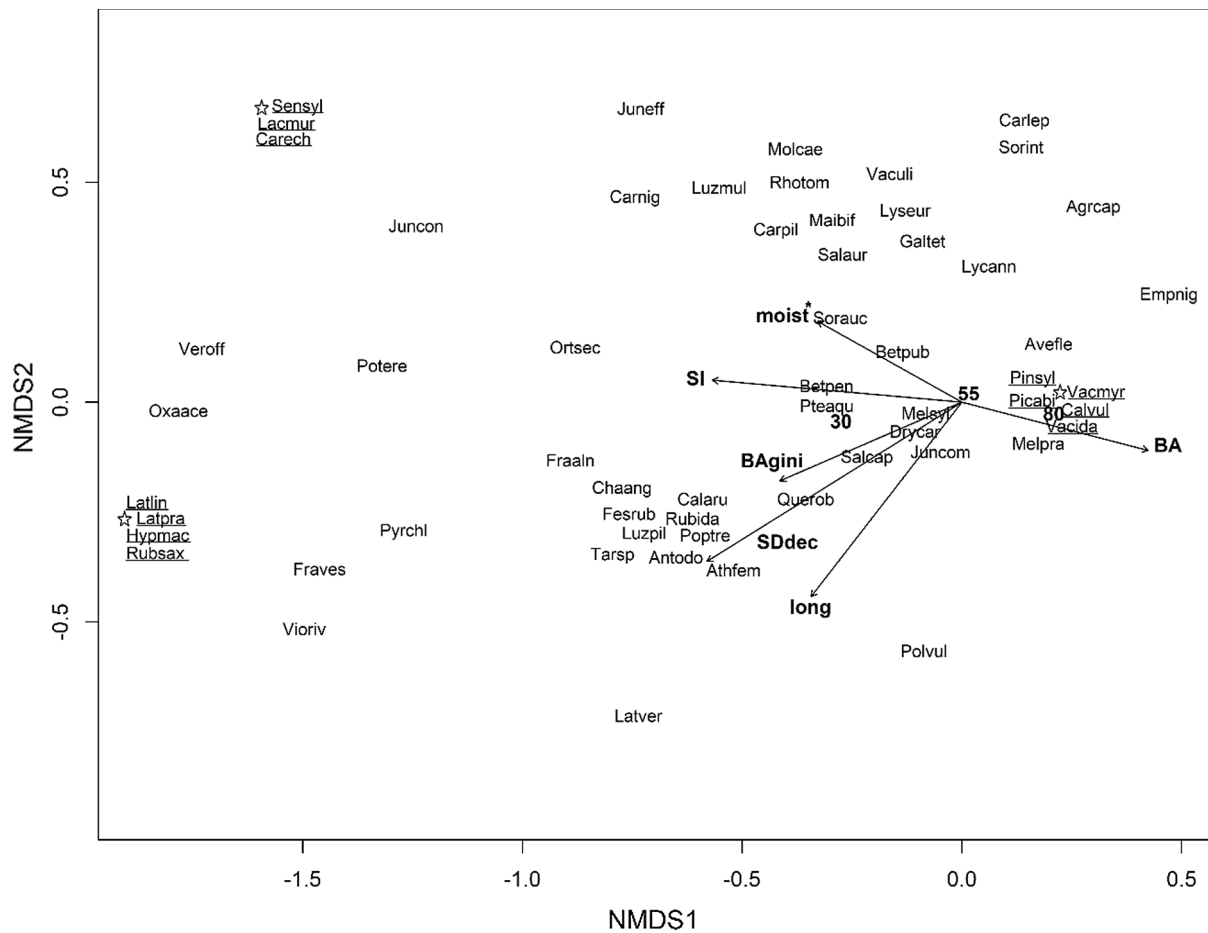
Fig. 10. Two dimensional NMDS of understory species composition of 30 Scots pine stands, with arrows showing unconstrained explanatory variables positions in the ordination space. Arrow length is scaled by square root of their correlation. Species labels overlapping (underlined) where moved with stars indicating their original position. Species name codes consist of the three first letters if the genus and three first letters of the species names (see appendix Table 8). Stress value = 13.7. * Note that the gradient for moisture (moist) is included in the plot although it's not significant at 5% level.

Table 5
Environmental variables fitted to the ordination space of species data in (a) Norway spruce and (b) Scots pine stands. P values based on 999 permutations. Only significant variables are presented here. Full list of variables is presented in appendix: Table 7.

(a)	Environmental variable	Code	r2	Pr(> r)
	level of soil water	LSW	0.52	< 0.001
	disturbance (% of area)	dist	0.45	< 0.001
	longitude	long	0.38	0.004
	soil moisture	moist	0.34	0.005
	soil water movement	SWM	0.31	0.008
	basal area of deciduous trees	BAdec	0.28	0.01
	stand age	age	0.20	0.02

(b)	Environmental variable	Code	r2	Pr(> r)
	stem density deciduous trees	SDdec	0.58	< 0.001
	site index	SI	0.41	0.001
	longitude	long	0.39	0.002
	Gini coefficient of basal area	BAgini	0.25	0.02
	stand age	age	0.24	0.01
	basal area	BA	0.23	0.02
	soil moisture	moist	0.18	0.07*

established on forest land, the tree species composition of these preceding forests remains unknown, and may be a source of some the observed variability in the understory vascular plant community. For example, some Norway spruce stands had remnants of old Scots pine stumps, indicating that these lands were once occupied by Scots pine. Likewise, some of the 80 year old Norway spruce stands may have been established on abandoned agricultural land, as understory species indicative of semi-natural grasslands sometimes encountered, i.e. *Hypericum maculatum*, *Lathyrus pratensis*, *Vicia cracca*, *Geum urbanum* and *Rumex acetosa* (Tyler et al., 2014). In support of this explanation, previous studies have found that grassland species can survive in forested areas (Dahlström et al., 2006, Jonason et al., 2016), and even being stored for 80 years in the seedbank of conifer stands (Milberg et al., 2019).

4.1.4. Stand age and SI

Overall, vascular plant species richness was comparably high in the young stands of both Norway spruce and Scots pine. This result may stem from the co-occurrence of mature forest vascular species (e.g. *Mainthemum bifolium*, *Lysimachia europea*, *Dryopteris carthusiana*, *Melampyrum sylvaticum* and *Viola riviniana*), that were just starting to establish, with ruderal remnants from the clearcut phase, e.g.

Chamaenerium angustifolium, Rubus idaeus, Urtica dioica. This observed peak in species richness in younger production stands has been observed in previous studies, in which it similarly resulted from an overlap of early and late succession plants (Widenfalk and Weslien, 2009). In the case of Scots pine, this early peak in species richness was followed by a consistent decrease with stand age. In Norway spruce stands however, a number of diversity metrics, including vascular plant species richness, dwarf shrub cover, and the number of saplings reached, were higher in the 80 year old than the 55 year old stands.

What remains unclear in these results is how differences in soil fertility might be affecting these outcomes. Site index (SI) from the management plans was used in order to reduce variation in fertility during stand selection and SI based on measured dominant height for Norway spruce and Scots pine, respectively, was used in the ordination analyses as explanatory variable. However, we could not separate SI from the age effect, as SI was generally higher in younger stands. This phenomenon of higher SI, i.e. increased fertility, in recently re-generated production forest is not limited to our study, but appears to be part of a wider phenomenon (Eriksson and Johansson, 1993). The role that fertility may be playing for understory vegetation is an important question that requires further investigation, as differences in fertility affect the understory communities that occur in managed stands (Hedwall et al., 2017), and this issue relates directly to current trends in the establishment of Norway spruce on Scots pine sites with lower SI.

4.2. Species-specific responses amongst understory species

The observed differences in species richness, abundance, and community composition invariably stem from underlying differences in the ecological requirements and competitive abilities of individual vascular plant species. For this reason explanations for species occurrence and abundance will vary depending on the individual species or group of species considered. In this regard, the results from the multivariate analysis of Scots pine understory communities revealed that for some species found in these stands, environmental gradients could explain aspects of the vascular species community composition. For example, juniper (*Juniperus communis*) was more commonly found in stands located in the eastern region of the study area, though the precise underlying drivers of this pattern remain unclear.

4.3. Ecosystem services and management implications

In the hemiboreal zone of Sweden, a steady decline in the coverage of dwarf shrubs has been observed in NFI data since the 1980s (Odell and Ståhl, 1998, Hedwall et al., 2013). Higher plantation densities are specifically thought to be driving these declines, especially among light demanding species (Hedwall and Brunet, 2016). Our results add to

these concerns, due to the lower understory light levels associated with Norway spruce compared to Scots pine stands. The associated implications for dwarf shrubs are of particular concern. The dwarf shrub bilberry is one of the most economically important wild berry species in Sweden and is widely collected for both consumption and sale (Lindhagen and Bladh, 2013; Sténs and Sandström, 2013). Furthermore, large herbivore game species, such as moose (*Alces alces*) and roe deer (*Capreolus capreolus*), feed extensively on dwarf shrubs (Cederlund et al., 1980). Our results should therefore raise concerns regarding the implications of stand conversions for two prominent recreational activities in this region. Additional concerns can be raised by the lower prevalence of young broadleaf trees encountered in Norway spruce stands, which are also an important food resources for browsing herbivores (Månsson et al., 2007). Furthermore, as the prevalence of dwarf shrubs and abundance of tree saplings was significantly lower in 55 year old than 80 year old spruce stands, additional concerns can be raised regarding future rotation lengths applied in Norway spruce stands. Shorter rotation times are being promoted in Sweden as a means of exploiting increased growth rates in production stands, and reducing stand susceptibility to disturbance (Felton et al., 2016; Roberge et al., 2016, Felton et al., 2017b). However, reduced rotation lengths have their own suite of negative implications for biodiversity and some ecosystem services (Roberge et al., 2016, Felton et al., 2017b), which our results lend further credence.

5. Conclusion

The understory vascular plant communities of Scots pine and Norway spruce stands differed in a wide range of important ecological aspects, including species richness, abundance and community composition. Furthermore, these differences extended to include substantial differences in the prevalence of major functional groups, including dwarf shrubs and regenerating tree species. Differences in light availability between the stand types appears to be playing a substantial role in the observed differences the understory communities. Concerns may thereby be raised regarding the resultant implications of converting Scots pine stands to Norway spruce for understory vascular plant, and the ecosystem services they provide.

Acknowledgements

Appendix A

See Tables 6 and 7.

Table 6

Light transmittance relation to the two tree species Scots pine (Intercept) and Norway spruce at different stand age (30, 55 and 80 year). The test includes 600 sites distributed in 60 stands (random effect).

Coefficients	Estimate	Std. Error	t-value	p-value
(Intercept)	4.1	0.07	55.4	< 0.001
basal area (nat. log)	−0.1	0.02	−5	< 0.001
Norway spruce	−0.6	0.04	−16.1	< 0.001
age 55	0.09	0.05	2	0.05
age 80	0.14	0.05	2.8	0.007

Table 7
Environmental variables tested in the ordinations. Stand averages are presented as the mean (μ) and standard deviation (σ) for Norway spruce (NS) and Scots pine (SP) stands. Integer variables are presented as the median and σ. Variables significant in ordination plots for SP and NS (Fig. 10, Fig. 9) are listed in column "significant".

Environmental variable	NS μ	NS σ	SP μ	SP σ	Significance
Ash layer thickness (cm)	3.3	3.1	3.967	2.1	
Basal area (m^3 ha^{-1})	24.4	8.5	18.3	4.4	SP
Basal area σ $_{\bar{x}}$ (0–1)	0.3	0.1	0.3	0.1	
Carbon content of humus layer	75.4	14.4	79.4	8.4	
Dead wood (m^3 ha^{-1})	10.2	12.6	4	2.9	
Deciduous basal area (m^3 ha^{-1})	0.6	0.9	0.2	0.2	NS
Deciduous stem density (stems > 4 cm ha^{-1})	50.4	55	10	11	
Disturbance (% of area)	3.5	3.8	1.8	2.5	NS
Forest plan stand age (± 5 years)	–	–	–	–	SP, NS
Gini-coefficient of basal area (0–1)	0.3	0.1	0.3	0.1	SP
Humus layer thickness (cm)	5.7	2.4	5.3	1.9	
Last management operation conducted	–	–	–	–	
Lateral soil water movement	2.2	0.4	1.9	0.5	NS
Latitude	56.9	0.1	56.9	0.9	
Light transmittance (%)	24.6	4.6	45.8	6.3	
Light transmittance σ $_{\bar{x}}$ (0–1)	0.6	0.1	0.3	0.04	
Longitude (degrees)	15.7	0.4	15.6	0.4	SP, NS
Nitrogen content of humus layer	1297	255	1183	164.3	
Site index (dom. hgt. in m after 100 years)	21.5	3	18.9	3	SP
Soil grain size	3	0.6	3	0.6	
Soil moisture	2.1	0.3	2	0.2	NS
Soil water level	2.1	0.3	2	0.2	NS
Stem density (stems > 4 cm ⌀ ha^{-1})	865.1	403.6	648.4	418.5	
Time since management (years)	12.5	5.9	11.1	6	

Species list

See Table 8.

Table 8
Species list with all species of vascular plants occurring in the study, and the number of occasions found in 300 plots each of Scots pine and Norway spruce. Abbreviations listed are the once used in Figs. 8–10. Nomenclature follows ArtDatabanken (2019).

Species	Abbreviation	Norway spruce	Scots pine
Vaccinium myrtillus	Vacmyr	257	298
Avenella flexuosa	Avefle	257	228
Picea abies	Picabi	234	246
Vaccinium vitis-idaea	Vacida	114	280
Calluna vulgaris	Calvul	90	278
Pinus sylvestris	Pinsyl	126	186
Melampyrum pratense	Melpra	80	184
Betula pubescens	Betpub	124	135
Luzula pilosa	Luzpil	171	63
Quercus robur	Querob	116	101
Sorbus aucuparia	Sorauc	149	34
Pteridium aquilinum	Pteaqu	85	59
Maianthemum bifolium	Maibif	119	23
Lysimachia europaea	Lyseur	72	62
Betula pendula	Betpen	27	100
Carex pilulifera	Carpil	84	7
Calamagrostis arundinacea	Calaru	49	28
Dryopteris carthusiana	Drycar	56	16
Melampyrum sylvaticum	Melsyl	66	3
Rubus idaeus	Rubida	37	26
Viola riviniana	Vioriv	55	8
Frangula alnus	Fraaln	47	16
Juniperus communis	Juncom	5	48
Oxalis acetosella	Oxaace	43	5
Veronica officinalis	Veroff	44	3
Empetrum nigrum	Empnig	0	36
Potentilla erecta	Potere	28	7
Carex digitata	Cardig	35	0

Table 8 (*continued*)

Species	Abbreviation	Norway spruce	Scots pine
Salix aurita	Salaur	16	19
Chamaenerion angustifolium	Chaang	17	17
Festuca rubra	Fesrub	20	11
Polypodium vulgare	Polvul	22	7
Populus tremula	Poptre	16	11
Carex nigra	Carnig	16	9
Lathyrus vernus	Latver	14	10
Corylus avellana	Corave	23	0
Hepatica nobilis	Hepnob	22	0
Lathyrus linifolius	Latlin	14	7
Hieracium sect *Hieracium*	Hie sp.	21	0
Lactuca muralis	Lacmur	20	1
Vaccinium uliginosum	Vaculi	0	19
Carex echinata	Carech	18	1
Fragaria vesca	Fraves	10	8
Rubus saxatilis	Rubsax	17	1
Juncus conglomeratus	Juncon	13	5
Athyrium filix-femina	Athfem	17	1
Orthilia secunda	Ortsec	16	1
Agrostis capillaris	Agrcap	16	1
Senecio sylvaticus	Sensyl	15	1
Solidago virgaurea	Solvir	16	0
Galeopsis bifida/Galeopsis tetrahit	Galtet	15	1
Lycopodium annotinum	Lycann	8	7
Anemone nemorosa	Anenem	14	0
Juncus effusus	Juneff	10	4
Veronica chamaedrys	Vercha	13	0
Salix caprea	Salcap	2	11
Molinia caerulea	Molcae	3	9
Sorbus intermedia	Sorint	9	3
Hypericum maculatum	Hypmac	10	1
Fagus sylvatica	Fagsyl	10	0
Lysimachia vulgaris	Lysvul	9	0
Anthoxanthum odoratum	Antodo	6	3
Deschampsia cespitosa	Desces	9	0
Taraxacum sp	Tarsp	5	3
Moehringia trinervia	Moetri	8	0
Agrostis stolonifera	Agrsto	8	0
Melica nutans	Melnut	7	0
Rhododendron tomentosum	Rhotom	1	6
Dactylis glomerata	Dacglo	6	0
Campanula persicifolia	Camper	6	0
Luzula multiflora	Luzmul	5	1
Milium effusum	Mileff	6	0
Clinopodium vulgare	Clivul	5	0
Pyrola chlorantha	Pyrchl	3	2
Lathyrus pratensis	Latpra	4	1
Convallaria majalis	Conmaj	5	0
Carex leporina	Carlep	3	2
Ribes alpinum	Ribalp	5	0
Acer platanoides	Acepla	5	0
Hieracium triviale		4	0
Geranium robertianum		4	0
Scorzonera humilis		1	3
Hypericum perforatum		4	0
Poa trivialis		4	0
Gymnocarpium dryopteris		4	0
Urtica dioica		3	0
Vicia hirsuta		3	0
Scrophularia nodosa		3	0
Vicia sepium		3	0
Cirsium palustre		2	1
Viola palustris		3	0
Stellaria longifolia		3	0
Hypochaeris maculata		0	3
Galium uliginosum		3	0
Ranunculus flammula		3	0
Juncus bufonius		3	0
Carex oederi		3	0
Goodyera repens		0	1
Peucedanum palustre		2	0
Campanula rotundifolia		1	1
Verbascum thapsus		2	0
Hedera helix		2	0
Galium odoratum		2	0

Table 8 (*continued*)

Species	Abbreviation	Norway spruce	Scots pine
Equisetum sylvaticum		2	0
Vicia sylvatica		2	0
Monotropa hypopitys		0	2
Galium palustre		2	0
Lathraea squamaria		2	0
Juncus squarrosus		1	1
Carex canescens		2	0
Linnaea borealis		2	0
Poa nemoralis		2	0
Lonicera xylosteum		2	0
Dryopteris filix-mas		1	1
Ajuga pyramidalis		1	0
Pimpinella saxifraga		0	1
Anthriscus sylvestris		1	0
Cerastium fontanum		1	0
Pyrola minor		1	0
Vicia cracca		0	1
Lycopodium clavatum		1	0
Geum urbanum		1	0
Rosa sp		1	0
Trifolium medium		1	0
Vicia tetrasperma		1	0
Rumex acetosa		1	0
Carex sp		0	1
Calamagrostis epigejos		1	0
Glyceria fluitans		1	0
Poa pratensis		1	0
Malus domestica		1	0
Sambucus racemosa		1	0
Rhamnus cathartica		1	0
Larix decidua		0	1
Tilia cordata		1	0
Prunus avium		1	0

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