



Riparian vegetation ecology

An observational study into the effects of forest management on understory vegetation communities along boreal headwaters

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Master's thesis • 60 credits

Swedish University of Agricultural Sciences, SLU

Faculty of Forest Sciences, Department of Forest Ecology and Management

Master program in Forest Ecology and Sustainable Management

Master thesis / Examensarbeten, 2023:6 • ISSN 1654-1898

Umeå 2023



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Credits: 60 credits

Level: Second cycle, A2E

Course title: Master's thesis in Forest Science at the Department of Forest Ecology and Management

Course code: EX0957

Programme/education: Forest Ecology and Sustainable Management

Course coordinating dept: Department of Forest Ecology and Management

Place of publication: Umeå

Year of publication: 2023

Cover picture: Lenka Kuglerová

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Title of series: Examensarbeten / SLU, Institutionen för skogens ekologi och skötsel

Part number: 2023:06

ISSN: 1654-1898

Keywords: riparian forest, forest management, understory vegetation, headwater streams, community ecology

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Abstract

Riparian forests along headwater streams have long been recognized for their role as an interface between the terrestrial and aquatic ecosystem. The over- and understory vegetation performs essential ecological and biochemical functions, which are important for stream functions. Headwaters and their riparian forests have historically long been overlooked in Swedish forest management, leading to clearcutting up to the stream's edge. Previous research found that the forest structure in production forests was significantly different from primary forests. This thesis focused on the possible effects of forest management on the understory vegetation communities.

I inventoried 7 production forests along a management gradient and compared their vegetation communities to 5 primary forests in forest reserves. In all forests a vegetation survey was conducted using 12 quadrates of 1x1m arranged in 6 transects. Vegetation communities were compared for species diversity, community composition and the environmental characteristics.

My results showed that forest type (production, reserve) did not significantly affect species diversity, although I did find that diversity related differently to forest age based on forest type. The community compositions were found to be different between the two forest types, although significant overlap has to be noted. Finally, light availability, as a function of canopy openness was found to be an important driver behind the vegetation communities. Earlier findings on canopy openness between the forest types were repeated with canopy openness being marginally, but significantly higher in the forest reserves.

Generally, this thesis showed that production forests contain large variation between different sites along a management gradient. Within this variation, production forests can house similar or larger number of species and are enormously relevant for the preservation of biodiversity. Therefore, management in the riparian zone may have important implications for the understory vegetation and by extend riparian functioning.

Keywords: riparian forest, forest management, understory vegetation, headwater streams, community ecology

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Abbreviations

ANOVA	Analyses of Variance
DBH	Diameter Breast Height
GLMM	General Linear Mixed-effects Model
GW	Groundwater
IDH	Intermediate Disturbance Hypothesis
LMM	Linear Mixed-effects Model
NMDS	Non-metric Multidimensional Scaling
PCA	Principle Component Analysis
PC	Principle Component

1. Introduction

1.1 Boreal headwaters and the riparian zone

In the boreal landscape, forests are intersected by numerous small, headwater streams (Bishop et al. 2008). These headwater streams are first order streams without permanent tributaries and typically drain catchments of less than 1500 ha (Jonsson et al. 2017). They are the first expression of flowing water (Richardson & Dudgeon 2022) and represent over 90% of the total drainage length (Bishop et al. 2008). They are recognised to have a large influence on, and provide important ecological services for the downstream river network (Wohl 2017). These influences and services include sediment transport, water chemistry and seed dispersal through hydrochory. Headwater streams are further differentiated from larger streams by their lower canopy openness, periodic minimum flows, dependence on terrestrial subsidies and low fish abundance (Richardson & Danehy 2007).

The terrestrial space immediately adjacent to these streams is the riparian zone and it functions as an interface between the aquatic and terrestrial ecosystems (Naiman & Décamps 1997). Through this interface, the terrestrial and aquatic ecosystems exchange subsidies (Sabo et al. 2005) creating a suitable habitat for many species. Riparian forests in the boreal zone are characterised by wet, organic matter rich soils (Ledesma et al. 2018). The forest floor is heterogenous and houses a mosaic of substrates forming micro habitat patches including deadwood, bare soil and litter (Crites & Dale 1998; Naiman et al. 1998; Lee & Sturgess 2001).

Riparian zones in the boreal forest have long been recognized as hotspots for species richness and biodiversity compared to upland forests (Naiman & Décamps 1997; Sabo et al. 2005). Although the riparian zone has been described as housing a unique species composition (Naiman & Décamps 1997), within the boreal forest they generally contain a larger concentration of the different species of vascular plants and bryophytes that are available throughout the entire forested area (Sabo et al. 2005; Kuglerová et al. 2014, 2015).

There has been a lot of research on the importance of the riparian forests, in particular riparian vegetation, for stream functions (Luke et al. 2007; O'Hara 2016). The riparian vegetation has been shown to stabilize stream banks (Naiman

& Décamps 1997; Polvi et al. 2014), filter nutrient inputs from the uplands (Naiman & Décamps 1997; Jansson et al. 2007; Richardson et al. 2012) and provide food sources for aquatic organisms (Webster & Meyer 1997; Saklaurs et al. 2022). It is well understood that structural diversity for riparian vegetation is important (O'Hara 2016), with trees having a strong impact on bank stabilization and nutrient storage (Langendoen et al. 2012), whereas herbaceous shrubs and ground cover vegetation plays an important role in nitrogen cycling (Mayer et al. 2007). The ground vegetation takes up nitrogen during the vegetation season but provide nutrient leaching during litterfall and decomposition. Additionally, Goudarzian et al. (2021) found that understory vegetation is involved in water quality regulation and that species composition in particular can be linked to stream quality and thus the effectiveness of ecosystem functioning.

1.2 Riparian vegetation dynamics

Ground vegetation community compositions are dictated by a large range of natural processes (Palmer 1994; Naiman & Décamps 1997). In the riparian zone, these natural processes are mostly controlled by forest structure and hydrology (Giesler et al. 1998; Zinko et al. 2005; Hart & Chen 2006).

Forest structure

Forest structure, succession and disturbance have important effects on the forest floor vegetation. Recent and intermediate disturbance has been linked to an increase in species richness and alpha diversity (Pollock et al. 1998). This increase has been linked to the increased light availability, which was the result of canopy removal (Schmiedinger et al. 2012). Early successional grasses and herbs disappear as the forest stand matures and light availability decreases (Grandpré et al. 2011; Schmiedinger et al. 2012), reiterating that high light availability leads to higher species richness. Increasing stem volume has further also been shown to decrease the total plant cover of ground cover vegetation (Odell & Ståhl 1998; Hedwall et al. 2013). In contrast to vascular plants, bryophyte diversity has been found to increase with stand maturation (Hart & Chen 2006).

In addition to stand dynamics, the forest floor heterogeneity can have important effects on vegetation. Certain herbaceous and bryophyte species are dependent on the presence of large deadwood or bare soil for establishment (Lee & Sturgess 2001). Litter often acts as an inhibitor for bryophyte establishment (Crites & Dale 1998). In turn, dense bryophyte cover has been known decrease colonization areas for certain vascular plant species and promoting vegetative regeneration (Nilsson & Wardle 2005).

Hydrology

Understory species composition in coniferous forests is driven by edaphic conditions (Närhi et al. 2011). In the riparian zone, soil moisture plays an important role in regulating soil properties (Giesler et al. 1998; Zinko et al. 2005). Silvertown et al. (1999) found that species rich communities were organised along

gradient axis of soil drying and aeration. Soil moisture in the riparian zone is driven by groundwater (GW) dynamics. Furthermore, the presence of local GW discharge has been linked to higher pH (Giesler et al. 1998; Zinko et al. 2005; Kuglerová et al. 2014) and lower C:N ratios (Zinko et al. 2005; Jansson et al. 2007). This led to higher species richness in vascular plants (Giesler et al. 1998; Jansson et al. 2007; Kuglerová et al. 2014), dominance of arbuscular mycorrhizae (Giesler et al. 1998) and dominance of sphagnum moss among bryophytes (Kuglerová et al. 2016).

Additionally, fluvial regimes have been linked directly to local habitat properties (Naiman & Décamps 1997), like rearranging litter distributions (Maridet et al. 1995) or sediment transport (Hupp et al. 2012). Further, the extend of the riparian zone is determined by stream size and increases downstream (Kuglerová et al. 2015). This increase of riparian area has been shown to be important for species richness (Naiman & Décamps 1997; Kuglerová et al. 2015), with the increase in riparian extend resulting in a larger species richness of both vascular plants as well as bryophytes (Kuglerová et al. 2015, 2016). Stream size can therefore be an important driver for vegetation communities. However, this study is looking at headwater streams which have small riparian zones, therefore stream size should have a limited effect on the vegetation communities.

1.3 Current and historical forest management

Apart from the natural processes, forest composition is also formed by human activities (Hjältén et al. 2016; Ring et al. 2018). Sweden has a long history of forestry (Östlund 1995) with high-grading and selective logging progressively moving further north throughout the 19th century until it covered the vast majority of the country. Regeneration after harvesting became mandatory in the 20th century (Lundmark et al. 2013), at the same time as the demand for smaller tree dimensions increased as a result of the growing pulp industry (Östlund et al. 1997). During that period, it also became common practice to ditch peatlands and wetlands, and to straighten small streams to increase water flow and drainage (Maher Hasselquist et al. 2021). During these operations riparian forests along small streams were typically cut down to the stream bank. The current-day rotation forestry system was introduced in the middle of the 20th century (Lundmark et al. 2013) with clear cutting and soil scarification as common harvesting techniques and thinning operations throughout the stand development. In addition, herbicides (agent orange) were used during the period 1960-1970 to reduce competition for coniferous species (Östlund et al. 2022).

These practices had harmful effects on vegetation and water quality and old growth forests became scarce and highly fragmented in the Swedish landscape (Östlund et al. 1997). The accompanied loss of biodiversity can have strong negative effects on ecosystem functioning, like plant productivity and decomposition (Kardol et al. 2018). To account for this, environmental consideration became equally important to the financial objectives in the forestry act of 1993 (Ring et al. 2018). Currently, it is policy to leave a buffer of

unharvested forest along natural streams. Nonetheless, Oldén et al. (2019) found that current buffer widths would not protect vascular plant communities. Other authors called for forest management which mimics natural forest (disturbance) dynamics as a more sustainable alternative (Kreutzweiser et al. 2012; Kuglerová et al. 2017; Kuuluvainen et al. 2021). However, to be able to achieve this, more knowledge about the disparity between managed and natural forest dynamics in terms of forest structure and vegetation communities is needed.

1.4 Using forest reserves as references

In order to create more knowledge about the differences in forest structure between managed and natural riparian forests, Lundqvist (2022) conducted research along headwater streams in mature production riparian stands and in untouched forest reserves (called primary forests based on the European primary forest database - Sabatini et al. 2021). Primary forests differ from old-growth forests as they encompass a wider range of forest types, including primeval, near-virgin and long-untouched forests. Primary forests do not necessarily need to be in a late successional state, which is the case for old-growth forests (Buchwald 2005). This makes primary forests good references to be compared to managed forests. In his research, Lundqvist (2022) found that the forest structure differed significantly in several aspects between the primary forests and the inventoried forest reserves (i.e., primary forests). The managed forests were found to have lower light availability because of a more closed canopy, as well as lower stem density than the forest reserves. Furthermore, the diameter distribution followed a unimodal distribution in the production forests, whereas the forest reserves showed an inverse J-shape.

Given the striking differences in the riparian forest structure documented by Lundquist (2022), it can be assumed that understory vegetation follow those patterns. Although there are many publications on the response of understory vegetation to management practices or the natural stand dynamics and succession (Jonsson 1995; Linder et al. 1997; Widenfalk & Weslien 2009), none of them aimed to compare riparian zones. It is therefore unknown if riparian understory vegetation communities develop differently along headwater streams in these structurally different forest stands or if the natural dynamics of the riparian zone are a more dominant factor in determining community composition and diversity.

1.5 Aim and research questions

The purpose of this study is to fill the knowledge gap about understory vegetation communities along boreal headwater streams in production forests and forest reserves. I do this by building upon the work done by Lundqvist (2022) and through answering the following three questions:

1. Do boreal forest reserves and production forests differ in biodiversity in their riparian ground vegetation communities along headwaters in northern Sweden?
2. Do riparian zones along headwaters in northern Sweden harbour different plant communities in production stands and forest reserves?
3. What environmental variables drive biodiversity differences in riparian vegetation communities along boreal headwaters? Are those environmental conditions different for production and reserve sites?

Based on the literature, I anticipate a greater total number of species in forest reserves due to a more heterogeneous forest type (Keeton et al. 2007; Lundqvist 2022). Moreover, I expect vegetation quadrats in forest reserves to have generally higher species richness but also a larger variation within the sites due to the higher heterogeneity (Keeton et al. 2007). Additionally, I predict higher species richness in vegetation plots that are situated at the stream edges (near-stream quadrats) due to higher fluvial disturbance (Kuglerová et al. 2016) and light availability. In line with Jonsson et al. (2020), I also expect higher species richness and diversity with increased age after clearcut in the production forest as all niches will be filled over time. The forest reserves are likely to have higher Shannon diversity scores due to the ‘hotspot’ nature of riparian zones, which is expected to result in a large variability among the forest reserve sites. However, the vegetation communities among sites and forest types will overlap because of the limited total number of species in boreal forests.

In addition, I anticipate more sphagnum mosses will dominate in the vegetation quadrats with higher soil moisture. I further expect the distribution of functional groups of vascular plants is expected to be roughly equal between the two forest types, with more species in different functional groups in forest reserves. Finally, I expect that from site environmental conditions light availability will be a key driver, with more exposed plots having higher diversity. From the findings of Lundqvist (2022), I expect that forest reserves will have increased light availability (higher canopy openness) compared to production forests.

2. Methods

2.1 Site selection and plot placement

In this project, the selection of headwater streams through forest stands was based on the sites used by Lundqvist (2022), as his work provides valuable additional data of the riparian forest structure. As my aim for this research is to assess if the differences he found translate into the understory vegetation, his work and by extension his sites form the basis for this project.

The five production sites used by Lundqvist (2022) were selected to be a more extreme representation of production forests, that is single diameter, single-story spruce dominated riparian forests, which expand all the way to the stream edges. I decided to supplement further four production sites in order to increase the applicability to a broader range of management intensities. This was done by selecting additional forest sites using a set of criteria that aimed to represent typical managed forests of mature age, with differences in the level of



Picture 1 Streams from a forest reserve (Kålhuvudet 1, top left), Lundqvist's extreme production sites (Krycklan 1, top right) and a more moderate production site (Site 294504, bottom)

Site	Forest type	Lundqvist	Age	Wetness	Altitude	Catchment size	Canopy openness	Bankful depth	Bankful width	Deadwood	Litter	Bare soil	Rocks
Site 31	production	Yes	60	mesic	235	1.17	26.90	40.83	27.83	3.17	30.42	1.33	2.08
Site 395501	production	No	89	dry	115	2.51	22.20	72.67	136.50	3.00	14.83	10.17	0.00
Krycklan 1	production	Yes	101	mesic	225	0.24	21.31	29.67	101.33	6.50	21.92	5.58	0.42
Site 294504	production	No	110	mesic	195	0.72	27.20	43.00	77.50	4.00	28.25	6.92	0.00
Site 61	production	Yes	120	mesic	145	3.62	18.20	41.50	166.67	1.17	17.00	16.58	0.00
Site 30977	production	No	125	moist	235	1.00	17.42	32.33	50.33	2.50	17.33	8.92	0.00
Site 9277	production	No	141	mesic	290	0.61	20.43	40.17	47.67	0.42	18.58	3.08	0.17
Gammtratten 1	reserve	Yes	150	moist	465	0.52	29.57	45.33	64.67	1.67	23.92	0.92	0.00
Gammtratten 2	reserve	Yes	150	wet	420	0.26	34.39	25.50	162.67	2.00	9.42	1.50	0.00
Kalhuvedet 1	reserve	Yes	200	mesic	410	1.35	24.51	52.33	121.00	3.08	37.67	1.00	0.50
Kalhuvedet 2	reserve	Yes	200	moist	395	0.23	26.78	33.33	31.17	0.83	14.83	1.08	0.17
Vandatberget	reserve	Yes	300	mesic	285	0.66	22.16	42.17	61.50	5.50	40.33	2.33	0.00

management intensity along a gradient. The sites were chosen from available stands from previous research projects. In particular, the production forests were managed differently, ranging from single diameter spruce dominated stands achieved by previous thinning and cleaning to relatively heterogeneous stands with some deciduous trees. As one of Lundqvist's (2022) sites had been harvested, this resulted in total of 8 production sites suitable for this project (Table 1, Fig. 1).

The five forest reserves which served as references where not supplemented beyond the sites used by Lundqvist (2022, Table 1) due to difficulties to find more sites in the region that fitted the criteria. The forest reserves were required to have never been cut with modern clearcutting methods. These sites were critical for understanding the natural processes that occur in ecosystems that are undisturbed by modern forestry.

Data was collected during summer 2022. Stream reaches used in the previous thesis by Lundqvist (2022) were located using GPS and field notes. At each stream I placed six transects along regular intervals (15 meter unless the reach was shorter) on alternating sides of the stream edge (Fig. 1, right). In cases of wetland conditions or large exposed boulders without vegetation, transects were moved upstream. For each transect, there were two 1x1m vegetation quadrats which were inventoried. The first quadrat was placed along the stream edge (near-stream quadrat), with the centre of the second quadrat being placed at a 20cm elevational increase from the first quadrat's centre (elevated quadrat), perpendicular to the stream (Fig. 1, right). Elevational increases are influential in riparian zones in terms of soil moisture

Table 1 Site characteristics per stream . This table shows the site characteristics for each stream. It lists age (years), forest type and whether or not Lundqvist (2022) used it in his study. Production sites that were included in Lundqvist's study are therefore the more extreme production sites. Further included are the averages of the recorded values for wetness (4 point scale, dry-wet), altitude (m asl), catchment size (km²), canopy openness (%), bankful depth (cm), bankful width (cm), deadwood (cover %), litter (cover %), bare soil (cover %) and exposed rocks (cover %). Only 7 production sites are shown as one was later removed due to unknown age.

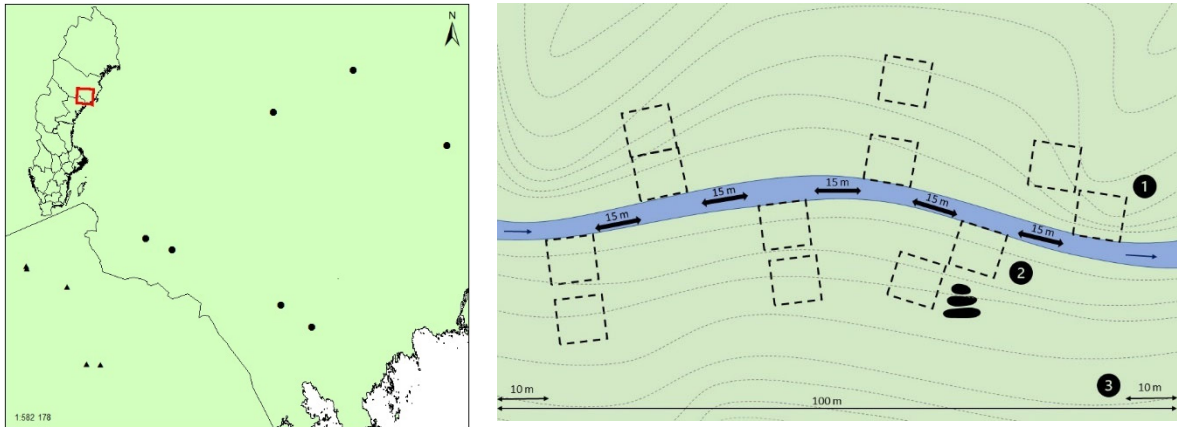


Figure 1 (left) shows the locations of the forest sites used in this study. The circular marks represent the production forests whereas the triangles show the locations of the forest reserves. Figure 1 (right) shows a schematic drawing of transect and quadrat placement within a site. The full reach was 100m with 10m buffer on either end (that is upstream and downstream) (3). All transects were placed on alternating sides of the stream with 15m space in between. The distance between the two quadrats in each transect was determined by the elevational gradient (20 cm elevational increase between the two centroids). Quadrats were adjusted in the upstream direction in case steep slopes forced them to overlap (1) or large boulders prevented vegetation access to soil (2).

and the disturbance regime (Kuglerová et al. 2016). Therefore, an elevational gradient allows to more accurately capture the wider range of species between the stream's edge to the upland than a distance based gradient would be able to, due to varying slopes.

Landowners were contacted for additional information on the sites, most importantly the forest age. During analysis, age turned out to be an important factor, but I was unable to get the age of one of the production stands and it was therefore excluded from the study (table 1). Further, the ages for the nature reserves are estimates, because the county administrative board provided an estimated age of the oldest tree cohort for the entire forest reserves, not just the inventoried stream reach.

2.2 Vegetation survey

To sample vegetation, I build a frame of 1 by 1 meter with ropes along the central axis, dividing the frame into four equal quadrats. This helped with estimating cover percentages of species.

Species were identified using the flora (Mossberg & Stenberg 2010) and the mobile app PlantNet (Goëau et al. 2013; Institut de recherche pour le développement et al. 2022) and their abundance (cover percentage) was estimated based on the vertical plant shoot area projection, or stem count and stem size (Mueller-Dombois et al. 1974; Wikum & Shanholtzer 1978). This estimation method was chosen to account for differences in vegetation development over time between sites. In the field I encountered cases where some sites had fully developed foliage and others were still developing. Visually identifying a full

quadrat limits the chances of underestimating species richness which has been shown to be the case for methods such as the pin point method (Bråkenhielm & Qinghong 1995). The practice of visually estimating cover percentages has been criticized for subjectivity (Milberg et al. 2008; Vittoz et al. 2010). To account for this I was the only one estimating the coverage. This allows observations to be comparable within this study but limits the abundance data from use outside of this project.

Specimen that showed too difficult to identify in the field were brought home, dried and identified at a later date. One exception to this rule was the distinction between the sedges: *Carex brunescens* and *Carex canescens*, which were recorded as *Carex brun/can* as distinguishing proved too difficult or time consuming.

2.2.1 Environmental variables

After the inventory of plant species, I inventoried the present bryophytes, for five distinct groups: sphagnum, feather mosses, polytrichum, mniun and liverworts . These groups were chosen because species belonging to them have shown significant changes in abundance as a result to harvest intensities and environmental conditions in the riparian zone in field observations by Kuglerová et al. (2016) and experiments in Oldén et al. (2019) . For bryophytes, stem count is not a viable option so here surface cover was estimated. The same was done for substrates: bare soil, dead wood, rock and litter, as these were found to have an effect on vegetation and bryophyte communities (Crites & Dale 1998; Lee & Sturgess 2001). At last, other site characteristics were measured. For each quadrat the canopy openness was measured using a picture of the canopy, using a fish-eye lens for mobile phones and the GLAMA mobile app (Tichý 2014). For each transect the stream bankfull was also measured to gauge stream size, as well as the distance between the two quadrats per transect as a proxy for bank slope. Furthermore, the wetness of the soil was assessed on a 4 point scale (Dry, mesic, moist, and wet) by touch.

The size of the catchment for each site was calculated using the flow accumulation raster derived from digital elevation models in the ArcGIS and Whitebox software (Ågren et al. 2014). The digital elevation model also provided the altitude for all streams.

2.3 Analyses

Data analysis was performed using R studio (RStudio Team 2022) and R markdown using knitr (Xie 2022), the packages “plyr”, “dplyr”, “tidyr”, “readxl”, “patchwork”, “ggpubr” and “ggplot2” for data manipulation and plotting (Wickham 2011, 2016; Wickham et al. 2019, 2022; Kassambara 2020; Pedersen 2022; Wickham & Bryan 2022; Wickham & Girlich 2022).

2.3.1 Plant diversity

Species richness

To answer my first research question and to assess the differences in species richness between the forest types, all species in the vegetation quadrats were counted. Species richness per quadrat was used as a response variable and explanatory variables were forest type (production vs. reserve), forest age and quadrat elevation (near-stream, elevated). I also included all two-way interactions between the three explanatory variables and used general linear mixed-effect model with Poisson distribution, because species richness is count data. Site represented a random factor, as there were multiple plots per site. (Zuur et al. 2009b; Bates et al. 2015; Kuznetsova et al. 2017; Bates n.d.). The selection of the final models, for this particular case and the ones later to be discussed in this section, was based on iterative selection with the AIC criterium (Zuur et al. 2009a; Peng & Lu 2012). This meant that models were first optimized for the random effects by comparing all possible random effects in various models and dropping the model with the lowest AIC. This process was repeated until no significant difference was found between the models (<10 units difference in AIC value), in those cases the model with the simplest random effects would be selected. Afterwards the same process would be conducted for the fixed effects and their interactions. Interactions would only be involved up to a two-way interaction level to avoid overcomplication. Selection of the final model was done, again based on the AIC value, but paired with the p-value of a type 2 ANOVA. The models were validated by checking the normality of the residuals (Zuur et al. 2009a). The variables in the model were assessed for significance using an analysis of variance (ANOVA; Fox & Weisberg 2019) type 3, which is best suited when interaction of explanatory variables is involved (Gardener 2017). Additionally, I summed up all species per site (combining all 12 plots) to see if sites were more species rich between the forest types using the Wilcoxon rank-sum test for non-normal data (Gardener 2014; Ott & Longnecker 2015).

Finally, I compared species richness of all sites in a one-to-one comparison (Ogle et al. 2023) using the Dunn test with Bonferroni correction. This was done to evaluate the overall differences among all the sites.

Shannon diversity

As final analysis for the first research question, I assessed the Shannon diversity of the vegetation quadrats. Using a diversity index like the Shannon (also known as Shannon-Wiener index) provides additional information to complement the species richness analysis. The index is calculated using the abundance data and gives a probability for the occurrence of a random individual from the community in the sample. There are many diversity indexes in existence, the Shannon index along the Simpson index are the most widely used, here the Shannon index is preferred as it focusses more on evenness of the species abundance where the Simpson index emphasizes the dominance of a small number of species.

Using the estimated cover percentages for each species, I calculated the Shannon diversity score for each vegetation quadrat (Nagendra 2002; Gardener 2014; Oksanen et al. 2022). Similar to species richness, the Shannon index was compared for the two forest types, elevations above stream, forest age and their interactions using linear mixed effects modelling and the ANOVA type 3 statistical test (Zuur et al. 2009c).

Species accumulation

I also analysed the slope of the species accumulation curves. These curves are used for quantifying and predicting species diversity in an ecosystem. They estimate the number of species present in a given area, even when not all individuals have been sampled. This occurs because the curve only notes newly found species, therefore, as more sampling events occur, the number of new species encountered decreases, and the curve begins to level off, indicating that the majority of the species present in the ecosystem have been sampled. The slope of these curves therefore can give an indication of the rate of discovering new species in plots at the different sites (Colwell et al. 2012; Gardener 2014; Oksanen et al. 2022). To compare the slope of accumulation curves of the different sites and the two forest types, I used the Wilcoxon rank-sum test.

Plant cover

Total plant cover in the vegetation quadrats was analysed using linear mixed-effects modelling to test the effects of forest type and stand age. Sites were included in the models to account for random effects. The significance of the effects on plant cover was tested using a ANOVA type 2. I used the same test to assess the effects of forest type and elevation from the stream on the total bryophyte cover. I further analysed if the five individual bryophyte types had a difference in dominance between the two forest types and elevations by comparing their mean cover per vegetation quadrat. Significance of the differences between the two forest types was calculated using the Wilcoxon rank-sum test as the cover data of individual bryophyte groups per quadrat did not follow a normal distribution for the production forests.

I also calculated the cover for the dispersal types of all plant species per quadrat to assess on which dispersal agents species relied on most and whether this differed between the forest types. I used the data provided by Tyler et al. (2020) who compiled a list of primary dispersal agents for the Swedish flora. To compare the different dispersal types, weighted averages for the dispersal types per forest type were calculated based on the plant cover percentages of the corresponding species per quadrat. This resulted in a single value for average cover per quadrat per forest type for all dispersal types.

2.3.2 Community composition

In order to address my second research question and compare the community compositions in the two forest types, I used Non-metric multidimensional scaling

(NMDS) and the Bray-Curtis ordination metric to compare the community compositions of the forest types, elevations and individual sites using abundance data. Significance of the differences was assessed using permutational analysis of variance (Gardener 2014; Roberts 2019; Oksanen et al. 2022).

Plant functional groups

The different vascular plant species were divided into 8 functional groups: shrubs, dwarf shrubs, ferns, forbs, grasses, sedges, trees and overstory. Trees reflect the regeneration layer of tree species, which are not yet part of the overstory (DBH < 5cm). The total cover for each functional group was summed up per vegetation quadrat and forest site. These data were compared between the two forest types using the Wilcoxon Rank-Sum test because of the non-normal data.

2.3.3 Environmental variables

For the third research question, the environmental variables of the vegetation quadrats and sites were assessed using a principle component analysis (PCA). The variables which were included in this analysis were: bankful width, bankful depth, slope (perpendicular to stream derived from the distance between the quadrats in each transect), wetness, canopy openness, altitude, catchment size and the proportions of: bare soil, rocks, dead wood, litter, and total plant cover. The principle components (PCs) that cumulatively explained >60% of the variation were assumed to have identified the important driving forces in variability of local habitat conditions in the correlating variables (<0.4). The quadrats and sites were plotted in a biplot, against the two PCs which explain most of the variation (Vu 2011; Csárdi et al. 2021).

To get a deeper understanding of local habitat conditions and environmental variables which have not been inventoried, I used indicator values of Swedish plant species (Tyler et al. 2020). These indicator values are an alternative to the Ellenberg values (Ellenberg et al. 1994) and provide more detailed information on the traits of plant species, especially in a Swedish context. The data are based on a broad survey of individual species and vegetation types in Sweden, as well as already available data, including Ellenberg values. The authors aimed to facilitate direct usage of the data in studies analysing changes in space or time based on vegetation compositions.

To calculate a single value per indicator per quadrat I calculated the average of all indicator values of the present species per plot, weighted by their abundance (Persson 1981; Diekmann 2003). The average scores of the following five indicator values were assessed for each site: biodiversity relevance, nitrogen availability, light conditions, soil disturbance and soil moisture (Appendix 1).

Lastly, the Shannon scores of the quadrats were plotted against the scores of the five indicator values with LOESS smoothing to explore possible relationships these variables have with the diversity found in the two forest types.

3. Results

3.1 Plant diversity

3.1.1 Species richness and alpha diversity

On average (\pm SE) , 10.06 (\pm 0.28) species of vascular plants were found per quadrat (production: range = 5-18, mean = 10.11 ± 0.34 ; reserve: range = 2-22, mean = 10.00 ± 0.46). The total number of species at forest sites averaged 24.50 ± 2.06 (production: range = 15-39, mean = 25.57 ± 3.13 ; reserve: range = 19-33, mean = 23.00 ± 2.55).

The data analyses showed that the interaction of forest age and forest type had a significant effect on the species richness in the vegetation quadrats (GLMM & ANOVA type 3: interaction forest type & age: $p = 0.02$ $df = 1$; forest type: $p = 0.01$, $df = 1$, Fig. 2 left). In the production forests, species richness increased significantly (Linear regression; $p = 0.03$, $df = 82$) with age ($r^2 = 0.03 \pm 0.01$) while in reserves, the opposite trend was observed. The stand-alone effect of forest type (without interaction with other variables) was not significant for quadrat species richness (GLMM & ANOVA type 2: $p = 0.90$, $df = 1$). Elevation above stream was not found to play a significant role for species richness with near-streams quadrates and elevated quadrates having similar species richness ($p = 0.32$).

The Shannon diversity index showed the same responses in alpha diversity as species richness. Meaning that the interaction between forest type and forest age significantly affected Shannon diversity of the quadrats (LMM & ANOVA type 3; $p = 0.02$, $df = 1$, Fig. 2 right), causing the index value to increase with age for production forests and decrease with age for forest reserves. When disregarding the other variables, forest type was found to have no significant effect on Shannon diversity (LMM & ANOVA type 2: $p = 0.95$, $df = 1$). The Shannon diversity index in production forests increased significantly with age (linear regression; $p = 0.04$, $df = 82$).

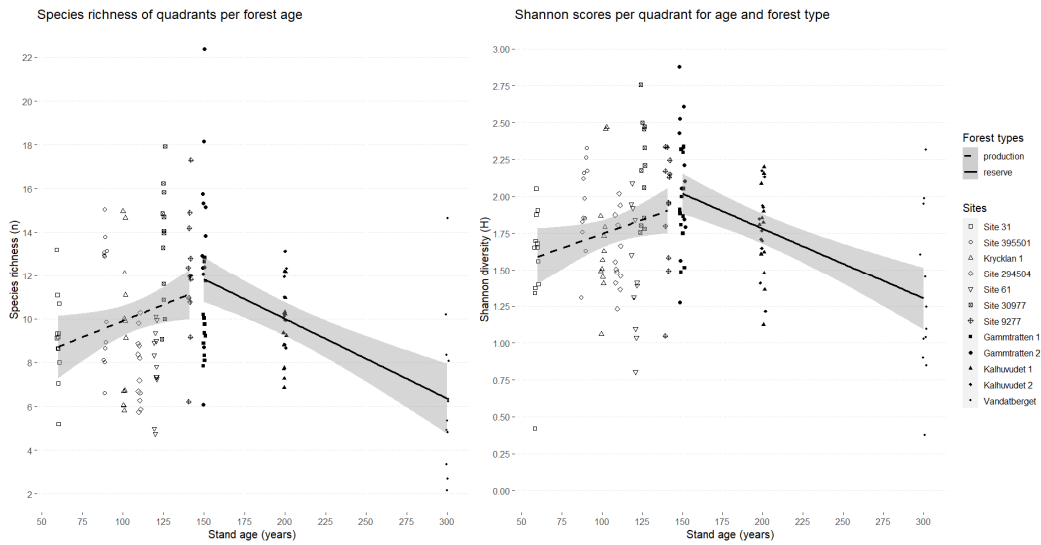


Figure 2 (left). Species richness of vegetation quadrats shown over stand age with linear trend lines for the two forest types (production and reserves). The quadrats of each site have their own symbol with the open or open-with-cross symbols belonging to the production forests and the filled symbols being forest reserves. The same applies to the dashed line for production forests and solid line for forest reserves. Figure 2 (right). Linear relationships of species richness and the Shannon diversity score respectively as a function of the interaction of age and forest type. GLMMs showed that the interaction between forest type and forest age had a significant effect on species richness ($p=0.01$) and Shannon diversity ($p=0.02$). Forest type was also shown to be significant ($p=0.01$ in both cases)

The total number of species found per forest site (all quadrats summed up) did not differ significantly between the two forest types (Wilcoxon rank-sum test; $p=0.74$; production: 25.57 ± 3.13 ; reserve: 23 ± 2.55 , Fig. 3), neither did the slope of the species accumulation curves for the sites (Wilcoxon rank-sum test, $p=0.53$).

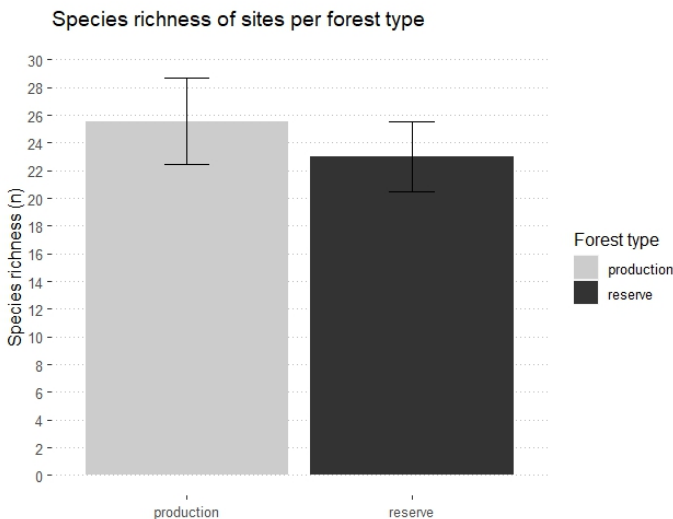


Figure 3. Comparison of the species richness of sites between the two forest types. This includes the average number ($\pm SE$) of all vascular plant species found per forest site belonging to the two forest types.

3.1.2 Plant cover

Bryophytes covered the soil most abundantly ($74.37\% \pm 2.83\%$) followed by vascular plants ($63.95\% \pm 2.31\%$). *Vaccinium myrtillus* and *Vaccinium vitis-idaea* were most commonly found vascular plant species (83% and 82% of all quadrats respectively, Appendix 2). Total vascular plant cover decreased significantly with increased forest age in the production forests (LMM & ANOVA type 2, $p=0.002$, Fig. 4), the same trend was found for forest reserves (LMM & ANOVA type 2, $p=0.01$, Fig. 4). The total vascular plant cover per quadrat did not differ significantly between forest reserves and production forests ($\Delta=1.03\%$, LMM & ANOVA type 2: $p=0.93$).

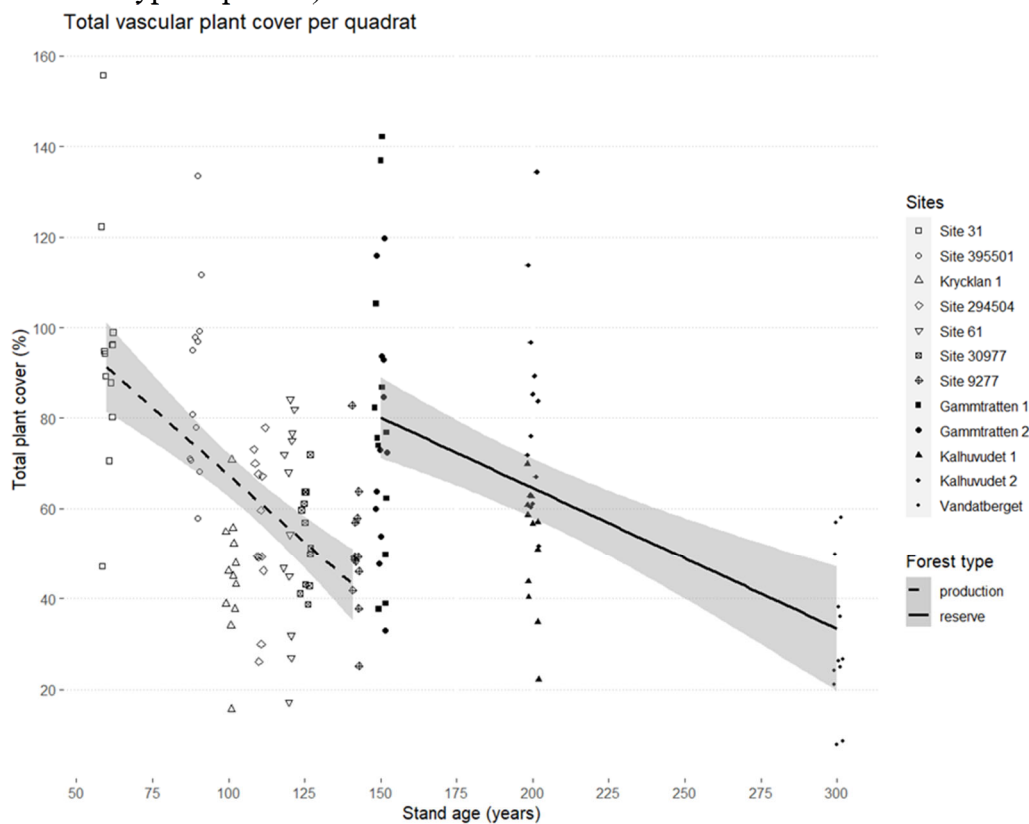


Figure 4. Total plant cover per quadrat over age. The dots signify their respective forest sites as described for figure 2. Trend lines for both production forest and forest reserves is shown.

The plant species in the inventoried communities rely heavily on three types of dispersal (Fig. 5): Passive (fruits without functional adaptations to any particular vector, $37.83\% \pm 2.91\%$), Birds ($36.50\% \pm 1.83\%$) and Air through small and light fruits ($26.58\% \pm 3.80\%$).

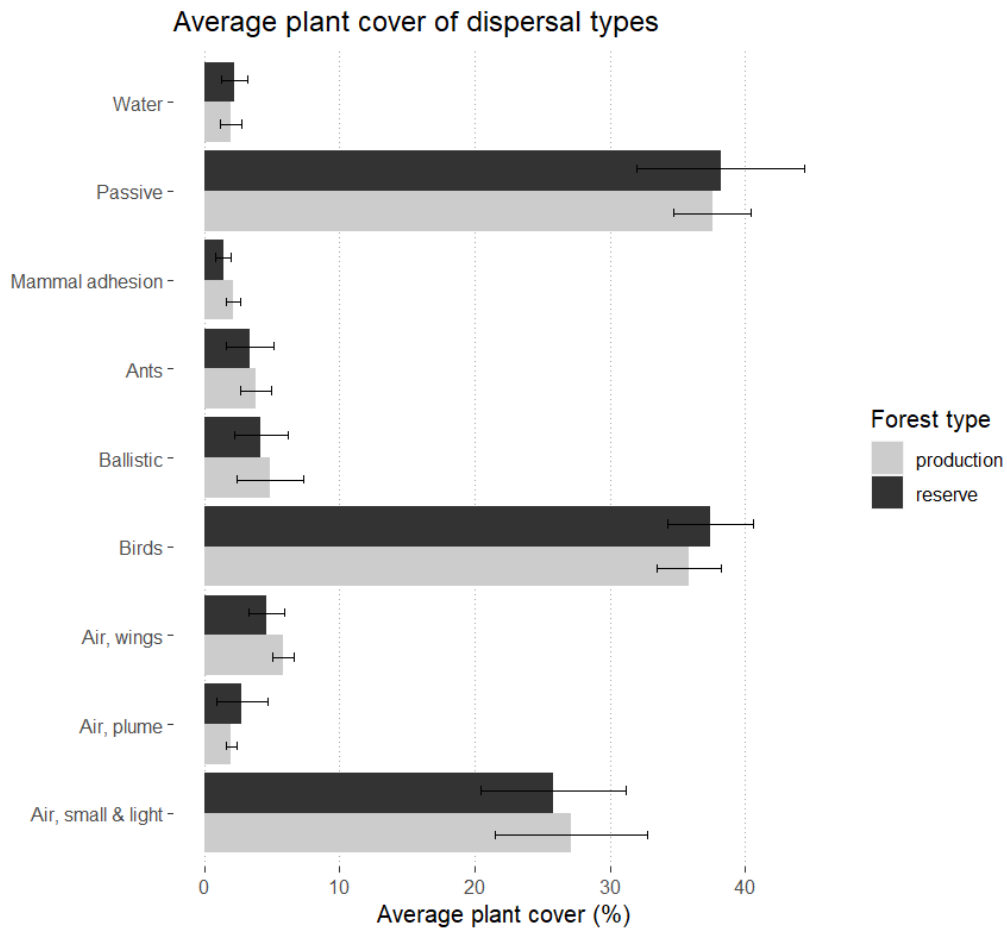


Figure 5. Average plant cover of different dispersal types, as a proxy for the success of plant species dependent on those dispersal types. The results are split between the two forest types but both show the same dominance of passive dispersal, dispersal by birds or dispersal through the air by means of small and lightweight seeds.

Bryophytes

The total cover of bryophytes per quadrats at the forest reserves were found to be higher (LMM & ANOVA type 2: $p = 0.02$ Fig. 6) and less varying (range = 11-137, mean = 93.87 ± 3.37 , $sd = 26.09$) than production forests (range = 1-132, mean = 60.44 ± 3.50 , $sd = 32.08$). Furthermore, I found that the total cover of bryophytes varied heavily between the production sites (range of cumulative bryophyte cover of all 12 quadrats per sites: 331– 1172, Appendix 8).

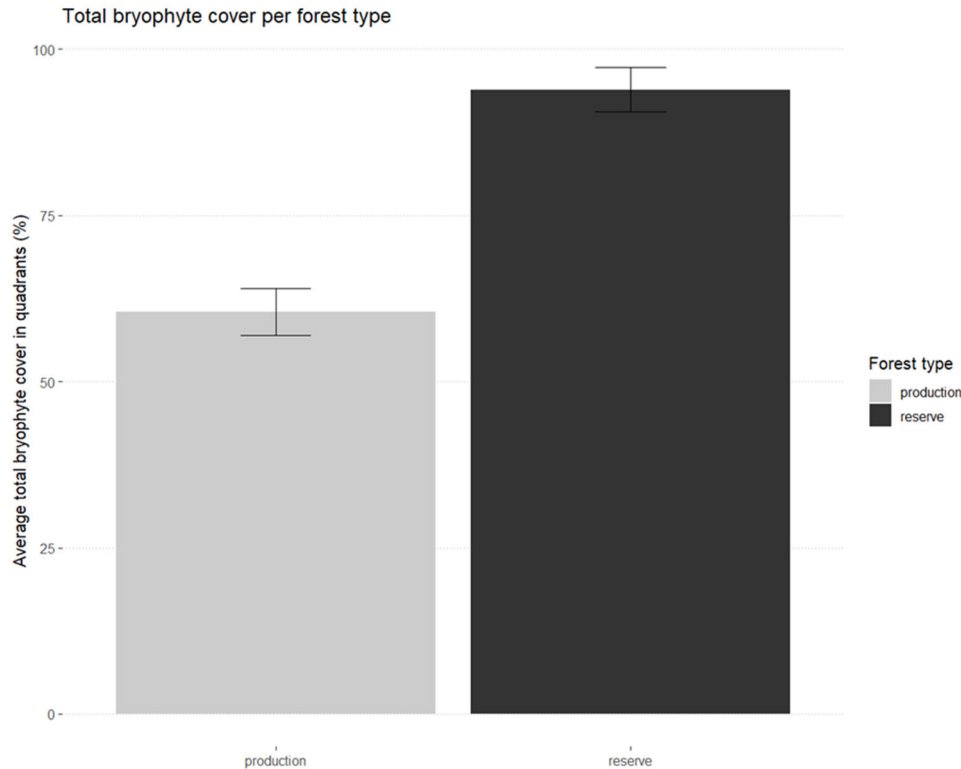


Figure 6. The average of the total cover (\pm SE) of bryophytes for production forests (light grey) and forest reserves (dark). The difference between the two forest types was found to be significant ($p=0.026$).

Elevation was also found to have a significant effect on total bryophyte cover (LMM & ANOVA type 2: $p=0.01$) with higher cover in the near-stream quadrats ($80.53\% \pm 3.81\%$) compared to elevated quadrats ($68.21\% \pm 4.08\%$). Sphagnum moss was usually found to be the most dominant moss in the vegetation quadrats (mean = 39.30, SE=2.83, 46.6% of total moss cover). Sphagnum was also found to be nearly twice as abundant in reserve forests ($53.07\% \pm 4.27\%$), than in production forests ($29.46\% \pm 3.38\%$, LMM: $p=0.009$) and higher in the near-stream quadrats ($49.38\% \pm 3.81\%$) compared to elevated quadrats ($29.22\% \pm 3.82\%$, LMM & ANOVA type 2: $p < 0.01$). Feather mosses was second most dominant (mean = 20.90, SE=2.12, 28.4% of total moss cover) and were found to be more abundant at the elevated quadrats ($27.29\% \pm 3.33\%$, near-stream: $14.50\% \pm 2.41\%$, LMM: $p < 0.01$)

Splitting the five inventoried bryophyte groups shows that only mniium, polytrichum and sphagnum differ significantly in abundance. Mniium was found to be more abundant in production forests ($2.42\% \pm 0.65\%$) compared to forest reserves ($0.48\% \pm 0.16\%$, Wilcoxon rank-sum test: $p < 0.001$, Fig. 7). Contrastingly, both polytrichum and sphagnum moss were significantly more abundant in the forest reserves ($13.15\% \pm 1.62\%$ and $53.07\% \pm 4.27\%$ respectively) than in production forests ($6.20\% \pm 0.95\%$ and $29.46\% \pm 3.38\%$ respectively, Wilcoxon rank-sum test: $p < 0.001$, Fig. 7).

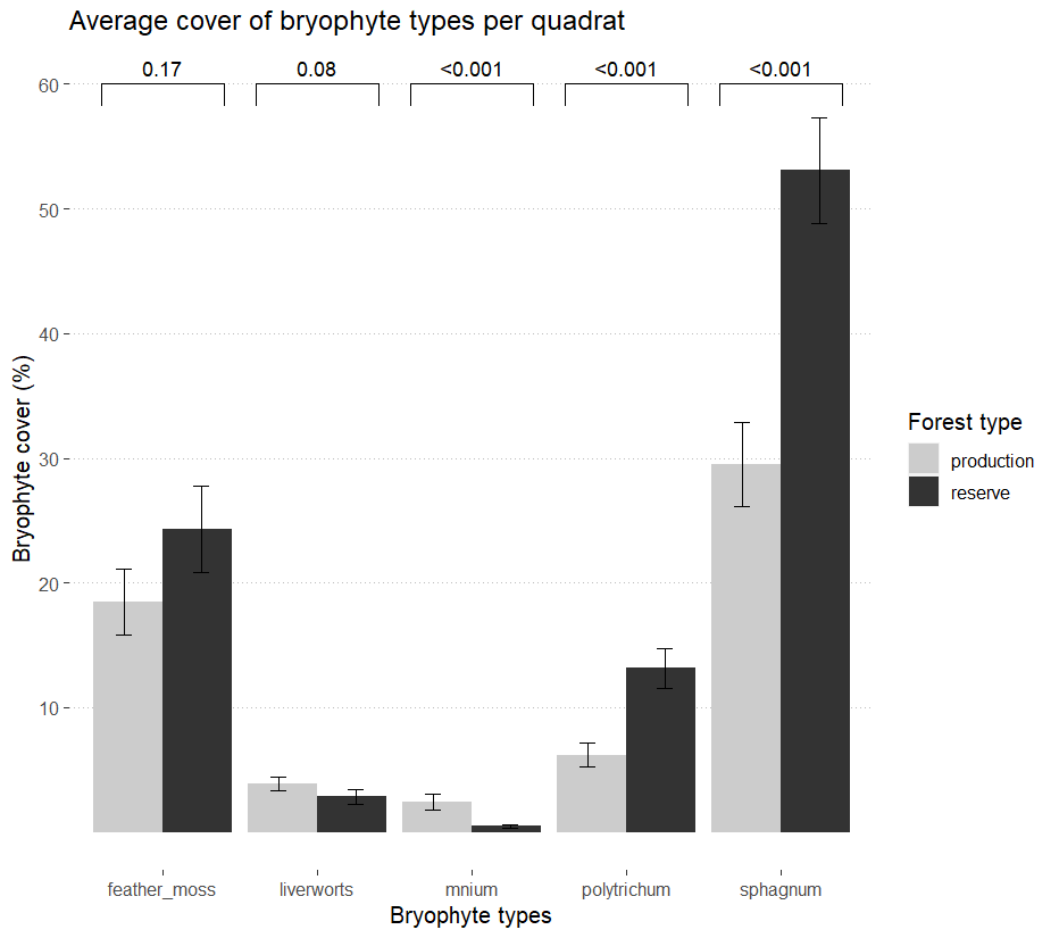


Figure 7 Average cover (\pm SE) of different bryophyte groups in quadrats for production forests (light grey) and forest reserves (dark). The differences were significant for mniium, polytrichum and sphagnum ($p < 0.001$ in all three cases).

3.2 Community Composition

3.2.1 NMDS

The community composition in vegetation quadrats was different between the two forest types (PERMANOVA; $p < 0.01$, $df = 1$, Fig. 8). The NMDS for individual sites (Appendix 5) shows the great variation between and within the different forest sites. PERMANOVA further confirmed that the individual sites differ significantly in their community composition ($p < 0.01$). The data also show that the community composition is different depending on the elevation of the quadrat (PERMANOVA; $p < 0.01$, $df = 1$, Appendix 5), as well as the interaction, or combination of forest type and elevation (PERMANOVA; $p < 0.01$, $df = 1$, Appendix 5).

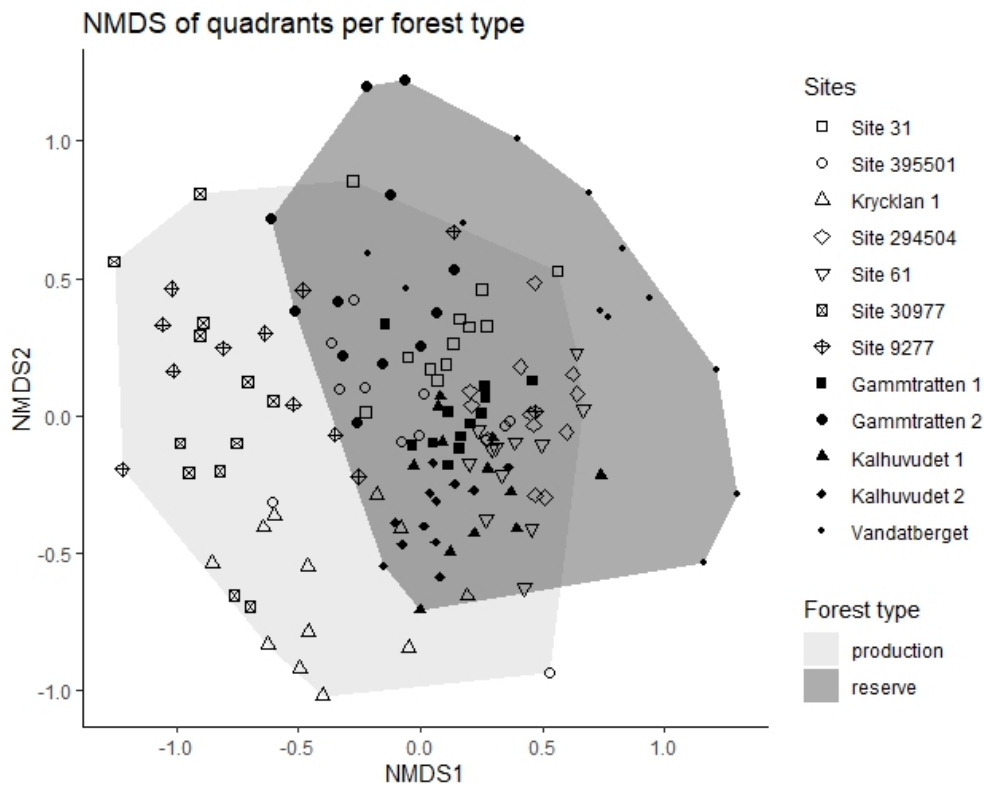


Figure 8. Non-metric dimensional scaling graph based on the Bray-Curtis dissimilarity metric to show the vegetation composition of the quadrats as mark –each mark representing one quadrat. The outer points of each forest type are connected to show their range on the axis. PERMANOVA shows that community compositions of forest reserves differ significantly for those in production forests ($p < 0.001$)

3.2.2 Plant functional groups

Out of the seven identified plant functional groups, Forbs were the most species rich, with a total of 27 species found across both forest types (Table 2, Appendix 3 for full list of species and functional groups). The biggest differences in species richness of a functional group between the two forest types were found in the grasses and sedges, with 100% more sedge and 80% more grass species in production forests compared to forest reserves. Shrub species were predominantly Salix, being found in single quadrats and therefore no overlap of species was found at all between the two forest types.

Table 2 Counts of species per functional group per forest type

	Production forests	Forest reserves	Total	Δ (% increase in production forests)
Forbs	22	19	27	15.8%
Grasses	9	5	9	80.0%
Sedges	8	4	8	100.0%
Ferns	4	4	4	0%
Shrubs	3	3	6	0%

Dwarf shrubs	4	3	4	33.3%
Trees	6	4	6	50.0%
Total	57	44	65	29.5%

I found that the vegetation quadrats had significantly higher cover of sedges in forest reserves compared to production forests (Wilcoxon rank-sum test; $p < 0.01$, production: 5.3% , reserve: 10.2% cover, Fig. 9). Production forests also had sporadic quadrats with very high fern cover (>40% with one up to 82%), however, statistically the production forests did not differ significantly from forest reserves (Wilcoxon rank-sum test; $p = 0.223$). No other functional groups significantly differed between the production and reserves. The cover of different functional groups varied between the individual sites, this variation is shown in Appendix 9.

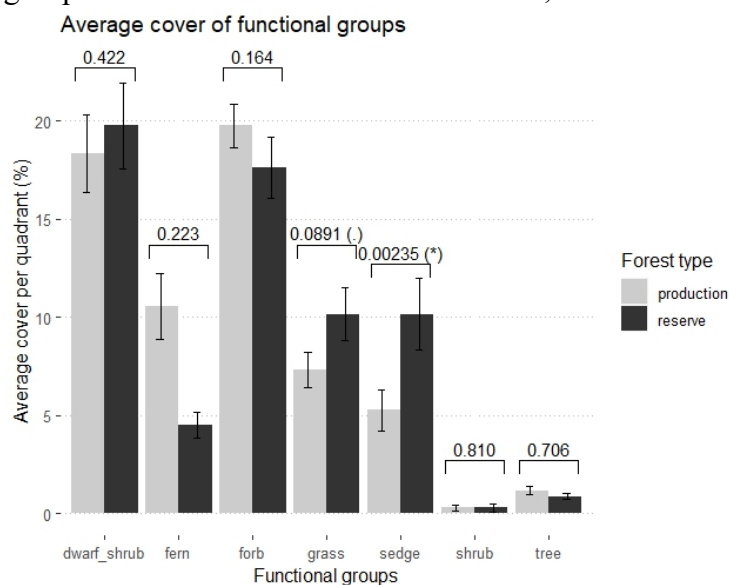


Figure 9. Average (\pm SE) cover of the 7 functional groups, split between the two forest types. The values above the bars are the p-values from the Wilcoxon rank-sum tests.

3.3 Environmental variables

The inventoried forest sites ranged between 60 and 300 years old. All forest reserve sites were older than production forest sites (reserve: mean = 200, sd = 61.2. production: mean = 106.6, sd = 26.5).

The canopy openness was low in both forest types, but the forest reserves were slightly more open than production forests, with the near-stream quadrats receiving more light than the elevated quadrats (canopy openness in; reserve-near-stream: mean = 28.24 %, SE = 1.20, reserve-elevated: mean = 26.72%, SE = 1.18; production-near-stream: mean = 22.52%, SE = 0.96, production-elevated: mean = 21.38%, SE = 0.87). The difference in canopy openness was found to be significant between forest types in general (LMM & ANOVA type 2: $p = 0.03$, $df = 1$), elevation or the interaction of elevation and forest type did not have a significant effect on canopy openness.

3.3.1 PCA

The principle component analysis explained >60% of the variation using the first 4 PC's which correlate mostly with the following environmental variables: Catchment size (PC1: 0.46), Altitude (PC1: -0.47), Wetness (PC1: 0.42), Litter (PC2: 0.53), Dead wood (PC2: 0.43), total plant cover (PC3: -0.57 & PC4: -0.42), bankful width (PC4: 0.66).

Plotting the Principle Component Analysis (Fig. 10) further showed a large variation between and within the sites. The different sites are organised along the horizontal axis, which corresponds to changes in catchment size, altitude and the amount of bare soil in the quadrats. The forest reserves are found left from the centroid of the plot, indicating smaller catchment sizes, less bare soil and higher altitudes. The variation within the sites is primarily organised along the vertical axis which corresponds to changes in the amount of litter and deadwood.

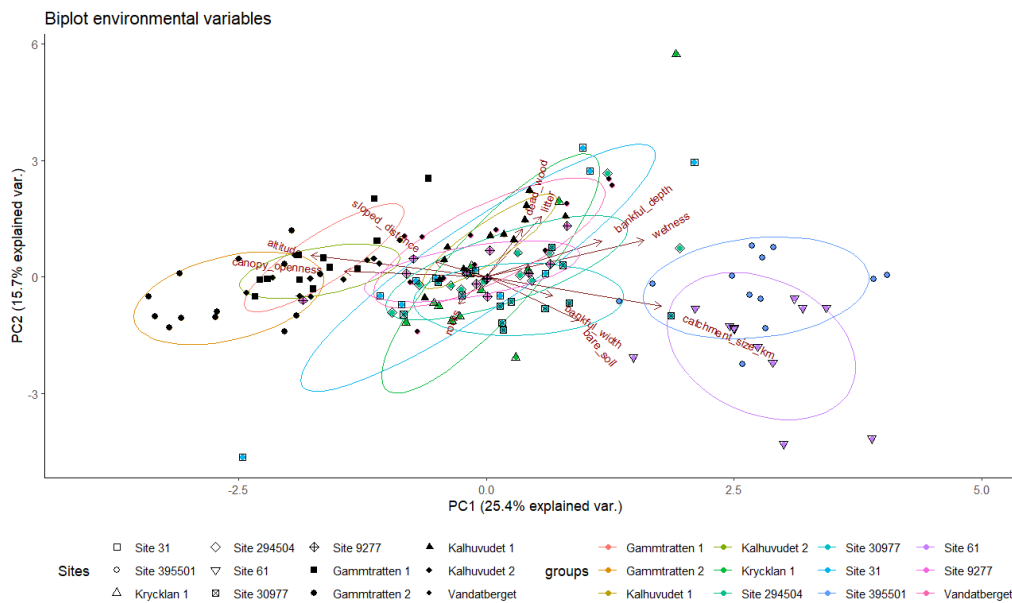


Figure 10. Biplot for PC 1 and 2, showing a total of 37.8% of the variation of the environmental variables found at the different sites. PC1 and 2 correlated most highly with the following variables, Catchment size, Altitude, Wetness (all PC1, horizontal orientation), Litter and Deadwood (PC2, vertical orientation)

3.3.2 Indicator values

The five indicator values, biodiversity relevance, light conditions, moisture conditions, nitrogen conditions and soil disturbances, are shown by their range and mean (\pm SE) for the two forest types below (table 3). The range of indicator values shows a lot of overlap, but the production forests have broader ranges for biodiversity relevance, light conditions and nitrogen conditions. The average indicator value for nitrogen conditions is also half a unit higher in production forests compared to forest reserves, with scores corresponding to a range of

“moderately N-poor” and “moderately N-poor - moderately N-rich” conditions. Additionally, biodiversity relevance has a 0.4 unit higher mean value for forest reserves. This is scored on a logarithmic scale with the indicator values of 3 and 4 corresponding to 13-24 and 25-50 associated species respectively.

Table 3 Indicator value ranges and averages (\pm SE) for both forest types

	Production forests	Forest reserves		
	Range	Mean	Range	Mean
Biodiversity relevance	1 – 6	3.30 \pm 0.13	2 – 6	3.75 \pm 0.13
Light conditions	2 – 5	3.48 \pm 0.07	3 – 5	3.78 \pm 0.07
Moisture conditions	4 – 7	4.95 \pm 0.06	4 – 7	4.93 \pm 0.07
Nitrogen conditions	1 – 6	3.44 \pm 0.12	2 – 4	2.97 \pm 0.09
Soil disturbance	1 – 2	1.80 \pm 0.04	1 – 2	1.97 \pm 0.02

4. Discussion

4.1 Using forest reserves as references

The purpose of this study was to fill the knowledge gap about the understory vegetation communities along boreal headwater streams in production forests and forests reserves. I tried to answer research questions with the aim of identifying differences in plant diversity, community composition and the driving environmental variables between forest reserves and production forests. I did this by building upon recent work by Lundqvist (2022) who found significant differences in forest structure between the two forest types. In the following paragraphs I will discuss my findings and relate those to existing literature in order to discuss possible explanations.

Lundqvist (2022) stated that the forest reserves can be classified as either minimally disturbed, old-growth or long-untouched forests. This means that they fit the definition of primary forests (Sabatini et al. 2021). A limitation of these forest reserves as references is that they are all significantly older than the production sites. However, as un-clearcut forests, matching the criteria of primary forests, of the same age do not exist, these forest reserves function as the best available references to my production forests.

The differences between the forest reserves and the production forests in Lundqvist (2022) are plenty. The diameter distribution formed an inverted J-shape for forest reserves, while it showed a lightly skewed unimodal distribution for production forests. These findings are comparable to earlier results in both forest reserves (Linder et al. 1997) and production forests (Burkhardt & Tomé 2012). This combined with the fact that the forest reserves contained almost twice the number of stems per hectare (1130 compared to 617 in production forests), while the proportional species composition was similar (also found in Nilsson et al. 2003). They further found more dead wood in the riparian zone of forest reserves as well as a higher degree of canopy openness when comparing to the production forests.

In my thesis, I wanted to know whether these differences in forest structure, resulting from forest management, led to different understory vegetation communities in the riparian zone. As stated before, the riparian zone acts as a biodiversity hotspot (Naiman & Décamps 1997; Sabo et al. 2005) and performs

important functions to regulate stream water quality and ecological functioning (Naiman & Décamps 1997; Luke et al. 2007). The extent to which the riparian zone is able to perform these functions is affected by the structural diversity (O'Hara 2016) and species composition (Goudarzian et al. 2021), with the herbaceous layer playing a significant role in the cycling of nitrogen (Langendoen et al. 2012). Differences found in biodiversity or community composition of the understory vegetation could therefore have implications for the ecological functioning of the riparian forest.

The forest reserves in this thesis fit the definition of primary forests (Sabatini et al. 2021; Lundqvist 2022) and are chosen to represent natural stand dynamics. However, anthropocentric influences have even impacted the stand structures in these forests (Linder et al. 1997). Even in the absence of active forest management practices, the extensive fire suppression throughout the entire Swedish forest landscape removed a very important natural disturbance dynamic (Linder et al. 1997; Linder & Östlund 1998). This has resulted in denser forest stands as well as a decrease or elimination of canopy gaps in the riparian zone. Even with these structural changes, forest reserves have been shown to protect important biodiversity (Hedwall & Mikusiński 2015), but it is important to realise that they represent an altered form of natural stand dynamics.

4.2 Plant diversity

4.2.1 Species richness and alpha diversity

In total, I found 64 species of vascular plants. 53 of these species (83%) were found in the production sites and 48 occurred in the forest reserves (75%). All species were endemic for Sweden and none were classified as threatened. The total number of species per site ranged between 15 and 39 which is in line with vegetation surveys along streams of similar sizes by Kuglerová et al. (2015).

My data showed that neither species richness nor alpha diversity in the vegetation quadrats or between entire forest sites differed significantly between the two forest types (production and reserves). Forest type however did affect the significant correlation of stand age with both species richness per quadrat and alpha diversity. This meant that species richness and alpha diversity increased in production stands with increasing stand age, while the opposite trend was observed for forest reserves, where species richness in the quadrants decreased with increasing stand age. When looking at all sites together, Fig.s 2_{ab}, show that plant species richness and alpha diversity peak around a forest age of 130-150 years before decreasing. This result follows the “intermediate-disturbance theory” (IDH, Grime 1973; Huston 1979), stating that a maximal value for local species diversity is reached when disturbance is not too frequent nor too rare. My results are further in line with results found by Hart & Chen (2008). They found that species richness was highest in stands with intermediate ages (72-90 years) since

stand replacing fires and stated that understory vegetation communities in the central boreal shield follow the intermediate-disturbance theory.

It is important to state that very little evidence for the IDH was found (Mackey & Currie 2001) and it has received major criticism (Fox 2013). Moreover, I believe that my results cannot be interpreted as a confirmation or rejection of the IDH. This is because the stand ages of the two forest types do not overlap and importantly, the variable 'age' has a different connotation for the two forest types. For the production forests, it states the stand age, i.e. time since last clear cut. In contrast, the forest reserves were never clear cut using modern techniques and as such, age refers to the age of the oldest cohort in the stand, as estimated by the county administrative board. Therefore I would argue that the opposing two linear trends between forest age and species richness/alpha diversity should rather be considered separately. This would indicate a simple positive relationship between diversity in understory vegetation and time since clear cut. This result was also found by Jonsson et al. (2020) who stated that ecosystem services related to diversity were highest in the oldest (120-185 years) stands in production forests .

A possible explanation for the negative relationship between plant diversity (species richness and alpha diversity), and the forest age in the reserves is harder to identify. This relationship goes against research by Wardle et al. (1997, 2012) that found that species richness and diversity of vascular plants increased through ecosystem retrogression in unmanaged forests on boreal island systems. Meaning that in forests without catastrophic disturbances, which reset the successional clock, species richness and diversity increased over time. The indicator values for the species in my research further showed very low levels of soil disturbance (table 3) without any significant variation between the sites. This shows that disturbance or a lack thereof might not be the driving mechanism for species diversity in the forest reserves. In contrast, my data showed a positive correlation between canopy openness and species richness (Pearson correlation: $\rho = 0.45$), with canopy openness also decreasing with age in the forest reserves (appendix 4). This correlation is probably the result of the altered natural stand dynamics in forest reserves as a result of fire suppression. With the older forests further along the development to denser forest stands as shown by Linder et al. (1997) and Linder & Östlund (1998). Therefore it is likely that canopy openness (or light availability) is a driver for plant diversity in my forest reserves, something that has been found in earlier literature too (Grandpré et al. 2011; Schmiedinger et al. 2012).

My data further showed that there were certain individual forest sites that had significantly higher species richness per quadrant compared to some of the other sites (Appendix 7). The individual differences between the production sites might be explained by the differences along the management gradient as I selected them. The extremely dense and spruce dominated stands used by Lundqvist (2022) generally had lower species richness per quadrat than the other production sites. Whereas the two sites with highest species richness per quadrat were a site with Sami reindeer herding and a site that was also classified as Nature2000. Important is that each site is unique and many things may influence a species' occurrence

even within the driving force of habitat dynamics and the presence or absence of forest management.

My data did not show any effect of elevation above the stream on species richness in the quadrants or alpha diversity. This is not in line with earlier results from Kuglerová et al. (2014, 2016) who found that higher elevation from the stream resulted in less influence by fluvial disturbance, leading to lower species richness, unless groundwater discharge acted as an extension to the riparian zone. The disparities between my data and earlier published results are probably due to the quadrat size I used in my design. Kuglerová et al. (2014) used narrow 80x20cm sampling plots as opposed to my 1x1m. Kuglerová et al. (2015) further show that the habitat breadth of the riparian zone increases along stream size gradient. My data were collected only along headwater streams where the riparian elevation zones, typical for larger streams (Jansson et al. 2019), are clustered within the first meter from the stream. This means that possible elevational gradients would have existed within a single quadrat and my sampling method may have therefore not been able to record this. Instead, I may have sampled the entire riparian elevational gradient in the near-stream plots and/or recorded riparian and upland communities in the elevated plots.

4.2.2 Plant cover

My results showed no significant difference between the production forests and forest reserves for the summed cover of vascular plants per quadrant. For both forest types this total cover of vascular plants per quadrant decreased with increasing stand age. Long-term studies found a declining trend of total plant cover over time in boreal forests (Odell & Ståhl 1998; Hedwall et al. 2013). Both studies correlated this decline to an increase in tree volume. Stand age was not identified as a driver for plant cover by Odell and Ståhl (1998). Hedwall et al. (2013) even found the opposite effect from my results with decline of total plant cover correlating with a 4% decline in stand age. Therefore, increasing tree volume (and perhaps accompanying decreasing light availability) might be the driver behind the decline in vascular plant cover. It could be that tree volume, canopy openness and age are highly correlated in my sites, explaining the age effect I found. There is further evidence that low light availability is driving plant cover, with only 2 to 6% of light reaching the forest floor in a mature stand (Constabel & Lieffers 1996; Messier et al. 1998; Hart & Chen 2006). Light data from my own sites does show the same trends for both forest types (appendix) indicating that light is probably the limiting factor for the total vascular plant cover.

My results further showed that forest reserves had a higher cover of bryophytes compared to the production forests, with sphagnum mosses being the most dominant bryophyte type. The increase in bryophytes in forest reserves has two likely explanations. First, the soils in forest reserves were wetter than in the production forests (table 1), with 53% of quadrats being moist or wet in forest reserves compared to only 22% in production forests (data not shown). Secondly, Hart and Chen (2008) found that bryophyte cover establishes slowly after major

disturbances, but, in contrast to vascular plants, increases indefinitely. Therefore, the higher age of the forest reserves might indicate a longer period of development for the bryophytes resulting in higher cover. Additionally, elevation from the stream seemed to play an important role in determining the presence of the two most dominant bryophytes (sphagnum and feather mosses), with sphagnum having higher cover percentages at the lower, or near-stream, quadrats, which was also found by Ring et al. (2018). The increase of sphagnum mosses at the near-stream quadrats can be explained by the higher moisture levels in the soil. Whereas feathermoss increased at the drier, elevated quadrats.

The dispersal types (Tyler et al. 2020) that were correlated to the species covering most of the forest floor, and can therefore be seen as the most successful, were dispersal by birds, passive dispersal or dispersal through the air by means of small lightweight seeds. Interestingly, even though one might expect hydrochory, or dispersal through water, to be prevalent in riparian zones, my data do not show it. This can be explained by the small catchment areas of my streams. The importance of hydrochory increases with catchment size and stream order (Nilsson et al. 2010; Kuglerová et al. 2015) as more branches of the dendritic river network contribute seeds to the downstream riparian zones. It is therefore not surprising that Kuglerová et al. (2015) found increasing success of species dependent on hydrochory and decreasing success of species dependent on wind and animal dispersal downstream in the sampled river networks. Since I looked at small headwater streams, the importance of the stream for seed dispersal into my vegetation quadrats is very small and instead, the plant species rely on passive dispersal or dispersal by the wind or birds.

4.3 Community composition

4.3.1 Community composition and NMDS

The community composition of vascular plants was influenced by multiple variables. Most notably, I found that forest type, elevation above the stream and their interaction all significantly altered the community composition. This is not to say that there wasn't significant overlap between the communities in different groups (Appendix 5). The influence of elevation from the stream on community composition might be explained by higher disturbance closer to the stream and different soil conditions. (Närhi et al. 2011) found that edaphic conditions are often drivers of understory species compositions in coniferous forests. Furthermore, the elevational gradient in riparian zones heavily influences soil properties through moisture conditions (Hefting et al. 2004) caused by GW fluxes from the uplands (Fisher et al. 2004), waterlogging (Silvertown et al. 1999) and flooding (Naiman & Décamps 1997; Renöfält et al. 2005).

When examining the NMDS plot of individual sites (Appendix 5) however, more distinct shapes can be identified with some sites having little to no overlap with sites of the other forest type (Vändåtberget, Krycklan 1, Site 30977 and 9277). The differences in community compositions between all sites was found to be

significant, but it is interesting to zoom in on these particular sites as they include the oldest forest reserve and the two oldest production stands. It is therefore interesting to note that forest age seems to affect the two forest types differently. Most of the younger production stands (31, 395501, 294504 and 61) have significant overlap with most of the forest reserves (Gammtratten 1 & 2 and Kålhuvudet 1 & 2), but the oldest production sites (30977 and 9277) have little to no overlap and are positioned at the left side of the graph while the oldest forest reserve (Vändåtberget) has little overlap with the younger production stands and is positioned on the right. This might indicate that the development and aging of production stands does not develop the same understory plant communities as forest reserves. Even though species richness and alpha diversity became more comparable with the old production stand age and young ($\Delta 5$ year) forest reserve stand age, their community composition seems to diverge, showing that both metrics should be considered as neither tells the full story. Schmiedinger et al. (2012) also found community composition to be a good indicator of forest management and supported earlier conclusions that it works as a better indicator than alpha diversity (Brososke et al. 2001; Hart & Chen 2006).

There were however, a number of species that were exclusively found in either the production forests or the forest reserves. In total, 22 species were exclusive to the production forests, and 7 to the forest reserves. The full list of the exclusive species can be found in appendix 6. The exclusive species in the forest reserves belonged to the functional groups of forbs and shrubs (*Salix* spp.) whereas the exclusive species in production forests had all functional groups represented. Most notably, the production forests had two deciduous tree species (*Betula pendula* and *Alnus incana*) in the ground regeneration layer while these were not found in the reserves. In contrast, *Salix* spp. was found in the shrub layer only in forest reserves. The higher number of exclusive species for production forests could be explained by the higher number of sites that were inventoried. Unfortunately, I was not able to locate more reserve sites within the desired region where I was certain of the forest age and no industrial forestry impacts. This should, however, be an endeavour of future study.

4.3.2 Plant functional groups

As for functional groups, I found that forbs was the most species rich plant functional group. It, together with dwarf shrubs dominated the ground cover of most forest sites. The cover of different plant functional groups did not differ significantly between forest reserves and production forests except for the sedges, which were significantly more abundant in forest reserves than production forests. This is interesting as sedges are generally more common in younger maturity stands (Widenfalk & Weslien 2009). Sedges, as well as grasses, were however, much more species rich in production forests than forest reserves with about double the number of species. Production forests further had slightly more species of forbs as well as tree species in the understory. All of this further shows that species and plant functional group data is not interchangeable and both should be considered when assessing differences in plant communities.

4.4 Environmental variables

4.4.1 Recorded environmental variables

It has well been established that environmental variables play an important role for species compositions (Giesler et al. 1998; Zinko et al. 2005; Kuglerová et al. 2014, 2015, 2016), which in turn affects the functioning of the riparian forests (Mayer et al. 2007; Goudarzian et al. 2021). To reiterate, light availability, driven by overstory canopy openness (Grandpré et al. 2011; Schmiedinger et al. 2012), soil chemistry and wetness (Zinko et al. 2005; Kuglerová et al. 2014) and disturbance linked to fluvial regimes (Naiman & Décamps 1997; Lind & Nilsson 2015) are all important drivers of understory riparian communities. Therefore, in addition to analysing the differences in understory plant communities, it is also important to understand any possible environmental differences at play.

The results showed that forest reserves had a significantly higher degree of canopy openness than production forests, although in absolute terms the difference was small (5.5%). The difference in canopy openness might be linked to forest age as Bechtold et al. (2017) found that darkest conditions were found in intermediate forests (aged 80-158 years), while old forests (>300 year) had very open canopies. This trend is not consistent for my individual forest sites. Only when the averages of production forests (intermediate age) and forest reserves (old) are compared can the correlation be observed. My results differ from Lundqvist (2022), who found quite large differences. However, he took the canopy measurements at 5 meters from the stream whereas my measurements were done at half a meter and 2.25 meters (on average, depending on the bank slope) from the stream. For both our measurements this constituted the centre of our quadrats. As my measurements were closer to the stream and stream edges have higher canopy openness, the differences in my measurements were smaller between the forest types. However, as shown, light availability is important for species richness and plant cover (Messier et al. 1998; Grandpré et al. 2011; Schmiedinger et al. 2012; Kaylor & Warren 2017), so although small, these differences are important.

All of the forest reserve stands were also older than the production sites. It is important to reiterate that the measure of age differs between the two forest types. For the production forests it is the time since the last clear cut, this is in absolute years and an accurate measure. Whereas for the forest reserves it is an estimation of the oldest tree layer, since the forests were never clear cut using modern methods. This estimation was provided by the county administrative board of Västernorrland. While I cannot be certain of the exact age of the riparian forests I inventoried for this thesis, it is rather clear that those stands are considerably older compared to the production sites. Further, it is unlikely that the ages of the forests in the reserves are of by several decades, meaning that they are likely correctly ordered along the age gradient. This means that the slope for species richness and Shannon score might not be fully reliable for forest reserves, however, we can be quite certain that the correlation of both variables and the stand age is negative.

The PCA plot shows that catchment size and altitude are the most correlated environmental variables with PC1 (Fig. 10), explaining most of the variation in the environmental properties among all sites. The biplot shows 395501 and 61 (right) and Gammtratten 1 & 2 and Kålhuvudet 2 (left) on opposite sides, without overlap with other sites, which are concentrated in the middle. Interestingly, these environmental differences did not lead to differences in community composition; as Fig. 8 and Appendix 5 show all five of these sites in the centre of the NMDS plot overlapping with each other. This means that, although we were able to identify a gradient in catchment size among the forest sites, in contrast to earlier studies (Kuglerová et al. 2015, 2016), it did not translate in different plant communities. This can be explained by the fact that my streams are all still small headwaters with low stream power and small riparian extend, limiting the driving forces of fluvial disturbance on riparian vegetation communities. A similar conclusion can be made for elevation above the stream. Although proven to be a driver for vegetation communities within stream networks (Renöfält et al. 2005; Kuglerová et al. 2015), it did not translate into meaningful changes along the gradient in my study. This might be because the elevational gradient had been clustered within the first meter from the stream, similar to what I described about the lack of effect on species richness and alpha diversity. It is further important to understand that the PCA works more in a deductive manner, than with statistical analysis. As a tool for ordination and the reduction of variable numbers, PCAs have long been in use and is considered a variable tool (Nichols 1977; Kuglerová et al. 2019). But, they have been known to perform poorly when applied to indirect gradient analysis (Nichols 1977).

4.4.2 Plant indicator values

The additional environmental variables correlated to the functional traits of the inventoried plant communities can provide additional insights and serve as a proxy for micro site properties (Tyler et al. 2020). This allows me to link vegetation directly to the environment, which was not possible with the PCA. As the unit scale for each of these values is different, it is hard to set a general threshold to identify when a difference in the mean value is to be considered as a different environment. Instead, all five evaluated indicator values will be discussed individually before general conclusions can be made.

First of all, the index for biodiversity relevance corresponds to the number of dependent organisms (Tyler et al. 2020). The biodiversity score could therefore be used as a proxy for carrying capacity or total potential biodiversity of a vegetation quadrat. Forest reserves, although not richer in species, do show a slightly higher biodiversity relevance than the production forests. Both scores fall between 3 (13-24 dependent species) and 4 (25-50 dependent species), but because of the nature of the logarithmic scale, the value of 3.75 for forest reserves could mean that it has significant higher biodiversity relevance than the score of 3.30 for production forests. This then fits with the expectation of old-growth forests providing a higher level of ecosystem services like biodiversity (Watson et al. 2018).

The vegetation dependence on soil disturbances for colonisation as indicated by the present plant species ranged between the scores 1 and 2 for both forest types. This corresponds to a range between plant species that colonize established vegetation that will persist as long as there is no soil disturbance and plant species that colonize established vegetation and will persist for some time, but will be outcompeted in the long run in the absence of soil disturbance. This indicates that the vegetation communities are prone to very low levels of soil disturbance. Although the range was identical and low for both forest types, it had a higher mean for forest reserves. Riparian zones are often considered to be prone to disturbances through hydrological and fluvial dynamics. These processes have been found to significantly influence the vegetation composition (Kuglerová et al. 2015; Lind & Nilsson 2015). The fact that the vegetation communities in my forests point to very low levels of disturbance might again be explained by the fact that these headwater streams are too small to cause significant disturbance. Similar results for headwater streams were found by Kuglerová et al. (2015).

The nitrogen availability ranged in production forests from 1 to 6, corresponding with a range from very N-poor to moderately-very N-rich. The forest reserves had a considerable smaller range, with 2 to 4, corresponding with moderately-very N-poor to moderately N-poor – moderately N-rich. Some of the higher nitrogen availability in some of the production forests can be explained through fertilization as I received data, which confirmed repeated fertilisation for site 30977. However it does not explain all the variance, as Krycklan 1 showed similar levels of nitrogen availability (this has also been found by other researchers, e.g. Blackburn et al. 2017), but the site has not received fertilisers. Nitrogen is a limited resource in the boreal forest where atmospheric deposition is low. The riparian zone acts as a hotspot with higher dissolved organic nitrogen and ammonium levels than the upland forests (Blackburn et al. 2017). The riparian vegetation has been known to play an important role in cycling the nitrogen, acting both as a sink and source throughout the vegetation season (Mayer et al. 2007). The wider range of nitrogen availability may play an important role in the greater number of unique species, which were found in the production forests.

The mean light condition scores of both forest types fall between 3 and 4, translating to half-shade to moderate shade and half shade, respectively. The difference in light conditions is in line with the canopy openness data I collected in the field, as well as data collected in 2021 (Lundqvist 2022), and show forest reserves having higher light availability values than production forests (mean score of 3.78 and 3.48, respectively). This shows that forest management has impacted light availability in the riparian zone through a lower canopy openness. It may be important to discuss, which ecological mechanisms are affected through the decrease of canopy openness by forest management. The resulting lower light availability may influence understory vegetation, but also other riparian and stream ecological processes (Mallik et al. 2013; Kaylor & Warren 2017). My data showed a strong correlation between canopy openness and species richness and plant cover in the forest reserves. Other sources also found positive effects on species richness and diversity of understory species through increased canopy openness (Grandpré et al. 2011; Mallik et al. 2013). Additionally, canopy

openness has been shown to positively influence the primary production in the stream and the bottom up drivers of the stream food web (Kaylor & Warren 2017).

Moisture conditions do not differ in range or mean between the two forest sites when consider the indicator values. This is in line with expectations as the plots were placed based on elevation from the stream, which dictates much of the soil moisture properties through flooding and GW fluxes (Fisher et al. 2004; Hefting et al. 2004). My own estimations of soil moisture in the field did show a difference between the two forest types with production forest being dominantly mesic and forest reserves being mesic-moist. The fact that the indicator values did not show this difference might be because those values are based on the plant communities. The differences I found when out in the field are single measurements in time and variation in soil moisture may occur, leading to similar conditions for plant communities. Another explanation to consider is that plants can occur in a range of environmental conditions, the indicator values are based on the most dominant environmental condition the species is found in, this does not have to be the same for all places the species is found.

5. Conclusions

My research showed that forest type did not significantly affected species richness or alpha diversity. However, both species richness and alpha diversity responded differently to forest age based on forest type. Species richness and alpha diversity were found to increase with age in production forests and decrease in forest reserves. I found no significant difference for total plant cover or the cover of plant functional groups between the two forest types. However, total plant cover decreased with age in both forest types. Bryophytes were found to be more abundant in forest reserves than production forests.

Canopy openness was found to be higher in forest reserves and was further identified as probably being one of the primary drivers behind the community compositions in my forests. Incidentally, I found that vegetation communities differed between the forest types as well as between individual forests.

Furthermore, plant indicator values have suggested that the production forests encompassed a wider range of biodiversity relevance and light and nitrogen availability. Nitrogen availability was indicated to be higher in the production forests, but forest reserves scored on average better in biodiversity relevance and light availability. Finally, when considering plant communities, the variety in my results showed that it is important to approach the subject from multiple angles as neither species richness, alpha diversity, community composition, functional groups, plant cover can tell you the whole story and all should be considered.

All in all, my research showed that on average, forest reserves have a higher relevance for biodiversity, higher bryophyte cover, a higher canopy openness and different community composition than production forests. However, production sites were not different in species richness, alpha diversity, cover of plant functional groups and overlapped significantly with forest reserves in terms of community composition. The production forests further encompassed a wider range of indicator values. The huge variation is based on large differences between individual sites, as well as the management gradient. This goes to show that individual management may determine whether riparian zones in production forests can be as diverse and ecologically important as in primary forests. Therefore, these ecologically important zones should be considered when applying management.

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Popular science summary

Riparian forests that grow along small streams in northern Sweden have a crucial role in connecting the land and water ecosystems. These forests perform essential functions for stream health, such as filtering water, providing nutrients, and stabilizing stream banks. However, in Sweden, these forests have been neglected in forest management, which has led to clearcutting up to the stream edge.

This study aimed to examine the impact of forest management on the understory vegetation in these forests. The study inventoried seven production forests with different management practices and compared them to five primary forests in forest reserves. I conducted a vegetation survey in each forest to compare the number of species, the different communities and growing conditions.

The results of the study showed that forest management did not significantly affect diversity. However, the study did find that forest age had a different effect on diversity depending on the forest type. The community compositions were also found to be different between the two forest types, but with significant overlap. The study also found that the primary forests had a more open canopy, which meant that more light could reach the vegetation. This was an important factor that drove the vegetation communities.

Despite the variation in forest management practices among the production forests, the study found that these forests can house similar or larger numbers of species than primary forests. Therefore, the management of riparian zones in production forests can have important implications for the preservation of biodiversity and the functioning of riparian ecosystems. This study highlights the need for more research on the effects of forest management on riparian vegetation communities, and the importance of including riparian zones in forest management plans. Overall, my thesis emphasizes the critical role of riparian forests in maintaining healthy stream ecosystems and the need for sustainable forest management practices to protect these vital habitats.

Acknowledgements

I would like to take the opportunity to thank my supervisor Lenka Kuglerová for supporting me through a full year of sampling, data-diving and of course, writing. The thesis wouldn't be what it is without the buckets of comments and good advice on taking breaks – message received! I won't show my face for a little while ;)

I would also like to thank my awesome field assistant Angela, who ventured out with me into the mosquito infested forests.

Last, but surely not least, I would like to thank the fellow members of the thesis ring: Julia, Magda and Gaya. We might not have ended as consistent as we started but it was great to have you as a sound board and be able to bounce ideas and graphs off of you.

Appendix 1. Description of indicator values

The concept of biodiversity relevance for a species refers to the number of organisms that depend on or use it as a food source, substrate, shelter, or mutualistic partner. a logarithmic eight-degree grading scale (1-8) is used to denote the biodiversity relevance of a plant species based on the number of associated species. A score of 1 corresponds to <6 associated species, while a score of 8 corresponds to >400.

Nitrogen availability refers to the amount of nitrogen in the soil that is available for plants to use. The grading scale ranges from 1 to 9, with 1 being very nitrogen-poor and 9 being mostly found on artificially nitrogen-enriched soils. The scale is based on data from experiments and published reports where nitrogen and other nutrients were measured and/or manipulated independently.

The concept of light condition refers to the ideal amount of light/shade required for a species to grow optimally. A grading scale of 1 to 7 is used, with 1 being deep shade and 7 being always full sun. The classification is based on the authors' experience and information provided by regional flora atlases.

The grading scale used for moisture conditions ranges from 1 to 12, with 1 being very dry and 12 representing deep permanent water. The scale is based on Ellenberg et al. (2001) and is used to categorize plant species based on their moisture preferences. Values 10-12 refer to the depth of standing water, rather than water availability.

Soil disturbance refers to the relationship between the occurrence and survival of plant species and the amount of soil disturbance. The grading scale is a nine-degree scale that represents the species' dependence on soil disturbance, and it does not differentiate between natural and anthropogenic disturbances. The scale ranges from 1 to 9, with 1 being a species that colonizes already established vegetation and successfully competes with it, while 9 is a species that requires yearly soil disturbance and is not competitive in closed vegetation.

Appendix 2. List of plant species

The table shows the percentage of quadrats where the species was found and their average cover percentage per quadrat.

	Plant species	Average cover when found (%)	Proportion of quadrats where found (%)
1	<i>Vaccinium myrtillus</i>	13.6	82.6
2	<i>Vaccinium vitis-idaea</i>	8.7	81.9
3	<i>Maiantum bifolium</i>	6.4	75.0
4	<i>Linnaea borealis</i>	3.6	70.8
5	<i>Trientalis europaea</i>	3.8	70.1
6	<i>Deschampsia flexuosa</i>	10.0	66.0
7	<i>Carex globularis</i>	10.6	53.5
8	<i>Equisetum sylvaticum</i>	4.4	47.9
9	<i>Gymnocarpium dryopteris</i>	5.2	39.6
10	<i>Phegopteris connectilis</i>	12.6	39.6
11	<i>Picea abies</i>	3.3	37.5
12	<i>Oxalis acetosella</i>	6.8	27.8
13	<i>Dryopteris expansa</i>	3.2	25.7
14	<i>Lycopodium annotinum</i>	6.2	25.0
15	<i>Sorbus aucuparia</i>	1.9	20.8
16	<i>Orthilia secunda</i>	2.2	16.0
17	<i>Carex brun/can</i>	5.3	15.3
18	<i>Luzula pilosa</i>	2.1	15.3
19	<i>Rubus saxatilis</i>	3.2	14.6
20	<i>Rubus chamaemorus</i>	4.8	13.2
21	<i>Carex vaginata</i>	3.6	12.5
22	<i>Calamagrostis purpurea</i>	2.7	11.1
23	<i>Melica nutans</i>	3.0	11.1
24	<i>Geranium sylvaticum</i>	1.7	10.4
25	<i>Cornus suecica</i>	4.1	9.0
26	<i>Filipendula ulmaria</i>	3.7	9.0
27	<i>Deschampsia cespitosa</i>	2.9	8.3
28	<i>Listera cordata</i>	1.9	8.3
29	<i>Viola epipsila</i>	3.3	8.3
30	<i>Solidago virgaurea</i>	1.5	6.9
31	<i>Betula pubescens</i>	2.9	6.3

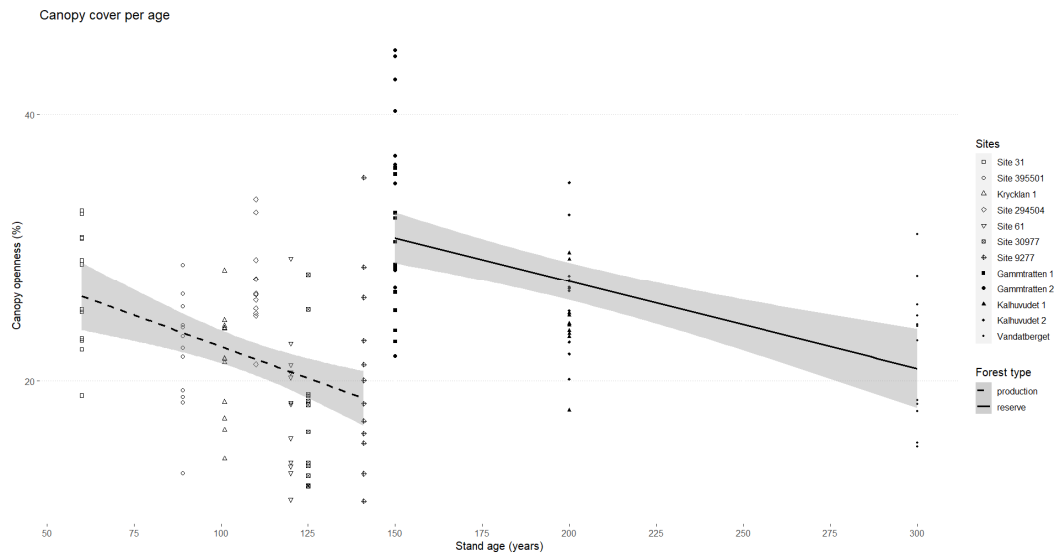
32	<i>Viola palustris</i>	6.1	5.6
33	<i>Athyrium filix-femina</i>	3.1	4.9
34	<i>Pyrola minor</i>	1.6	4.9
35	<i>Epilobium angustifolium</i>	1.3	4.2
36	<i>Equisetum arvense</i>	2.2	4.2
37	<i>Rubus idaeus</i>	2.5	4.2
38	<i>Calamagrostis canescens</i>	13.2	3.5
39	<i>Populus tremula</i>	2.8	3.5
40	<i>Potentilla palustris</i>	1.3	2.8
41	<i>Pyrola rotundifolia</i>	2.3	2.8
42	<i>Valeriana sambucifolia</i>	2.0	2.8
43	<i>Carex disperma</i>	3.7	2.1
44	<i>Juniperus communis</i>	5.0	2.1
45	<i>Lycopodium selago</i>	6.0	2.1
46	<i>Agrostis capillaris</i>	11.5	1.4
47	<i>Alnus incana</i>	4.0	1.4
48	<i>Cicerbita alpina</i>	2.0	1.4
49	<i>Juncus filiformis</i>	3.0	1.4
50	<i>Melampyrum sylvaticum</i>	2.5	1.4
51	<i>Betula pendula</i>	1.0	0.7
52	<i>Caltha palustris</i>	2.0	0.7
53	<i>Carex echinata</i>	13.0	0.7
54	<i>Carex loliacea</i>	1.0	0.7
55	<i>Carex nigra</i>	24.0	0.7
56	<i>Carex rostrata</i>	2.0	0.7
57	<i>Crepis paludosa</i>	5.0	0.7
58	<i>Dactylorhiza maculata</i>	1.0	0.7
59	<i>Milium effusum</i>	5.0	0.7
60	<i>Prunus padus</i>	2.0	0.7
61	<i>Salix caprea</i>	5.0	0.7
62	<i>Salix myrsinifolia</i>	8.0	0.7
63	<i>Salix myrtillus</i>	1.0	0.7
64	<i>Salix phylicifolia</i>	12.0	0.7

Appendix 3. List of functional groups

	Plant species	functional groups
1	<i>Vaccinium myrtillus</i>	Dwarf shrub
2	<i>Vaccinium vitis-idaea</i>	Dwarf shrub
3	<i>Rubus saxatilis</i>	Dwarf shrub
4	<i>Rubus idaeus</i>	Dwarf shrub
5	<i>Dryopteris expansa</i>	fern
6	<i>Gymnocarpium dryopteris</i>	fern
7	<i>Phegopteris connectilis</i>	fern
8	<i>Athyrium filix-femina</i>	fern
9	<i>Equisetum sylvaticum</i>	forb
10	<i>Linnaea borealis</i>	forb
11	<i>Maianthemum bifolium</i>	forb
12	<i>Rubus chamaemorus</i>	forb
13	<i>Trientalis europaea</i>	forb
14	<i>Oxalis acetosella</i>	forb
15	<i>Melampyrum sylvaticum</i>	forb
16	<i>Epilobium angustifolium</i>	forb
17	<i>Lycopodium selago</i>	forb
18	<i>Orthilia secunda</i>	forb
19	<i>Dactylorhiza maculata</i>	forb
20	<i>Geranium sylvaticum</i>	forb
21	<i>Listera cordata</i>	forb
22	<i>Lycopodium annotinum</i>	forb
23	<i>Pyrola rotundifolia</i>	forb
24	<i>Solidago virgaurea</i>	forb
25	<i>Cicerbita alpina</i>	forb
26	<i>Crepis paludosa</i>	forb
27	<i>Cornus suecica</i>	forb
28	<i>Filipendula ulmaria</i>	forb
29	<i>Viola epipsila</i>	forb
30	<i>Viola palustris</i>	forb
31	<i>Valeriana sambucifolia</i>	forb
32	<i>Pyrola minor</i>	forb

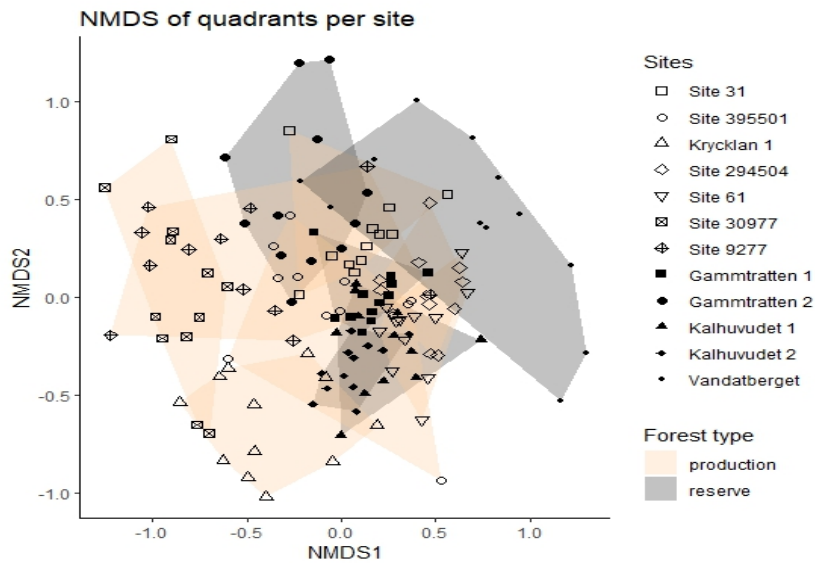
33	<i>Caltha palustris</i>	forb
34	<i>Potentilla palustris</i>	forb
35	<i>Equisetum arvense</i>	forb
36	<i>Deschampsia flexuosa</i>	grass
37	<i>Luzula pilosa</i>	grass
38	<i>Deschampsia cespitosa</i>	grass
39	<i>Calamagrostis purpurea</i>	grass
40	<i>Juncus filiformis</i>	grass
41	<i>Melica nutans</i>	grass
42	<i>Calamagrostis canescens</i>	grass
43	<i>Agrostis capillaris</i>	grass
44	<i>Milium effusum</i>	grass
45	<i>Picea abies</i>	overstory
46	<i>Alnus incana</i>	overstory
47	<i>Betula pubescens</i>	overstory
48	<i>Carex globularis</i>	sedge
49	<i>Carex vaginata</i>	sedge
50	<i>Carex disperma</i>	sedge
51	<i>Carex loliacea</i>	sedge
52	<i>Carex rostrata</i>	sedge
53	<i>Carex echinata</i>	sedge
54	<i>Carex nigra</i>	sedge
55	<i>Salix myrtilillus</i>	shrub
56	<i>Salix phylicifolia</i>	shrub
57	<i>Juniperus communis</i>	shrub
58	<i>Prunus padus</i>	shrub
59	<i>Salix myrsinifolia</i>	shrub
60	<i>Salix caprea</i>	shrub
61	<i>Picea abies</i>	tree
62	<i>Populus tremula</i>	tree
63	<i>Sorbus aucuparia</i>	tree
64	<i>Betula pendula</i>	tree
65	<i>Alnus incana</i>	tree
66	<i>Betula pubescens</i>	tree

Appendix 4. Canopy cover over age

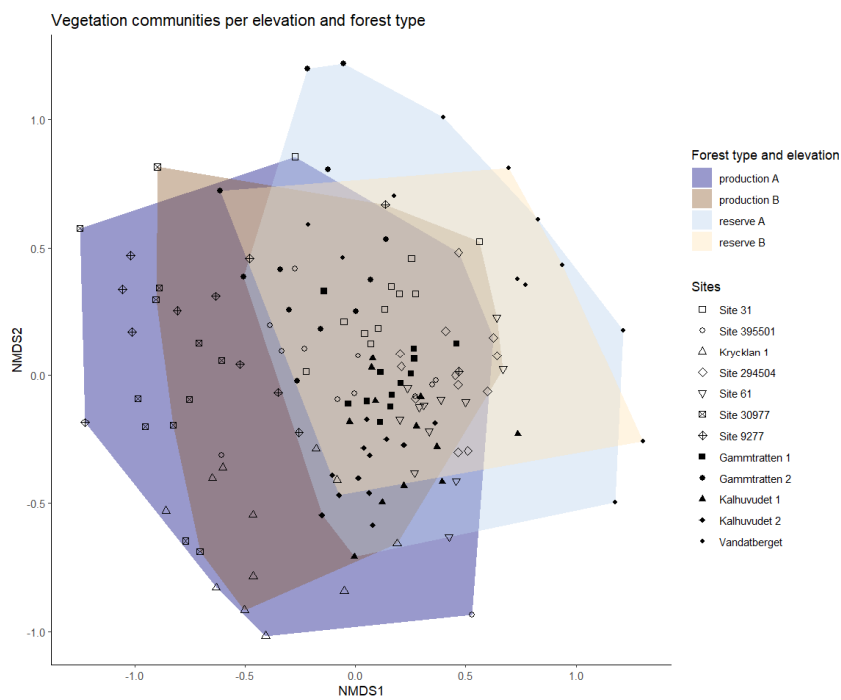


This figure shows the decreasing trend canopy openness for forest reserves (dashed line) and production forests (solid line) over stand age. Measurements were taken for each quadrat and are therefore represented by a site-specific icon.

Appendix 5. Additional NMDS analyses



These NMDS plots show the different communities per site (top) and per elevation and forest type (bottom). Near-stream plots are denoted with an A, while elevated plots are marked with a B.



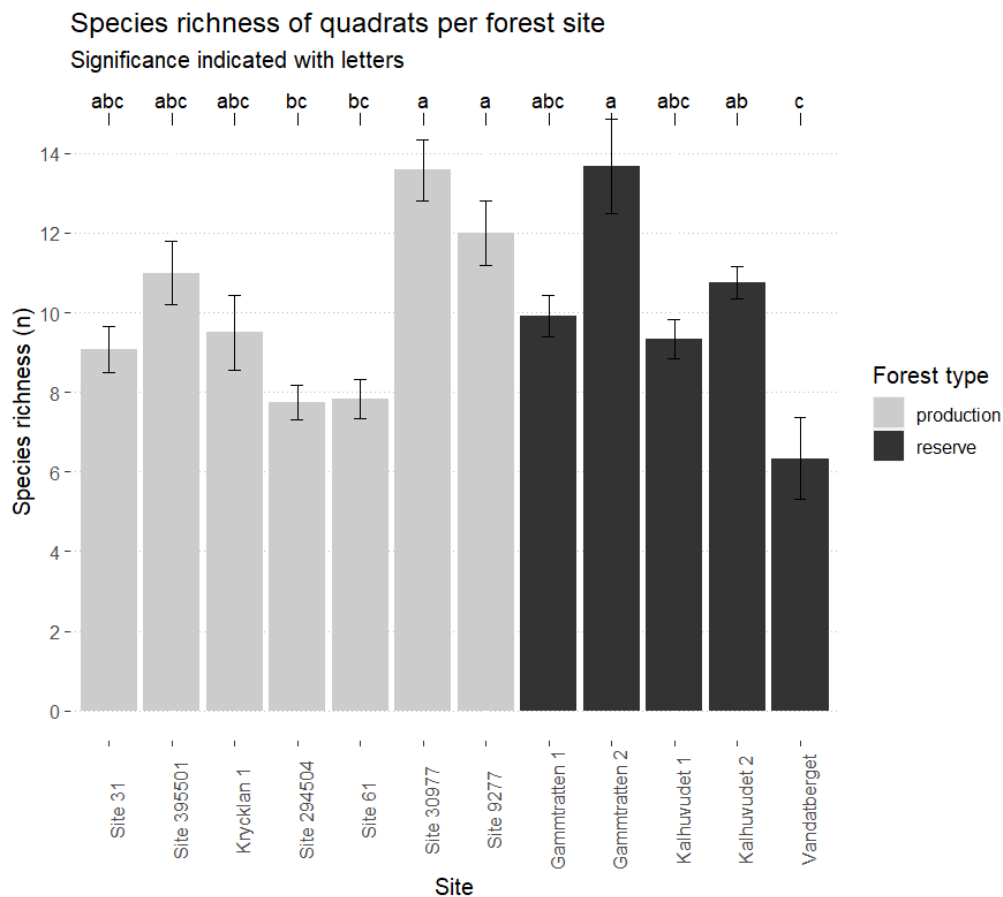
Appendix 6. Species unique to forest types

Unique to production	Plant species	Functional group
1	Rubus idaeus	dwarf shrub
2	Filipendula ulmaria	forb
3	Viola epipsila	forb
4	Viola palustris	forb
5	Valeriana sambucifolia	forb
6	Pyrola minor	forb
7	Caltha palustris	forb
8	Potentilla palustris	forb
9	Equisetum arvense	forb
10	Melica nutans	grass
11	Calamagrostis canescens	grass
12	Agrostis capillaris	grass
13	Milium effusum	grass
14	Carex loliacea	sedge
15	Carex rostrata	sedge
16	Carex echinata	sedge
17	Carex nigra	Sedge
18	Betula pendula	Seedling / sapling
19	Alnus incana	Seedling / sapling
20	Juniperus communis	shrub
21	Prunus padus	shrub
22	Salix myrsinifolia	shrub

Unique to reserves	Plant species	Functional group
1	Dactylorhiza_maculata	forb
2	Listera_cordata	forb
3	Cicerbita_alpina	forb
4	Crepis_paludosa	forb
5	Salix_myrtillus	shrub
6	Salix_phylicifolia	shrub
7	Salix_caprea	shrub

Appendix 7. Species richness at individual forest sites

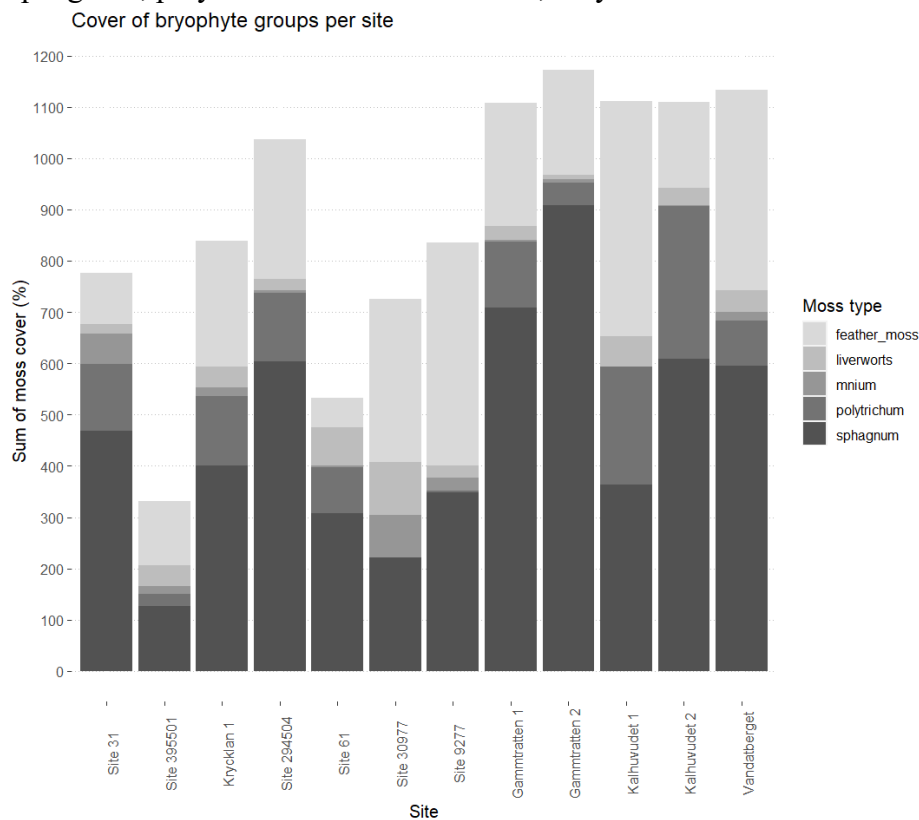
The Dunn test with Bonferroni correction showed that there were significant differences in species richness per quadrat between multiple individual sites (Gammtratten 2 and sites 30977 & 9277 had higher species richness than Vändåtberget and sites 61 & 294504, Kålhuvudet 2 was only significantly more species rich than Vändåtberget). The Dunn test with Bonferroni correction further showed that Site 30977 had higher alpha diversity than Vändåtberget and sites 61, 31 & 294504 ($p < 0.01$; $p < 0.01$; $p = 0.04$ & $p = 0.05$ respectively). Gammtratten 2 was found to have higher alpha diversity than Vändåtberget and site 61 ($p = 0.01$ and $p = 0.04$ respectively).



Average (\pm SE) species richness of quadrats per site. The sites are ordered based on forest age (youngest to oldest) and the bars are coloured by forest type. Above the bars the significance of the difference between species richness is indicated by letters.

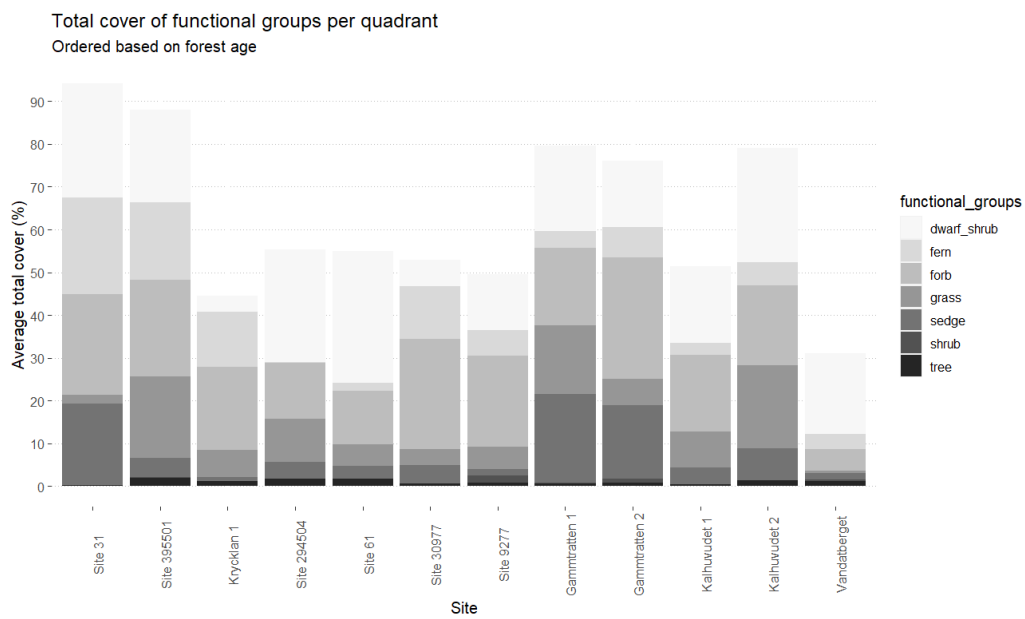
Appendix 8. Bryophyte cover at individual forest sites

The total cover of the five inventoried bryophyte groups varied heavily per quadrat at the 7 production sites (range = 1-132, mean = 60.44 sd = 32.08, SE = 3.50), resulting in large differences of total cover (range = 331– 1172). It is clear that there is a lot of variation in the production forests (Site 31 - Site 30977) on a site scale as well as on the scale of vegetation quadrats. The total sum of bryophyte cover for the forest reserves (Gammtratten 1 – Vändåtberget) shows less variation, although the individual moss types within these sites, especially Sphagnum, polytrichum and feather moss, vary.



Bar stack plot showing the total sum of the five inventoried bryophytes (Feather moss, liverworts, mniium, polytrichum and sphagnum moss) per site.

Appendix 9. Plant functional groups at individual forest sites



Average cover of functional groups per quadrat for all forest sites. The different functional groups (bar colours) are stacked, giving the average total cover percentage of vascular plant per quadrat per site. The sites on the x-axis are ordered by increasing stand age.

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