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Differences in structure, diversity and ecological functions of riparian forests in production stands and nature reserves in Sweden

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ABSTRACT

Riparian zones play a crucial role for aquatic ecosystems and host a large number of organisms, but in regions with intensive forestry, such as Sweden, these areas have historically received inadequate protection from operations. The legacies of past management can be seen in todays' mature forests. We compared riparian forests in mature production stands with those in unmanaged nature reserves to describe structural, functional and diversity differences. Our findings reveal significant differences in forest structure, with production stands exhibiting larger average tree diameters but fewer stems. Tree species diversity was similar in both types of forests, but nature reserves had about double the number of individuals of most species. Further, nature reserves displayed greater structural diversity including more varied light conditions and higher volumes of large deadwood. Vascular plant diversity showed no significant difference between forest types, although community composition was different. The ground cover of *Sphagnum* sp. group was significantly higher in the nature reserves compared to production sites. The results presented here highlight the lasting impact of forestry practices on riparian ecosystems, emphasizing the need for better management to preserve their ecological functions through, for example, mimicking natural riparian forest regimes.

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Introduction

The riparian zone plays a vital role for aquatic ecosystems due to the many ecological functions it sustains. Forested riparian zones along streams control water temperatures and light regimes, provide organic material (both particulate and dissolved) to aquatic organisms, filter dissolved and particulate substance from groundwater and overland flow, and provide important habitats (Richardson and Danehy 2007). These functions are closely connected to water quality and quantity, biodiversity, and the ecosystem services that streams provide (Kuglerová et al. 2017; Wohl 2017; Richardson and Dudgeon 2020). All the functions are also highly affected by disturbances including land use. In countries with large and intensive forestry sectors, such as Sweden, streams and their riparian forests have been historically minimally protected from forestry operations, and this negligence continues even today (Kuglerová et al. 2024). Especially small streams, also referred to as headwaters, experience multiple forestry-related stressors, resulting in the loss and degradation of the stream-riparian habitats (Kuglerová et al. 2021). This is in sharp contrast with many local and transnational policies that advocate for good ecological status of all surface waters, sustainable use of natural resources and protection of biodiversity (e.g. Water Framework Directive, the EU Forest Strategy, Convention on Biological Diversity).

Several factors contribute to the inadequate protection of small streams from forestry in Sweden. First, headwaters are rarely of much value for recreational fishing and thus protecting them has not been a priority (Kuglerová et al. 2024). Second, many headwaters were, or still are, missing on property maps, hindering effective forestry planning (Ågren et al. 2015). Third, past policies permitted forestry in riparian zones, including planting, thinning, cleaning and harvesting, creating legacy effects that has shaped riparian forests to resemble production stands (Hasselquist et al. 2021). While the first two issues receive a significant research attention (Ågren and Lidberg 2019; Kuglerová et al. 2020; Lidberg et al. 2023; Ring et al. 2023), we have a limited understanding to what extent do mature riparian forests today carry the effects of decisions made in the

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past. Before the adoption of the new forest act in 1993, forest management has promoted coniferous, even-aged, single-story production stands all the way to the water's edge (Hasselquist et al. 2021). While a noticeable increase in protection of water was observed during the 1990s and 2000s through the application of riparian buffers, in 2013 still 50% of the stream length in the Krycklan catchment in northern Sweden (Laudon et al. 2021) lacked protection (Hasselquist et al. 2020). This demonstrates that production stands managed with rotation forestry along streams persisted well into twenty-first century, affecting natural riparian forest succession, and in turn modifying their ecological functions (Hasselquist et al. 2021; Kuglerová et al. 2021). As a result, it is highly likely that today most streams and their riparian areas in mature production forests are completely changed from what they used to be or would be without forestry. However, the extent to which managed riparian forest differ from unmanaged stands remains unexplored.

On the upland part of forests, the consequences of Swedish forest management are well documented. Large-scale transformation of the Swedish forest to even-age production system has been associated with changes in stand structure, composition and dynamics (Linder and Östlund 1998), a decline in biodiversity (Eide et al. 2020), and a decline in large dead wood (LW) (Siitonen et al. 2000), with ecological consequences for ecosystem services (Gamfeldt et al. 2013). Some of these aspects were also found in streams flowing through managed forests, such as the general low volumes of LW (Dahlström et al. 2005) and the dominance of spruce in riparian areas (Hasselquist et al. 2021). Yet, the full consequence of past forest management (i.e. planting, cleaning and thinning) for the structure, diversity and functions of the riparian zones are unexplored. Riparian forests are more dynamic compared to uplands, and their high biodiversity and rapid ecological processes have been attributed to the unique microclimate (Oldén et al. 2019), regular disturbance by floods (Kuglerová et al. 2015), wet soils (Kuglerová et al. 2014), heterogeneous surfaces (Hylander et al. 2005), and/or hydrochory (Nilsson et al. 1994). Because of the dynamic nature that drives the processes in riparian zones as well as in the water, and the long rotations (>80 years) in the boreal region, the consequences of forest management might be less evident in riparian forests compared to the well documented effects on the uplands. However, this theory has not been tested.

In this paper, we ask whether riparian forests situated in managed stands differ in their structure, diversity and ecological functions (i.e. provision of LW and shading) from forests situated in stands never managed for timber production. Nature reserves with a status of "primary" or "old-growth" forests were chosen to represent the unmanaged stands. This does not exclude the possibility that the forests in the reserves have been used by humans in the past, but the forests were never managed for production by modern forestry principles. The production stands were chosen to be typical even-age Norway spruce stands of mature age (>60 years old). We predict that all three aspects (structure, diversity and ecological functioning) will be different in the two forest types. In particular, we expect that riparian forests in the nature reserves will have broader range of tree sizes (wider DBH distribution) and a higher number of large diameter trees, but that species composition of mature and understory trees as well shrubs will be similar due to the limited pool of naturally occurring tree species in northern Sweden. Further, we expect that forests in the production stands will have less incident light due to uniform spruce canopies (high shading) and this could affect the ground flora composition. Finally, we predict that riparian forests in managed stands will provide less LW to streams and the riparian zone compared to the production stands.

Methods

Site selection

Ten riparian forests were surveyed in this study, five situated in mature production stands and five in nature reserves in the counties of Västerbotten and Västernorrland (Figure 1). The nature reserves that were included were selected based on their classification as "primary" forests in the European primary forest database (v2.0; Sabatini et al. 2021). We also confirmed their status as "primary" or "old-growth" forests with the local county administration board. However, precise stand age information was not available; the only documentation (on the nature reserve websites) indicated that individual trees within the reserves were estimated to be between 150 and 300 years old. Topographic maps were used to assess whether the reserves contain streams. Four of the reserves from this database that were in the desired region had small streams. The fifth nature reserve was found based on information from the county administration board having the status of "primary" or "old-growth" forest. The nature reserves used were: Gammtratten (2 streams), Kålhuvudet (2 streams), and Vändåtsberget (1 stream). In the reserves that had two streams, these streams are two different headwater systems, situated several kilometers apart. The production forest sites were used in previous projects (Chellaiah and Kuglerová 2021; Myrstener et al.

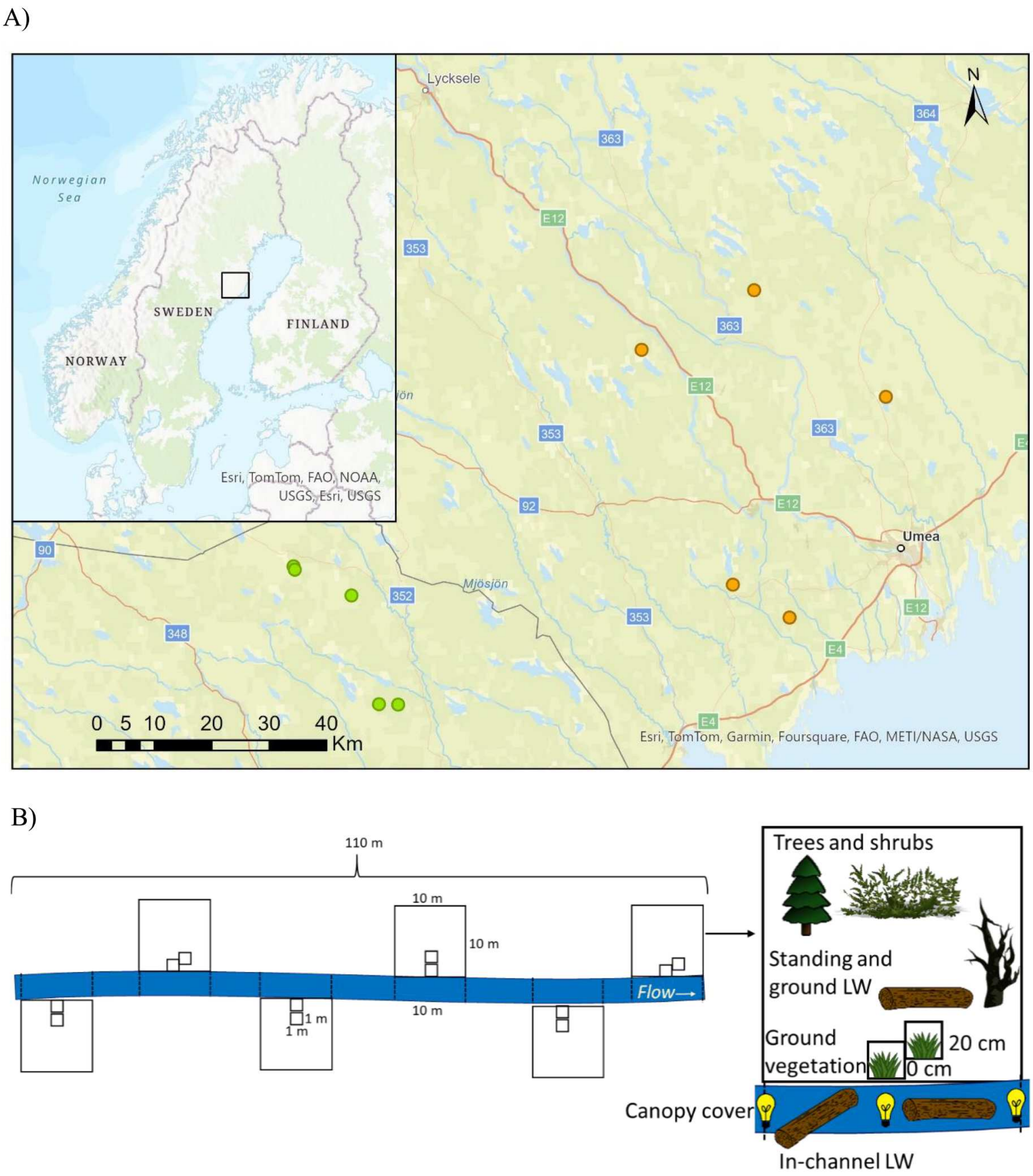

Figure 1. (A) Location of the studied streams within Sweden (inset map) and the region, orange points indicate production sites and green points indicate nature reserves. (B) Design of the surveys performed at each site, with 6 10 × 10 m large plots and 12 1 × 1 m quadrats. In the large plots, surveys of trees, shrubs, and large wood (LW) were conducted while in two small quadrats vascular plants and bryophyte groups were inventoried. The small quadrats were situated on the stream edge (0 cm) and at 20 cm bank elevation (20 cm). Canopy cover was measured at three places over the stream by each large plot, and channel deadwood was also recorded as displayed in the plot sketch.

2023) and have mature (>60 years old) Norway spruce forest stands all the way to the stream edges, with visible effects of previous cleaning and thinning (Hasselquist et al. 2021). While all the production sites are situated in a different county compared to the reserves (Figure 1), this geographical spread is not of a concern on these latitudes. All the sites are situated in Northern Boreal ecoregion (Bubnicki et al. 2024) with Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) as the dominant tree species (Brus et al. 2012). The vegetation period is the same for the two regions, on average 150–160 growing days per year (SMHI 2025).

Study design

All the selected streams were small streams of first or second order (headwaters) with catchment areas <4 km^2. All streams were situated in forests for at least 200 m of the stream length. In September 2021, six riparian plots (10 × 10 m) were established at each site along ca 110 m stream length with a distance of about 10 m apart from each other. Plots were placed in a zig-zag fashion (Figure 1B). The stream edge was used as borderline of the 10 × 10 m riparian plots. Surveys taken in the stream (channel LW, canopy cover and stream width) were performed in the 10 m stream length adjacent to each plot (Figure 1B). Within each plot, inventories of trees, shrubs, ground vegetation and large wood (LW) were carried out (Figure 1B). All trees ≥5 cm in diameter at breast height (DBH) in each plot were measured and classified into a species. For trees <5 cm DBH and shrub species, we counted the number of stems belonging to either coniferous or deciduous species. We did not count small trees and shrubs per species, however in each plot, we made a note which species were present (without abundance). Large wood was measured in three categories: riparian standing LW (standing dead trees and snags), riparian ground LW (situated on the ground in the riparian zone), and channel LW (situated in the stream channel or over the channel). All LW objects were identified into species (if possible) and measured for diameter. For standing riparian LW, diameter was measured at breast height. For riparian ground and channel LW, the mean diameter was recorded. Decay status (Maser et al. 1979) was recorded for the riparian LW, both on the ground and standing.

Canopy cover was assessed above the stream channels, taking three measurements at approximately 0, 5, and 10 m mark of each 10 m long plot side along the stream (Figure 1B). For canopy cover, we used the application GLAMA (Tichý 2016), with external fish-eye lens attached to a smartphone that calculates % of canopy cover in a hemispherical photograph. At the same locations of the stream (0, 5, and 10 m along each plot), we measured bankful channel width.

In July 2022, we established two 1 × 1 m ground vegetation quadrats at two different elevations – 0 and 20 cm above the stream bank vegetation border in each plot at all but one site. One of the production forest sites was subject to harvesting during the winter 2021/2022 with visible marks of machine operations within the riparian zone. Thus we considered this site as recently disturbed and excluded it from the ground vegetation surveys. At the remaining nine sites, the first quadrat (0 cm elevation) was placed along the stream edge, with the center of the second quadrat being placed at a 20-cm elevation increase from the first quadrat's center, perpendicular to the stream. If the two plots overlay (on steep banks), we moved the 20 cm plot upstream while keeping it at the 20 cm elevation level (Figure 1B). Each quadrat was surveyed for all vascular plant species using the flora (Mossberg and Stenberg 2010). Abundance (cover percentage) of each species was estimated based on the vertical plant shoot area projection, or stem count and stem size (Wikum and Shanholtzer 1978). Bryophytes were not identified to species, instead we estimated the cover of five different bryophyte groups: feather mosses, liverworts, Mnium-type, *Polytrichum* sp., and *Sphagnum* sp. Bryophyte groups' abundance was estimated using quadrate coverage in percent.

Data analyses

For all data analyses, the software R Studio (RStudio Team 2024) was used. Unless stated otherwise, linear mixed effect models (LMM, Baayen et al. 2008) were used for the analyses described below to account for spatial dependence of data taken within plots/sites. An overview of all tested variables and models can be found in the supplementary material (see Table S1). All LMMs were fitted with the function *lmer* in R package lme4 (Bates and Maechler 2009) and nested random factors were site ID and/or plot ID because multiple plots were measured per site and for most parameters multiple measurements were taken within a plot. Type of forest (production vs. reserve) was used as fixed factor in all LMMs and significance was assessed at the $\alpha = 0.05$ threshold. In some cases, a second fixed factor was used (in interaction with type of forest) and in case when we performed model simplification, we removed non-significant interaction and models were compared with Akaike Information Criterion (AIC). If AIC differed >2 units, the model with lower AIC was accepted. All models were checked for residual distribution and if it indicated non-normality or heterogeneity, input data were transformed. This was the case for stream width that was log-transformed.

Forest structure and diversity

To assess whether the structure of the two riparian forest types (production vs. reserve) differ from each other, we first performed two-sided Kolmogorov–Smirnov test on the tree DBH data distributions. We ran three separate K–S tests, one for the full data set, one for trees with DBH <25 cm, and one for trees ≥25 cm in DBH. Second, we compared the DBH as well as the number of stems of all trees between the production and reserve sites with two LMMs. In both models, we used type of forest (production vs. reserve) and tree species as fixed factors. We also tested the interaction between the two fixed factors to evaluate whether the potential differences in DBH and number of stems per plot differed for the different tree species on production and reserve sites. The random factor of plot ID was omitted in the model for number of stems because it had standard error of zero.

To assess if the understory trees and shrubs differ between the two types of forests, we evaluated both abundance (stem count) and diversity. For diversity, we used the number of different understory tree and shrub species found in each plot and used LMM to assess whether the species number differed at the two types of forests. Similar models were created to assess abundances that were separated to deciduous and coniferous types, not to species (see methods). Number of stems of either conifers or deciduous species per plot was compared between production and reserve sites with two separate LMMs.

Ground vegetation diversity

To evaluate whether ground vegetation communities of vascular plants differ in the two types of forests, we assessed both species richness and community composition. We used Shannon–Wiener index for diversity to account for unequal abundances of the different species found. Shannon index was generated for each quadrat, and LMM with type of forest, plot elevation on the stream bank (0, 20 cm) and their interactions was used. Moreover, we used non-metric multidimensional scaling (function metaNDS in package *vegan* – Oksanen et al. 2013) and the Bray–Curtis ordination metric to compare the community composition of the vascular plants across all quadrats using abundance data. Significance of forest type and plot elevation for the community composition was assessed by permutational analyses of variance (PERMANOVA) with Bray–Curtis dissimilarity. To analyze whether the five bryophyte groups differ in abundance between the two types of forests we initially used same LMM models as for the rest of the analyses. However, the standard error of both random factors (site ID and plot ID) was zero and as such, we omitted the random factors and analyzed the bryophyte groups with analyses of variance (Anova). Forest type, plot elevation and bryophyte group were used as explanatory variables for the response variable of bryophyte cover. We used all two-way interactions among the explanatory variables and remove insignificant interactions for model simplification. We performed Tukey post-hoc test on the final model (that contained two significant interactions) to compare bryophyte cover between production and reserve sites for each bryophyte group separately.

Ecological functions

We chose two variables, namely shading and provision of LW, as proxies for ecological functions that riparian forests are supposed to provide (Chellaiah and Kuglerová 2021). Canopy cover (a proxy for shading) was compared between the two forest types with LMM. Stream width was used as a second fixed factor and also in interaction with the forest type. Stream width was used as a covariate because with increasing stream width, trees do not enclose over the stream, affecting canopy cover. By testing the stream width interaction with type of forest, we were testing if the trend between canopy cover and stream width persists in the two types of forests. We also tested whether the stream width differed between the two types of forests with LMMs to avoid spurious correlations.

Finally, each category of LW (riparian standing, riparian ground, channel) was tested separately with LMM to evaluate the ecological function of LW provision. We used number of objects per plot as response and type of forest as explanatory variables. We also used descriptive statistics to evaluate if LW coarsens (size), diversity (species) and decomposition stage differed in the two types of forests.

Results

Forest structure and diversity

In total, we found seven species of trees in the mature tree class (≥5 cm DBH). Those species were: grey alder (*Alnus incana* L. Moench), aspen (*Populus tremula* L.), downy birch (*Betula pubescens* L.), Scots pine (*Pinus sylvestris* L.), rowan (*Sorbus aucuparia* L.), Norway spruce (*Picea abies* L.), and willow (*Salix* sp.). The most dominant species was spruce (79% of all recorded trees), followed by birch (15% of all recorded trees). Both spruce and birch were found at all 10 sites. Pine was the third most common species (4% of all recorded trees) and was found at four production sites but only one nature reserve site. Alder and aspen were found only at one production and one reserve site, while rowan was found only at two reserve sites and willow only at one reserve site.

The DBH distribution of all riparian trees recorded in nature reserves and production stands significantly differed from each other (Kolmogorov–Smirnof test: $p < 0.001$). The production stands had DBH distribution following the Gaussian pattern while the nature reserves had distribution following the inverse J curve (Figure 2). When the data set was split on trees either below or

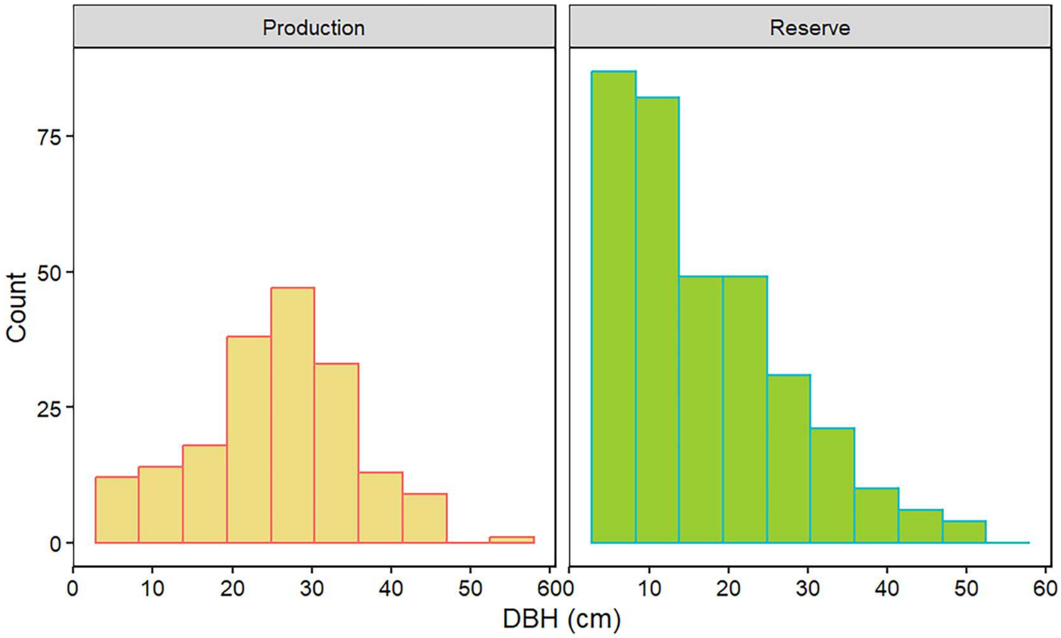

Figure 2. Histograms showing the diameter distribution of the two types of riparian forests with number of trees recorded on the *y*-axis and DBH (cm) on the *x*-axis. The distributions are significantly different from each other.

above 25 cm in DBH, the DBH distribution of trees with DBH <25 cm was still significantly different in the two forest types (Kolmogorov–Smirnof test: $p < 0.001$) while trees ≥25 cm DBH showed similar DBH distribution (Kolmogorov–Smirnof test: $p < 0.71$) in reserve and production sites.

The average DBH of all trees measured in all plots was significantly lower on the reserve sites compared to the production sites (estimate = 7.1, *t*-value = 2.6, $p = 0.03$). The interaction between type of forest and species was not significant ($p = 0.32$), indicating that the difference in DBH between the two types of forest was similar for all tree species found. Indeed, all species that were found per multiple plots and sites (alder, birch, pine, and spruce) had, on average, larger average DBH on the production sites (Table 1).

Table 1. Average (±SE) of diameter at breast height (DBH) and number of stems per plot of all trees found in the study and separate into species. Numbers are presented separately for sites situated in production stands and nature reserves. NAs mark missing individuals of particular species per forest type.

	DBH (cm)		Stem count	
	Production	Reserve	Production	Reserve
All trees	25.32 ± 0.73	16.95 ± 0.57	3.36 ± 2.34	5.95 ± 0.59
Alder	22.75 ± 0.75	9.44 ± 3.17	0.07 ± 0.07	0.17 ± 0.17
Aspen	26.00 ± 0.00	33.00 ± NA	0.07 ± 0.07	0.03 ± 0.03
Birch	20.97 ± 1.58	12.51 ± 0.77	0.90 ± 0.21	1.70 ± 0.41
Pine	35.44 ± 1.17	28.84 ± 2.83	0.30 ± 0.11	0.37 ± 0.23
Rowan	NA	9.33 ± 2.51	NA	0.10 ± 0.06
Spruce	25.52 ± 0.84	17.41 ± 0.66	4.83 ± 0.39	8.90 ± 0.72
Willow	NA	29.20 ± NA	NA	0.03 ± 0.03

On average, there was nearly double the number of stems of all tree species combined per plot on the sites situated in reserves compared to production sites (Table 1). This difference was close to be statistically significant (estimate = −0.7, *t*-value = −1.9, $p = 0.09$). Tree species and the interaction between type of forest and trees species were both significant in the model for stem numbers ($p < 0.001$), and this was caused by many species having no or a very few individuals in most plots (Table 1).

In the understory tree layer, we recorded in total 10 different species of small trees (<5 cm DBH) and shrubs. All species that were found in the mature tree layer were also common in the understory layer (alder, aspen, birch, pine, rowan, spruce, willow). In addition, we found several other species of shrubs at few sites, namely raspberry bushes (*Rubus idaeus* L., one production and one reserve site), juniper (*Juniperus communis* L., one production and one reserve site), and bird cherry (*Prunus padus* L., one reserve site). Overall, there were no statistically significant differences in the number of understory tree and shrub species between the two types of forests (estimate = −0.2, *t*-value = −0.3, $p = 0.74$). In production sites, the average number of understory trees and shrubs species per plot was 3.1 species and in reserve sites 2.8 species. When dividing the understory trees and shrubs to deciduous and coniferous species, we found no statistically significant differences in the number of individuals per plot for either group (conifers: estimate = −1.5, *t*-value = −0.3, $p =$

0.80, deciduous: estimate = −0.17, *t*-value = −1.6, *p* = 0.14). On average, 14.7 and 13.2 coniferous, and 35.4 and 18.1 deciduous individuals per plot were found in production sites, reserve sites respectively.

Ground vegetation diversity

It total, we found 53 vascular plant species in the surveyed quadrats. At all production sites combined, we recorded 40 species, while at all reserve sites combined, we recorded 42 species of vascular plants. We found no statistically significant effects of forest type (estimate = −1.1, *t*-value = −0.8, *p* = 0.46) and elevation above the stream channel (estimate = −0.04, *t*-value = −0.8, *p* = 0.57) on Shannon diversity of the ground vegetation recorded in the two quadrats in each plot. On average, plots situated on the 0 cm elevation had 9.9 species per plot in production riparian forests and 9.5 in reserves. Plots situated on the 20 cm elevation had on average 9.7 and 10.5 species per plot in the production, reserve sites respectively.

Community composition was significantly affected by both forest type (Permanova: *F* = 6.33, *p* = 0.001) and bank elevation (Permanova: *F* = 2.59, *p* = 0.005). While there was a large overlap between the nature reserves and production sites in ground vegetation composition, the non-metric multidimensional scaling revealed that there were quadrats with communities unique to both of the forest types (Figure 3). In all production sites combined, the five species with the highest average cover were *Phegopteris connectilis* (Michx.), *Oxalis acetosella* L., *Lycopodium selago* L., *Gymnocarpium dryopteris* (L.) Newman, and *Carex globularis* L., while the five species with the highest average cover in the reserve sites combined were *Vaccinium myrtillus* L., *Carex globularis* L., *Deschampsia flexuosa* (L.) Trin., *Salix phylicifolia* L., and *Vaccinium vitis-idaea* L. (Figure 3, Supplementary material, Table S2).

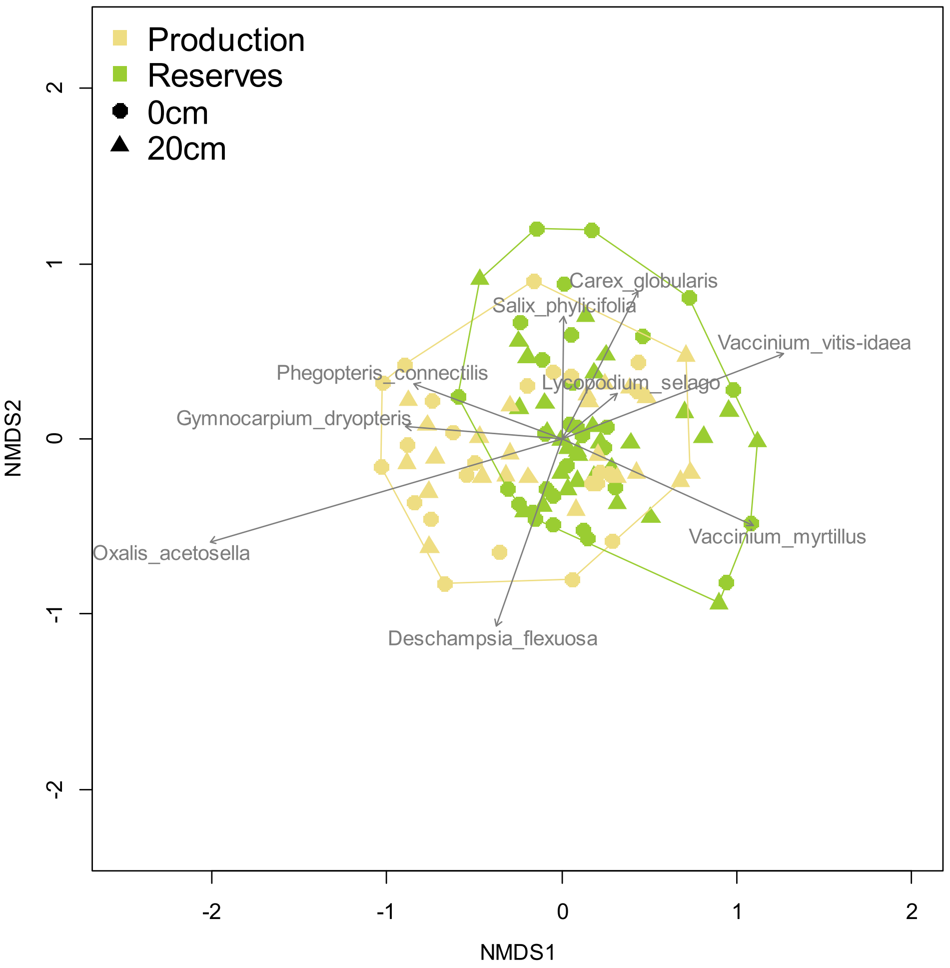

Figure 3. Non-metric multidimensional scaling graph based on Bray–Curtis dissimilarity matrix to show the vegetation composition of the quadrats (stress = 0.25). Each mark represents a quadrat from either reserves (light green color) or production sites (beige color) and situated either at 0 cm bank elevation (circles) or 20 cm elevation (triangles). The outer points of each forest type are connected to show their range on the axis. The five most abundant species in either forest type are displayed as vectors.

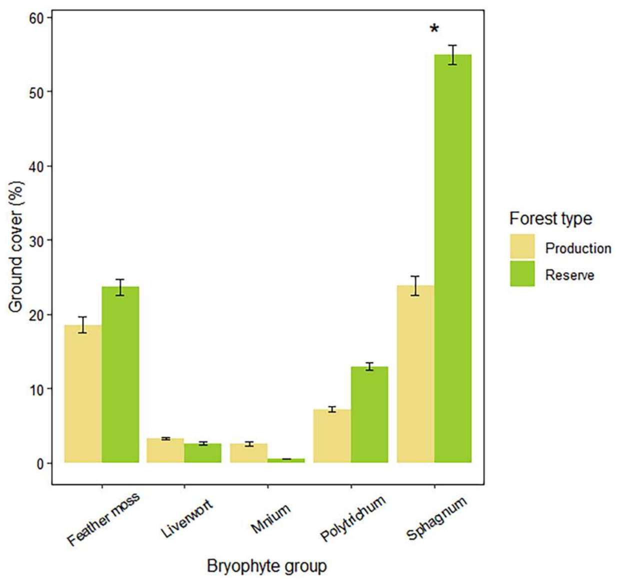

Figure 4. Average cover (±SE) of five bryophyte groups assessed in this study. The numbers are presented separately for nature reserves (green) and production sites (beige). Star indicates statistically significant difference between the types of forests within the bryophyte group.

Analyses of variance of the bryophyte groups' cover data revealed significant differences between the two types of forests, with reserve sites having on average, 1.6 times higher plot cover of bryophytes (Anova: F-value = 22.7, $p < 0.001$). This general difference was mostly driven by the significant difference of the Sphagnum group (post-hoc test: t ratio = −8.1, $p < 0.001$, Figure 4). The other groups did not show significant differences in plot cover between the two types of forests, although feather mosses were close-to-significant (post-hoc test: t ratio = −1.8, $p = 0.07$, Figure 4). Plot elevation had no significant effect on cover of bryophytes for any of the groups ($p = 0.1$).

Ecological functions

Canopy cover was on average 11% higher in the production sites compared to the reserve sites (Figure 5), and this difference was statistically significant (estimate: 11.1, t-value = 2.8, $p = 0.02$). Canopy cover was also significantly affected by stream width (estimate: −3.77, t-value = −2.71, $p = 0.008$) showing that with increasing stream width, canopy cover decreases (Figure 5). Stream width was not significantly different in production and reserve sites (estimate: −0.1, t-value = −0.2, $p = 0.79$).

Sites situated in nature reserves had on average 3.2 times higher the number of standing riparian LW objects (mean 2.57 objects) per plot compared to sites in production stands (mean: 0.8 objects, Figure 6). This difference was statistically significant (estimate = 1.77, t-value = 3.59, $p = 0.007$). Most of the riparian standing LW objects were spruce and birch (Table 2). The average DBH (coarseness) of standing LW of birch was 14.3 cm in reserve sites and 12.7 in production sites. Spruce standing LW had, on average, 13.3 and 20.4 cm in DBH at reserve, and production sites respectively (Table 2). The decomposition status at reserve and production sites for standing LW was 2–3 category (Table 2).

The number of LW objects recorded in the riparian zone on the ground (ground LW) did not differ between reserve and production sites (estimate = −1.8, t-value = −1.2, $p = 0.28$), the average at production sites was 2.5 objects per plot and at reserve site 4.3 objects per plot. The most common riparian ground

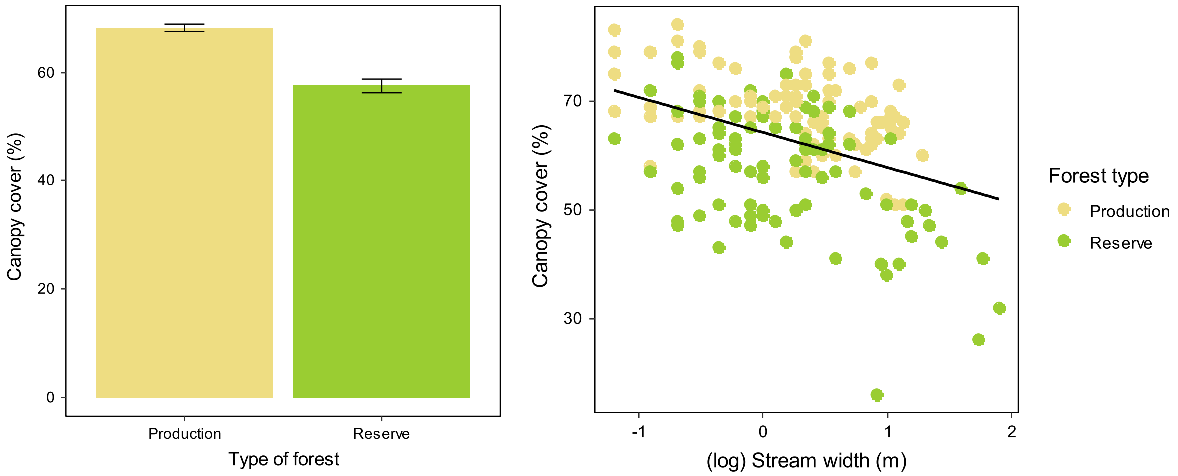

Figure 5. Average (±SE) of canopy cover (%) in production and reserve forest are displayed on the left panel. The right panel displays the significant linear trend (black line) between canopy cover (%) and stream width (on a log-scale) across all plots and sites, with points color-coded by forest type.

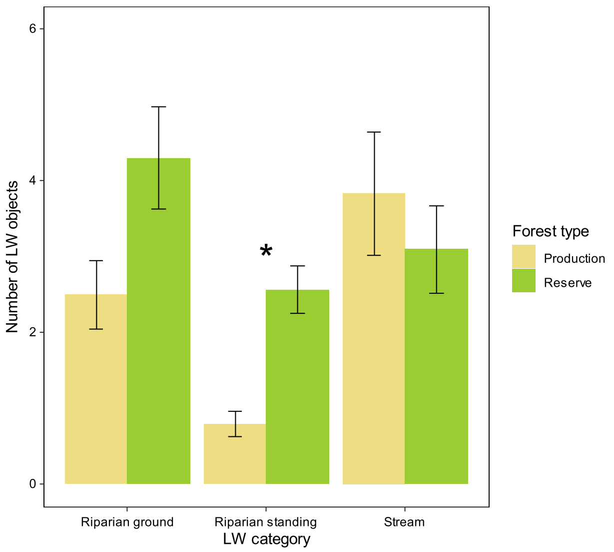

Figure 6. Average (±SE) of large wood objects per plot found in riparian zone (both standing and on the ground) and in the stream channels in production and reserve sites. Star indicates statistical significant difference between the types of forest within the LW category.

LW was, similar to standing LW, birch and spruce (Table 2) with average diameter of birch being 8.5 cm at production and 7.4 cm at reserve sites, and average diameter of spruce being 9.6 cm at production and 10.6 cm at reserve sites. Most ground LW objects were in decomposition stage 3 (Table 2).

The number of LW objects in the stream channels did not significantly differ in production and reserve sites (estimate = 0.7, *t*-value = 0.4, *p* = 0.70). On average, 3.8 objects per stream section bordering each plot were found in production sites and 3.1 object per stream section were found in reserve sites (Figure 6). The most common LW species in the stream channel was wood that was unknown (not possible to identify to species), spruce, and birch. Decomposition status was not measured for channel wood (difficult for submerged LW). In all three LW categories, the LW objects were more diverse in reserves compared to production sites (Table 2).

Discussion

Riparian forests in production stands and nature reserves included in this study clearly differed in number of structural parameters, diversity of organisms and ecological functions. Specifically, the riparian forests in the nature reserves that were never managed by rotation forestry were structurally more complex, had higher abundance of trees of most species, allowed more light to reach stream and riparian areas and supplied more large deadwood (LW). These structural differences to some extent also affected riparian plant communities as composition of vascular plants differed between the two forest types and bryophytes had higher abundance in nature reserves. The findings we presented in this study are important from ecological perspective but also from a management point of view. The riparian forests in the production stands will

Table 2. Number of objects, diameter and decay class of all large wood (LW) separated into different species found in the production and reserve sites. The LW data is divided on riparian standing LW, riparian ground LW and LW situated in the stream channels (this includes bridges over the channels). Where numbers are missing, no values were calculated due to no objects present. Missing data are identified by *x*.

Species	Objects (total number)		Diameter (cm) (mean ± SE)		Decay class (median)	
	Reserve	Production	Reserve	Production	Reserve	Production
Riparian standing						
Birch	22	4	14.3 ± 1.4	12.7 ± 2.8	2.5	3
Pine	5	2	12.6 ± 1.3	20.6 ± 6.7	2	2.5
Rowan	3	0	7.4 ± 0.7		2	
Spruce	46	18	13.3 ± 1.2	20.4 ± 2.9	2	2
Willow	1	0	16.2 ± 0		3	
Riparian ground						
Alder	1	0	15.5 ± 0		1	
Birch	44	20	7.4 ± 0.6	8.48 ± 1.1	3	3.5
Pine	4	1	11.3 ± 2.9	20.6 ± 0	2.5	4
Rowan	5	0	7.7 ± 1.6		3	
Spruce	62	51	10.6 ± 0.8	9.6 ± 1.3	3	2
Willow	5	0	7.3 ± 0.8		3	
Unknown	8	3	7.8 ± 0.8	12.9 ± 6.1	4	x
Channel						
Alder	2	0	9.7 ± 4.4			
Birch	27	21	8.7 ± 1.1	10.8 ± 1.1		
Pine	3	2	10.2 ± 1.9	13.3 ± 2.4		
Rowan	2	0	4.7 ± 0.7			
Spruce	27	50	14.2 ± 1.4	9.6 ± 1.1		
Unknown	32	42	7.4 ± 0.7	8.2 ± 0.7		

eventually become riparian buffers that are expected to protect streams from the adverse effects of logging, such as increased sediment transport to streams, changes in shading and thermal regimes, and biodiversity losses (Richardson et al. 2012). We clearly showed that those riparian forests are already compromised by the past management when compared to their unmanaged counterparts. Thus we cannot expect these forests to function well when they become buffers, a phenomenon that we see frequently across Sweden where riparian buffers are unable to sufficiently protect streams (Chellaiah and Kuglerová 2021; Hasselquist et al. 2024; Kuglerová et al. 2023). Mimicking natural conditions in riparian buffers has been suggested as improved water protection strategy, compared to fixed-width unharvested buffers (Kreutzweiser et al. 2012). The forest characteristics of the nature reserves investigated here can serve as an appropriate target for such management strategy (Kuglerová et al. 2024).

Forest structure

Previous research on the boreal upland forests showed that forests that developed under natural succession tend towards inverse J-shaped distribution of tree sizes while production stands develop a unimodal or slightly skewed distributions (Linder 1998; Bukhart and Tomé 2012). We found exactly the same result in the riparian forests investigate here. Given that all the production sites investigated here were mature forest (>60 years old), production stand conditions in the riparian forest were expected. Until the adoption of the forest act in 1993 that put an emphasis on both environmental and economic goals, even riparian forests were utilized as production stands, especially along small streams (Hasselquist et al. 2021). This means that most of the riparian forest that are mature today, including the sites investigated here, were planted, cleaned, and thinned to achieve single diameter spruce stands. This is supported by our results that show that the difference in BDH distribution is significant for trees <25 cm in DBH, but not for the larger ones (≥25 cm in DBH). Although cleaning and thinning of non-commercial trees from the riparian forests are no longer the norm in Sweden, and the Swedish Forest Agency (SFA) advocates for different management actions in riparian forests compared to uplands (Andersson et al. 2013), we will continue to see the legacy of the past actions for many decades to come.

Almost twice as many trees were recorded in the riparian forests in the nature reserves compared to the production stands for most of the tree species, a finding that is in contrast to Dahlström and Nilsson (2006) who found no differences in stem numbers between old-growth and production riparian stands in central and northern Sweden. The reason for the contrasting results could be the size of the streams and the difference in forest histories. Our streams were smaller than those of Dahlström and Nilsson (2006) and thus, our riparian forest likely experienced less fluvial disturbance that can suppress regeneration and growth. Nevertheless, the difference in number of trees between the two types of forest in this study was driven by the higher numbers of smaller trees (<25 cm DBH) in nature reserves compared to production stands, and this is the outcome of thinning practices in production stands that reduce competition for the targeted crop trees. We did expect to find higher number of large diameter trees (>34 cm DBH) in the nature reserves as those structures are more prominent in stands without management (Linder and Östlund 1998). However, the numbers of large diameter trees were similar in both forest types, likely indicating that even the nature reserves were subject to selective tree removal in the past. This is not surprising, considering that humans utilized the boreal forest long before the implementation of modern forestry (Östlund et al. 1997).

Both forest types investigated here were dominated by Norway spruce. Norway spruce is a late-successional species that is predicted to dominate in forest without natural (or anthropogenic) disturbances in boreal regions (Linder 1998). While riparian areas do get disturbed by flooding and are more susceptible to uprooting of trees due to the moist and less stable soils (Everham and Brokaw 1996), the streams that bordered the riparian forests investigated here were perhaps too small to drive typical floodplain dynamics that would promote deciduous trees to a larger degree (Kuglerová et al. 2015). Further, in the production stands, deciduous trees were removed during thinning. Nevertheless, we found nearly double the number of deciduous trees in the nature reserves compared to the production stands. Even though these numbers were usually in single digits per plot or per site, higher occurrence of deciduous trees, here birch, alder, rowan and willows can improve ecosystem functioning in conifer dominated riparian stands (Hasselquist et al. 2021). Higher occurrence of deciduous leaf litter supports more diverse microbial communities, both in water and on the land (Tolkkinen et al. 2020). Deciduous trees also provide more varied light regimes and are associated with different species of fauna and flora compared to spruce (Berg et al. 1994; Hasselquist et al. 2021). Finally, the fact that the production riparian stands had so low numbers of deciduous trees, something lacking completely, supports the idea that forest management in riparian zones should aim to promote deciduous trees (Hasselquist et al. 2021).

Diversity

The plant species communities found along the headwater streams in both forest types represented typical riparian vegetation diversity in the region (Kuglerová et al. 2016). There were no differences in the number of vascular plant species or alpha diversity index on sites situated in the nature reserves and in the production stands. This is not too surprising because riparian plant species richness is driven by the hydrological regimes of the streams and riparian zones (Kuglerová et al. 2015) and those were likely similar in the two forest types. All investigated streams were headwaters with similar width, depth and catchment area (Baan Hofman 2023) resulting in similar flow regimes. The overstory forest structure as well as heterogeneity in riparian habitat also contribute to riparian plant diversity (Kuglerová et al. 2016) and in this study we likely see the results of such differences between nature reserves and production sites reflected in the community composition. Each forest type was associated with slightly different communities, and this is the result of varied light (see section on canopy cover), tree species composition (see section on forest structure), riparian habitat structure (not measured here) as well as the forest history. Forest history is particularly important for bryophyte communities, which had higher cover for most groups, but especially for Sphagnum group and somewhat for feather mosses, in the nature reserves compared to the production sites. Hart and Chen (2006) found that bryophytes establish slowly after major disturbances but can continue increasing in abundance and diversity for many decades. While we were not able to obtain the exact stand age of the nature reserves, it is likely that they experienced major disturbances longer time ago compared to the production sites that were clear-felled sometimes around the mid-nineteenth century. More Sphagnum in the nature reserves also indicates that the riparian zone might be wetter there (Baan Hofman 2023). Higher soil wetness might be an outcome of differences in topography but more likely, in this region it is linked to the forest management. Vast areas of the production forest have been drained to facilitate forestry, affecting many headwater streams and their catchments (Hasselquist et al. 2018). Further, the reserve sites had on average, about the double the number of stems of birch, which has been shown to positively affect Sphagnum establishment (Sundberg and Rydin 2002).

Diversity of the tree and shrub layer was similar in nature reserves and production stands investigated here but as already mentioned the number of individuals was nearly double in the reserves for the tree layer. In the understory layer, deciduous species dominated over conifers in both forest types but surprisingly production stands had nearly double the number of deciduous individuals per plot compared to nature reserves. This indicates that riparian forests in production stands have the potential to regenerate and grow deciduous trees. This potential could be utilized in forest management actions that aim to increase deciduousness in riparian zones to create more functional, multi-layered, mixed-species riparian buffers in the future (Hasselquist et al. 2021).

It is important to mention here that other terrestrial and aquatic organisms than vegetation communities could show larger diversity differences between the nature reserves and production riparian forests. Organisms that are associated with older trees, LW, light heterogeneity and disturbance should be subject of future studies at these sites together with identifying bryophytes to species (Berg et al. 1994; Jonsell et al. 2007; Bell et al. 2015; Jonsson et al. 2017).

Ecological functions

Riparian forests provide many ecological functions that streams depend on (Richardson and Danehy 2007; Tolkkinen et al. 2020) and shading and provision of LW are some of the most important ones. In fact, the Swedish Forest Agency advocate for both shading and provision of LW to be maintained by riparian buffers after the upland forest is felled (Andersson et al. 2013). Yet, no concrete targets for what is sufficient light or what is sufficient amount and quality of LW are provided, leaving practitioners with no specific instructions. It has been suggested that to improve the protection of surface waters in production forests in Sweden, concrete targets for ecological values should be determined (Kuglerová et al. 2024) but it is unclear how. Using pristine or minimally impacted forests has been suggested as appropriate strategy (Stoddard et al. 2006) and as such, this study provides direct and specific template.

From our study, it is clear that riparian forests situated in nature reserves that experienced little or no forestry supply higher volumes of riparian standing LW. Standing snags but also laying logs are important features and provide unique habitat and substrate for many species of insects, bryophytes, lichens and many more (Gurnell et al. 1995; Esseen et al. 1997; Hylander et al. 2005; Johnson and Almlöf 2016). Those features are lacking in production forests where trees are harvested before they can die and create LW (Siitonen et al. 2000; Gustafsson et al. 2020). If riparian management is to emulate natural dynamics (Kreutzweiser et al. 2012), our results show that the volumes of LW must at least double. Over time, standing LW will eventually fall to the ground, likely increasing the volume of riparian ground LW, which in this study did not differ between reserve and production sites. This pattern is likely explained by a time lag, where standing LW gradually contributes to ground LW volumes. While we did expect the nature reserves to be old enough to supply LW to the riparian ground, it is possible that selective tree removal in the past, prior to formal protection, contributed to this time lag by removing the largest and oldest trees. Unfortunately, precise stand age data for the reserves are lacking, but anecdotal evidence suggests that while many trees exceed 150–300 years in age, the overall stand structure still reflect human use. This legacy could mean that the reserves are in an intermediate succession phase, where the full accumulation of ground LW has yet to occur.

We did not see statistically significant difference in channel LW between the two types of forests. Previous studies showed that streams in old-growth forests have substantially more LW in stream channels compared to streams flowing through production stands (Dahlström and Nilsson 2004, 2006) and given the differences in the riparian LW, we expected to find the same in the streams. One explanation for no differences in channel LW can be the presence of two log-jams in one of the production sites, generally increasing the average for production sites. Another explanation could be a possible increased input of logging residues from thinning operations into the streams in the production forests (Dahlström et al. 2005). This is quite likely considering the small diameters of the LW objects recorded. In fact, the diameter of the in-channel LW was small (<15 cm) in both nature reserves and production forests but the diversity was higher in the streams situated in nature reserves (two extra species of LW found in reserves compared to production sites). Species composition and volumes, as well as age and size, are all important for the LW dynamics in streams and the riparian zones (Bisson et al. 1984; Dynesius and Hylander 2007) and it is evident that the variation in those metrics was higher in the nature reserves compared to the production sites in this study. Nevertheless, the volumes of the channel LW were considerably smaller in the nature reserves studied here compared to similar studies (Dahlström et al. 2005; Kuglerová et al. 2024), most likely due to the small stream size and short stream sections (only 60 m per site) we studied.

We also recorded more varied and overall lower canopy cover in nature reserves compared to the production sites. Given the already presented differences in the forests structure and in the volumes of riparian LW, this result is not surprising and in agreement with previous studies (Stovall et al. 2009; Warren et al. 2013; Kaylor et al. 2017). The natural forest dynamic in the nature reserves creates canopy gaps that in turn provide a more heterogeneous light inputs into the stream channel and the riparian zone, likely benefiting aquatic and riparian organisms (Kiffney et al. 2003; Mallik et al. 2014). This difference in canopy cover is linked to management, or the lack of thereof, as well as to stand age. The nature reserves are approximately twice as old as the production stands, which are in the age range (>60 years old) associated with the densest, most closed-canopy conditions (Bechtold et al. 2017). This finding has high relevance for forest management in Sweden. While protecting streams against high light inputs via canopy shading is an important function of the riparian forests, intensive management has resulted in streams that flow through too dark mature second-growth stands (Warren et al. 2016). On the other hand, in Sweden, when such riparian forests become buffers, they tend to blow down resulting in too little shading of the stream and riparian habitat (Chellaiah and Kuglerová 2021). Riparian management should strive to achieve a heterogeneity in canopy cover within buffers so that both light and dark environments are available across small spatial scale (i.e. within one clearcut). This would require active management within wide buffers (>15 m wide) such as gap cutting or selective logging of spruce. Combined with the rest of the findings in this study, this could also promote regeneration and growth of deciduous trees, more varied LW dynamics and overall benefit the aquatic-riparian ecosystem in production stands.

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