



Do silver birch (*Betula pendula*) and hybrid aspen (*Populus tremula* × *P. tremuloides*) plantations on former agricultural land differ from the perspective of biodiversity?

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Abstract

Silver birch (*Betula pendula*) and hybrid aspen (*Populus tremula* × *P. tremuloides*) are widely planted tree species on former agricultural lands in Northern and Eastern Europe due to their fast growth, high biomass production and CO₂ sequestration. As few comparative studies on the biodiversity of silver birch and hybrid aspen plantations have been carried out, we aimed to evaluate above- and below-ground diversity in silver birch plantations (SBs) and hybrid aspen plantations (HAs) and associate the trends with environmental variables. For this, we collected data on herbs, ground-dwelling bryophytes, epiphytic bryophytes, lichens, closed forest species and soil fungi from 10 SBs and 10 HAs (<25 years of age) in Estonia. The richness and composition of herbs was similar in SBs and HAs, whereas all other groups differed either in species richness, composition or both. Overall, HAs hosted higher richness of ground-dwelling bryophytes and epiphytic lichens and lower richness of epiphytic bryophytes than SBs, which was associated with differences in litter and light conditions. The richness of closed forest species was similar between HAs and SBs and increased in correlation with the area of surrounding forests, whereas the compositions differed. The HAs hosted higher fungal richness of all soil fungi, as well as ectomycorrhizal, saprotrophic and plant pathogenic fungi and differed compositionally from SBs. Based on our findings, both birch and hybrid aspen plantations provide benefits with respect to biodiversity, as they support compositionally different assemblages of bryophytes, lichens, closed forest species and soil fungi.

Keywords Short-rotation forestry · Herbaceous species · Bryophytes · Lichens · Soil fungi · Forest species

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Introduction

The area of plantation forests increased by 55.8 million ha from 1990 to 2020, reaching 131 million ha worldwide (FAO 2020). Plantation forests can provide various ecosystem services ranging from wood production and carbon sequestration to accelerating forest succession, providing habitat for many species and increasing connectivity between fragmented forest patches (Brockerhoff et al. 2008; Pawson et al. 2013; West 2014). The effects of plantation forests on biodiversity have been found to vary greatly, depending on the geographic region (Tudge et al. 2023), previous land-use (Bremer and Farley 2010), management practices, rotation length (Hartley 2022; Spake et al. 2019) and plantation age (Tudge et al. 2023). The tree species used to establish the plantations also impacts biodiversity as native tree species and mixed plantations are often considered more favourable towards biodiversity than exotics and monoculture plantations (Hartley 2022; Messier et al. 2022; Suryaningrum et al. 2022). Overall, the response of biodiversity to the establishment of plantations varies among different groups of organisms (Felton et al. 2010; Wang et al. 2022).

In general, overstory trees affect understory diversity by determining the availability of resources (light, water, nutrients) as well as through litterfall and phytotoxic compounds (Messier et al. 1998; Barbier et al. 2008; Rodríguez-Calcerrada et al. 2011). The direct effects on biodiversity depend on the tree species (Pettersson et al. 2019) and the largest differences are usually observed between coniferous and deciduous trees (Barbier et al. 2008; Augusto et al. 2015), although understory characteristics can also vary significantly among different deciduous trees (Rola et al. 2021). The components of understory (shrub, herb and bryophyte layer) interact and are shaped by different factors (Bartels and Chen 2013). For instance, the diversity of the understory herb layer reacts strongly to light and nutrient conditions (Reich et al. 2012; Márialigeti et al. 2016), while ground-dwelling bryophytes are also strongly affected by litter. In deciduous forests litter has a detrimental effect on mosses due to the posed physical barrier, increased nutrient availability that favours the abundance of vascular plants and allelopathic effects (Márialigeti et al. 2009; Jean 2017).

The richness and composition of epiphytic bryophytes and lichens at the stand level also depend on overstory tree composition as epiphytes often prefer certain host trees mainly due to the variability of bark conditions among tree species (Ellis 2012; Kiraly et al. 2013; Ódor et al. 2013). The overstory effects on light conditions and microclimate are equally important in determining the diversity of epiphytes (Ódor et al. 2013; Wierzcholska et al. 2024).

While it is commonly known that above- and below-ground species richness and communities are linked in several ways or are mutually dependent on each other (Hiiesalu et al. 2014; Tedersoo and Bahram 2019), existing evidence of tree species impact on soil biota is mixed. Some studies highlight host plant species as a strong factor driving fungal communities (Tedersoo et al. 2008) with no effect on fungal richness (Li et al. 2021). Tedersoo et al. (2016) showed that the tree species of a pure stand has a strong effect on fungal communities, whereas the effect of tree diversity is low, but the magnitude and impact direction of a specific tree species are context dependent. As the physiological elements of trees vary between different species, the impact of each tree species on soil properties and below-ground biota is unique. A study where sporocarps in native sites and monocultures with different species were assessed showed that the mono-specificity of host trees involves several factors that could drive fungal diversity, such as absence of specific fungal species and canopy cover attributes (Buee et al. 2011).

Silver birch (*Betula pendula*) and hybrid aspen (*Populus tremula* × *P. tremuloides*) are fast-growing deciduous tree species that have been widely planted on former agricultural lands in Northern and Eastern Europe (Johansson 2007; Tullus et al. 2012b; Daugaviete et al. 2020). Several comparative studies have been published on the ecophysiological traits (Õunapuu-Pikas et al. 2022), acclimation to elevated air humidity (Rosenvald et al. 2014; Kukk et al. 2015; Tullus et al. 2017) and economics of plantations composed of silver birch and hybrid aspen (Tullus et al. 2012a). In addition, silver birch and hybrid aspen have been included in studies evaluating effects beneficial to the climate (Lutter et al. 2021), impacts on soil chemistry (Rytter and Rytter 2020) and growth and productivity of trees on abandoned agricultural land (Daugaviete et al. 2020; Rytter and Lutter 2020; Celma et al. 2022; McKay et al. 2022). A recent study also described mycorrhizal fungi on the roots of different clones of hybrid aspen and silver birch (Matisons et al. 2024). However, comparative studies on the effects of silver birch and hybrid aspen on biodiversity have so far focused only on the understory vegetation comprising vascular plants (Soo et al. 2009b) and bryophytes (Tullus et al. 2012c) at a young age (< 10 years). These studies concluded that the diversity of vascular plants and bryophytes was similar among birch and aspen stands and found a strong effect of previous agricultural land use on species composition (expressed in a low share of forest species and high share of open-habitat species) in both plantation types at the age of 7–9 years (Soo et al. 2009b; Tullus et al. 2012c). To date, understory data from older stands have not been compared and there have also been no reports comparing the epiphytic assemblages of bryophytes and lichens or soil fungal communities in hybrid aspen and silver birch plantations.

The general aim of the current study was to determine whether hybrid aspen and silver birch plantations on previous agricultural land host similar biodiversity. For this we compared the richness and composition of different organism groups in hybrid aspen and silver birch plantations of similar age (< 25 years) and associated the trends in biodiversity with environmental variables. More specifically, we aimed, firstly, to analyse the biodiversity of above-ground organism groups (herb and bryophyte layers, and epiphytes); we hypothesized that epiphytic bryophyte and lichen communities show substantial differences between the hybrid aspen and silver birch plantations while ground-dwelling layers are more similar in their species richness and composition in the two types of plantations. Secondly, we hypothesized that below-ground species groups (all soil fungi, saprotrophic, pathogenic and ectomycorrhizal fungi) do not exhibit large differences between the two plantation types. As a separate aim we explored if hybrid aspen and silver birch plantations provide similar habitats for forest biodiversity. For this we analysed whether the richness of ground-dwelling and epiphytic species typical to closed forests was similar in hybrid aspen and silver birch plantations and determined how light and soil conditions, litter characteristics and surrounding landscape affected closed forest species.

Materials and methods

Study area

Data were collected from hybrid aspen ($n=10$) and silver birch ($n=10$) plantations located in the continental part of hemiboreal Estonia (Fig. 1). All plantations were established in 1999 or 2000 on previous agricultural land, using either 1-year-old micro-propagated plants (for hybrid aspen) or 1-year old seedlings (for silver birch). The initial planting

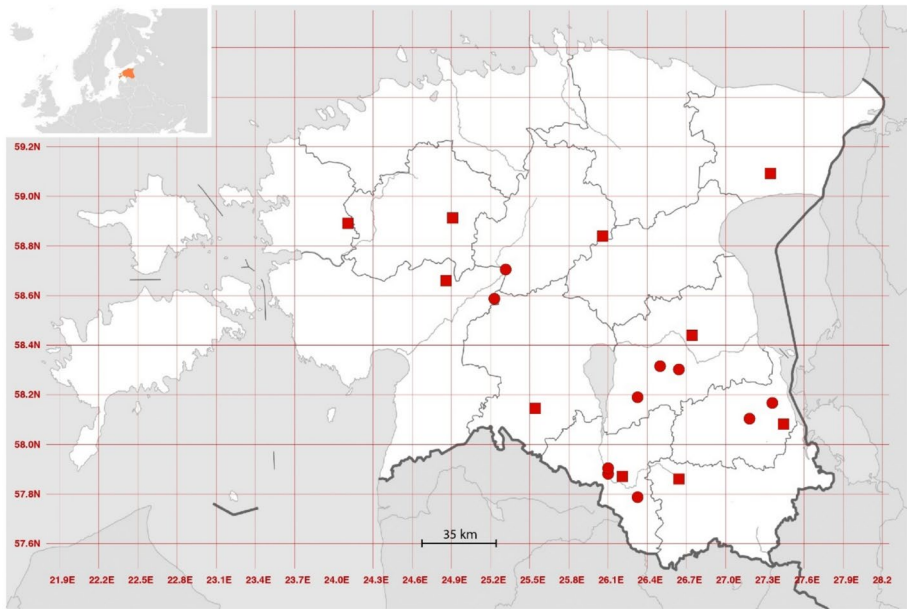


Fig. 1 Locations of the studied silver birch ($n=10$, marked as quadrats) and hybrid aspen ($n=10$, marked as circles) plantations in Estonia

density was considerably higher in silver birch plantations (SBs) than in hybrid aspen plantations (HAs) (Tullus et al. 2012a). No chemical vegetation treatment was applied after planting (Soo et al. 2009a; Tullus 2013). The size of each silver birch plantation was 1 ha, whereas the size of hybrid aspen plantations ranged from 7 to 34 ha. All plantations were established for timber production. In Northern and Eastern Europe, the predicted rotation length is 20–30 years for hybrid aspen (Tullus et al. 2012b) and 30–35 years for silver birch when grown in plantations on former agricultural land (Lutter et al. 2021; Tullus et al. 2012a).

Data collection

Above-ground biodiversity

In every plantation a 100 m² square plot (located in typical part of the respective plantation in terms of land relief and tree layer, excluding plantation edges) was established for biodiversity studies, where the species of shrubs and trees, herbs (including *Rubus idaeus*) and bryophytes were determined. The abundance of each species was estimated visually, following a scale of 1–5 based on coverage (1–1–5%, 2–6–20%, 3–21–50%, 4–51–75%, 5–76–100%). For species with a coverage < 1% an estimate of 0.5 was used). Tree bases, trunks (up to 2 m from the ground) and branches (up to ca 3 m from the ground, the branches which could be cut or bent downwards; also dead and broken branches on the soil) of hybrid aspen and silver birch were examined for epiphytic bryophyte and lichen species. If a bryophyte or lichen specimen could not be identified in field conditions, the samples were collected for further identification under a stereo or light microscope. In

hybrid aspen plantations, floristic inventories were carried out in the middle of the vegetation periods of 2021 and 2022 and lichen inventories in 2022 and 2023. In silver birch plantations, floristic data were collected in the middle of the vegetation period of 2019 and lichen surveys were carried out in 2015 (in five plots) and 2019 (in five plots). The nomenclature for vascular plants follows Kukk et al. (2020), for bryophytes Vellak et al. (2023) and for lichens Randlane et al. (2023). Data on vascular plants, bryophytes, lichens and tree layer collected from SBs were previously published by Tullus et al. (2022), however, in the current study we excluded a plantation on an island in western Estonia as none of the studied hybrid aspen plantations were situated on western islands.

Below-ground biodiversity

Soil sampling for molecular analyses was carried out according to Tedersoo et al. (2014) on a 2500 m² circular plot (located around the centre of a 100 m² square plot) per sampling site. At each site, 40 topsoil subsamples (5 cm diameter to 5 cm depth) were collected from 20 randomly selected trees at a distance of 1–2 m from two opposite sides. A separate plastic pipe was used to collect each soil sample after the woody debris and litter were removed from the ground. All 40 subsamples of each site were pooled into a plastic bag and set to air dry on a heated floor at 20 °C immediately after sampling to minimize mould overgrowth. Field sampling was carried out in the middle of the growing season (June and July) in 2017 (hybrid aspen plantations) and in 2019 (silver birch plantations).

After drying, the samples were homogenized and mixed thoroughly in plastic bags by hand. Subsequently, 0.2 g of each soil sample was weighed into a 2 ml tube. The samples were homogenised using two 3.2 mm diameter stainless steel beads (BioSpec Products, Bartlesville, OK, USA) by shaking for 5 min at 30 Hz with the Retsch Mixer Mill MM400 (Retsch, Haan, Germany). DNA was extracted from the 0.2 g of homogenised soil using DNeasy PowerSoil kit (Qiagen, Düsseldorf, Germany) according to manufacturer's instructions.

To evaluate potential differences among the fungal communities associated with birch and hybrid aspen stands, we used internal transcribed spacer (ITS) region sequencing data previously published by Lutter et al. (2023) and Rähn et al. (2024). Both studies used the PacBio platform to sequence the ITS region amplicons, which for Lutter et al. (2023) were generated using the primers ITS1catta and ITS4ngsUni (Tedersoo and Anslan 2019), and for Rähn et al. (2024) using the primers ITS9mun and ITS4ngsUni (Tedersoo and Lindahl 2016), both of which provide good coverage of fungal taxa. Supplementary information of the two previous studies is available searching by DOI (<https://doi.org/10.3389/fmicb.2024.1372938> and <https://doi.org/10.1016/j.foreco.2023.121100>). The associated species hypotheses are found under bioproject PRJNA936817 and PRJNA1152302 on NCBI.

Environmental variables

Tree layer characteristics were measured in each plantation using a 0.1 ha study plot surrounding the 100 m² sized square plot. To evaluate stand density, all silver birch or hybrid aspen trees inside the study plot were counted and converted to number of trees per ha. Diameter at breast height (cm) over bark was measured for all individual trees inside the 0.1 ha plot using a forest caliper. Stand basal area (m² ha⁻¹) was calculated by summing up the basal areas of individual trees and converting the plot-level basal area to the hectare scale.

Litter (including leaf and branch litter) was collected from eight 20×20 cm sub-plots located in a transect inside the study plot. First, the litter samples were dried at 70 °C to constant weight. Leaves and branches with a diameter < 1 cm and branches with a diameter ≥ 1 cm were then weighed separately (hereafter they are referred to as leaf litter and branch litter). Finally, averaged values of leaf and branch litter ($t\ ha^{-1}$) were calculated for each square plot.

Soil samples were collected from the upper 0–10 cm layer and the 10–20 cm mineral layer of the same eight sub-plots and analysed at the Centre of Estonian Rural Research and Knowledge to determine pH_{KCl} from 1 M KCl suspension, total nitrogen (N, %) using the Kjeldahl method; available phosphorus (P, $mg\ kg^{-1}$) and potassium (K, $mg\ kg^{-1}$) using the Mehlich III method. Total nitrogen of the soil samples collected from hybrid aspen plantations was determined at the Laboratory of the Department of Soil Sciences and Agrochemistry of the Estonian University of Life Sciences.

To characterise the amount of canopy-transmitted direct and diffuse solar radiation ($mol\ m^{-2}\ d^{-1}$), four hemispherical photos were taken at each study plot from above the herb layer using Sigma's 8 mm F3.5 EX DG Circular Fisheye lens attached to a Canon EOS 5D or 6D Mark II digital camera. The photos were analysed with Gap Light Analyzer 2.0 (Frazer et al. 1999) and the length of the growing season was set from April 22 to October 28, based on the averaged data of 1965–2013 (Kollo et al. 2023). Averaged values of the four hemispherical photos were used for further data analysis.

Based on orthophotos and spatial data provided by the Geoportal of the Land Board and the National Forest Register we estimated the percentage of area covered by forests, fields and grasslands in a 300 m radius area around each square plot. Following Márialigeti et al. (2016) we distinguished regenerating forests (all stands with age ≤ 20 years, referred hereafter as young forests) and older forests (all stands with age > 20 years, referred hereafter as forests). The area around the study plots covered by silver birch and hybrid aspen plantations aged < 25 years was categorized as young forests.

Data management

Above-ground biodiversity

We determined species that are largely restricted to closed forests based on literature sources, using Heineken et al. (2022) for herb layer species, van Zuijlen et al. (2023) for bryophytes and Schmidt et al. (2011) for lichens. These species are referred hereafter as closed forest species or forest species. *Impatiens parviflora* was excluded from the list of closed forest species as it is a non-native species for Estonian flora (Kukk et al. 2020). Closed forest species were distinguished into two groups: 1) ground-dwelling forest species (including all herbs and bryophytes recorded on the ground) and 2) epiphytic forest species (including all lichens and bryophytes recorded on trees). Two closed forest bryophyte species (*Eurhynchium angustirete* and *Lophocolea heterophylla*) were found growing on the ground as well as on trees in the studied plantations. Based on the number of occurrences on either of the substrate type *Eurhynchium angustirete* was classified as a ground-dwelling forest species and *Lophocolea heterophylla* as an epiphytic forest species.

Based on the abundance of shrub layer species we determined the Shannon diversity index of shrubs for every square plot using “vegan” package in R version 4.3.2 (R Core Team 2023).

Below-ground biodiversity

The two fastq format ITS sequencing datasets were first processed using *mothur* (Schloss et al. 2009) to remove reads < 100 bp and to demultiplex longer sequences allowing 1-base differences to the index and 2-base differences to the primer. Subsequently, the *Pipecraft* v1.0.0 pipeline was used to perform quality filtering, read clustering, and assigning taxonomy to the recovered operational taxonomic units (OTUs) (Anslan et al. 2017). Briefly, *UCHIME* (Edgar et al. 2011) was used to perform both de novo and reference-based (*UCHIME* reference dataset 16.10.2022) chimera filtering, and *ITSx* (Bengtsson-Palme et al. 2013) was then used to extract full-length Internal Transcribed Spacer (ITS) region sequences. The full-length ITS reads were subsequently clustered to OTUs using *VSEARCH* based on a 97% similarity threshold (Rognes et al. 2016). OTUs with > 97% sequence similarity to a reference were assigned to species hypotheses (SH) based on *UNITE* v.10 and higher-level classification was assigned according to Tedersoo et al. (2014). Finally, the OTUs were assigned to functional guilds based on the *FungalTraits* database (Pöhlme et al. 2020).

Statistical analysis

Above-ground biodiversity

All statistical analyses on above-ground biodiversity were conducted in R, version 4.3.2 (R Core Team 2023). A significance level of $\alpha=0.05$ was used in all statistical tests. The effect of the planted tree species on the richness of different species groups (herbs, ground-dwelling bryophytes, epiphytic bryophytes, lichens, ground-dwelling forest species, epiphytic forest species and all forest species) was tested using Generalized Linear Models (GLMs) with quasi-Poisson distribution. Principal component analyses (PCA) of the site and stand characteristics (soil pH, N, P, K, branch litter, leaf litter, number of trees, stand basal area, transmitted diffuse radiation, transmitted direct radiation, diversity of shrubs and landscape variables) was carried out. The associations of PCs with quantitative (species richness) and qualitative (plantation type) supplementary variables were tested with Pearson's linear correlation analysis and one-way-anova, respectively. Additionally, a Pearson's correlation matrix comprising environmental variables and the richness values of different species groups was compiled (logarithmic transformation was used to normalize the distribution of soil N, P, leaf litter, branch litter, area of young forests and area of grasslands).

The compositional differences of herbs, ground-dwelling bryophytes, epiphytic bryophytes, lichens, ground-dwelling forest species, epiphytic forest species and all forest species between silver birch and hybrid aspen plantations were evaluated using Permutational Multivariate Analysis of Variance (PERMANOVA) based on Bray–Curtis dissimilarity indexes as implemented in the function “*adonis2*” of the R package “*vegan*”. Non-metric multidimensional scaling was performed to study compositional variability of herb, bryophyte (combining bryophyte layer and epiphytic bryophytes), lichen and forest species assemblages (combining ground-dwelling and epiphytic forest species). Non-metric multidimensional scaling (NMDS) was applied using the function “*metaMDS*” and environmental variables were fitted to the ordination using the function “*envfit*” of the “*vegan*” package. The averaged values of the 0–10 cm upper soil layer and the 10–20 cm mineral layer soil samples were used in PCA and NMDS analysis. Indicator species of herb, bryophyte,

lichen and forest species assemblages were determined for SBs and HAs with the function “multipatt” from the package “indicpecies” and indicator species were plotted onto the ordination schemes. Taxa classified at the genus level were excluded from compositional analyses.

Below-ground biodiversity

Fungal diversity analyses were conducted using STATISTICA version 12 (TIBCO Software Inc). Fungal richness and relative abundance over all sampling sites ($n=20$) was computed for major functional guilds (all fungi, saprotrophs, ectomycorrhizal fungi (EcM), plant pathogens and arbuscular mycorrhizae (AM)) and separately for hybrid aspen ($n=10$) and silver birch plantations ($n=10$). The relative abundances of fungal guilds were computed by summing the proportions of individual OTU sequences relative to the total number of sequences per sample. To evaluate differences in fungal richness among birch and hybrid aspen plantations, we calculated estimated marginal mean OTU richness values using the total number of reads per sample as the control factor to adjust for variable sequencing depth in linear modelling (LM). Tree species impact on AM richness and communities was not tested due to insufficient number of AM reads in birch plantations.

Potentially significant covariables were tested with multiple regression before modelling and one of each two variables with $R>0.5$ was excluded from the analyses to avoid autocorrelation. The remaining factors with $R>0.3$ were included in the preliminary models. Best predictors for fungal relative abundance and OTU diversity (number of OTUs per sample) were analysed using LM where sequencing depth (total number of sequences per sample) was added as a covariate.

Community analyses were conducted in PRIMER-e version 7 (www.primers-e.htm). PERMANOVA+ (Anderson 2005) was used to compare fungal community compositions of silver birch and hybrid aspen plantations. OTUs with represented by <2 sequences (over all samples) and samples represented by <2 OTUs were discarded from the dataset. OTU abundance was standardized and square-root transformed by samples before the analysis to reduce the effect of dominant taxa. Bray–Curtis dissimilarity (Bray and Curtis 1957) was used as the distance measure. Additionally, NMDS as applied in R function “metaMDS” was used to evaluate compositional variability of all fungi, ectomycorrhizal fungi, saprotrophic fungi, and plant pathogenic fungi. Subsequently, to evaluate the effect of environmental variables on fungal community composition, we used R function “envfit” to fit environmental vectors onto the ordination.

Environmental variables

Differences in environmental variables between silver birch and hybrid aspen plantations were tested using the t-test in R.

Results

Above-ground species richness

Altogether 132 vascular plant taxa were found in the herb layer of the 20 plantations, including 123 classified at the species level and nine at the genus level due to the

juvenility of specimens (Supplementary Table S1). SBs and HAs shared 59% of herb species, with SBs hosting 101 species and HAs 94 species. The herb layer consisted mainly of native species frequently found in Estonia. We also recorded three non-native species: *Impatiens parviflora* with three occurrences, *Solidago canadensis* (1) and *Trifolium hybridum* (1) and three protected species: *Epipactis helleborine* (4), *Epipactis palustris* (1) and *Platanthera chlorantha* (1).

Altogether 48 bryophyte species and three taxa classified at the genus level were identified on the ground and on the trees in the 20 plantations (Supplementary Table S1). Out of these, 13 species were recorded on the ground, 18 species on trees and 17 species on both substrates. SBs and HAs shared 54% of bryophyte species, with SBs hosting 35 and HAs 39 bryophytes. All recorded bryophyte species are frequently found native species of Estonian bryoflora.

We identified a total of 62 lichen species on the tree trunks and branches, including 36 species in SBs and 47 in HAs (Supplementary Table S1). Ground-dwelling lichens were not present in the study plots. Overall, the two plantation types shared 33% of lichen species.

Out of 233 herb, bryophyte and lichen species recorded in the studied plantations 26 were considered to be closed forest species, including 16 ground-dwelling and 10 epiphytic species.

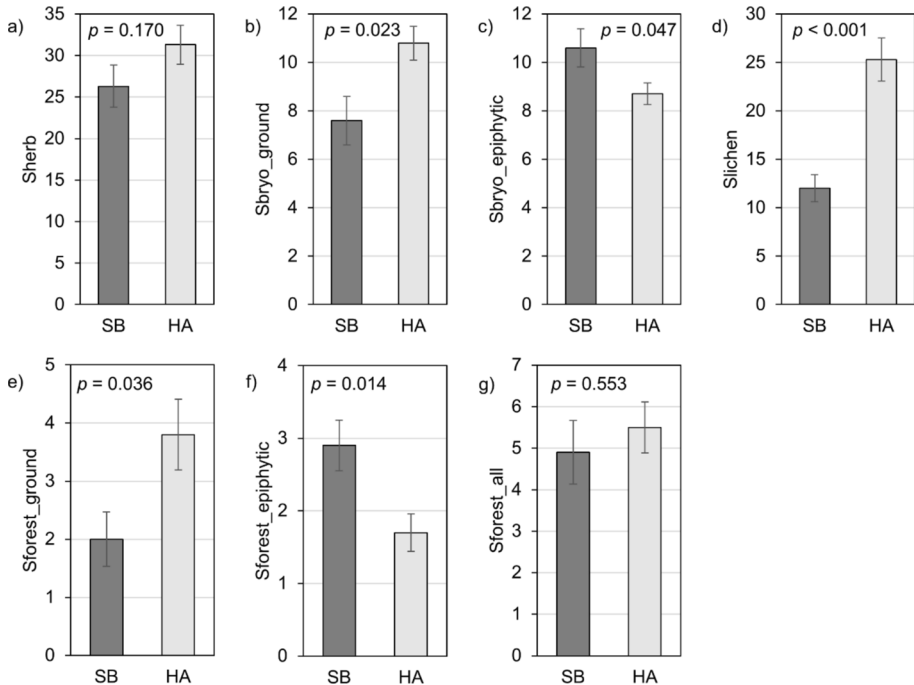


Fig. 2 The average species richness (S) of different organism groups: **a** herbs, **b** ground-dwelling bryophytes, **c** epiphytic bryophytes, **d** lichens, **e** ground-dwelling forest species, **f** epiphytic forest species and **g** all forest species in silver birch (SB) and hybrid aspen (HA) plantations. *P*-values indicate the results of GLM based on quasiPoisson distribution

The herb layer hosted similar species richness in SBs and HAs (Fig. 2a), whereas the bryophyte layer of HAs contained on average three species more than the bryophyte layer of SBs (Fig. 2b). An opposite trend was observed on tree trunks as the richness of bryophytes on silver birches was higher than on hybrid aspens (Fig. 2c). The trunks and branches of hybrid aspen hosted on average two times higher richness of lichens compared to silver birch (Fig. 2d). The richness of ground-dwelling forest species was considerably higher in HAs (Fig. 2e), while the richness of epiphytic forest species was significantly higher in SBs (Fig. 2f). The combined ground-dwelling and epiphytic closed forest species richness was similar for both tree species (Fig. 2g).

The first three principal components (PCs) explained 64% of the total variance of all included variables. Tree species (silver birch or hybrid aspen) was distinguished in PC1 ($p < 0.001$, Table 1). Number of trees, leaf and branch litter increased towards SBs and canopy transmitted radiation and the area of young forests towards HAs (Fig. 3a). The richness of epiphytic forest species increased towards SBs and the richness of lichens towards the less shaded HAs. Accordingly, bivariate correlations indicated that the richness of lichens and canopy transmitted direct and diffuse radiation were positively associated ($R = 0.52$, $p = 0.018$ and $R = 0.72$, $p < 0.001$, respectively; Supplementary Table S2). The richness of epiphytic forest species and the richness of all forest species were correlated with PC2 and increased together with an increasing area of surrounding forest. The positive impact of surrounding forest on the richness of epiphytic forest species ($R = 0.58$, $p = 0.007$) and all forest species ($R = 0.54$, $p = 0.015$) was also confirmed by bivariate correlation analysis (Supplementary Table S2). In addition, the richness of all forest species was associated with PC3, similarly to the richness values of ground-dwelling forest species and herb layer species that increased together with stand basal area and diversity of shrubs and decreased with increasing soil N (Fig. 3b). Correlation analysis also revealed a positive impact of higher stand basal area on the richness of ground-dwelling forest species ($R = 0.45$, $p = 0.048$) and on the richness of herbs ($R = 0.50$, $p = 0.025$), whereas other correlations were insignificant (Supplementary Table S2).

Below-ground species richness

The total fungal dataset contained 1422 OTUs, where the relative abundance of EcM sequences was 38.5%, saprotrophic fungi 26.6%, plant pathogens 3.4% and AM 0.31%. Other guilds taken together (other parasites, foliar and root endophytes, moss symbionts and lichenized fungi) comprised 2.5% of the OTUs and fungi with undetermined lifestyles represented 28.6% of all fungal OTUs. All recovered fungal reads and representative sequences of the OTUs are given in Supplementary Table S3. We found that the proportions of plant pathogens varied significantly between SBs and HAs ($p = 0.043$), whereas the relative abundances of EcM and saprotrophic fungi were similar ($p > 0.05$). The OTU richness estimates of plant pathogens, saprotrophs and all fungi were approximately two times higher in HAs compared to SBs (Table 2). EcM OTU richness varied less between tree species but was still markedly higher in HAs (Supplementary Table S4).

OTU richness of all fungi was affected by tree species ($p < 0.001$, Supplementary Table S4), sequencing depth ($p < 0.001$) and negatively by the area of forest around the study plot ($p = 0.046$). Plant pathogens and saprotrophic fungi were both affected by tree species ($p < 0.001$ and $p < 0.001$, respectively) and sequencing depth ($p = 0.007$ and $p = 0.005$, respectively). Additionally, tree species had a significant impact on EcM fungi ($p = 0.001$). Separate analysis of birch and hybrid aspen datasets revealed a near-significant

Table 1 Pearson's correlation coefficients (*R*) between the first three principal components (Dim1, Dim2, Dim3), environmental variables and richness (S) values of different species groups

	Dim1 (33.2%)		Dim2 (19.3%)		Dim3 (11.9%)			
	<i>R</i>	<i>p</i> -value	<i>R</i>	<i>p</i> -value	<i>R</i>	<i>p</i> -value		
Leaf litter	0.83	< 0.001	Soil K	0.65	0.002	Basal area	0.73	< 0.001
Stand density	0.76	< 0.001	Area of fields	0.60	0.005	Diversity of shrub layer	0.62	0.003
Area of fields	0.66	0.002	Soil P	0.58	0.007	Soil N	-0.53	0.017
Branch litter	0.57	0.009	Soil pH _{KCl}	0.55	0.012			
Soil pH _{KCl}	0.48	0.031	Leaf litter	-0.47	0.037			
Area of young forest	-0.76	< 0.001	Branch litter	-0.54	0.013			
Direct radiation	-0.80	< 0.001	Area of forest	-0.81	< 0.001			
Diffuse radiation	-0.83	< 0.001						
S_lichens	-0.67	0.001	S_epiphytic forest species	-0.70	0.001	S_herbs	0.60	0.005
Tree species	<i>R</i> ² = 0.52	< 0.001	S_all forest species	-0.49	0.028	S_ground-dwelling forest species	0.59	0.006
						S_all forest species	0.46	0.042

Significant correlations (*p* < 0.05) are presented in bold

Fig. 3 Principal component analyses (PCA) based on environmental and site variables (cyan arrows) of hybrid aspen (HA) and silver birch (SB) plantations. Biplots of principal components 1 and 2 (a) and 2 and 3 (b); supplementary variables (species richness values) are shown as blue arrows with dashed lines and 95% confidence ellipses encircle the centroids of plantation types

negative impact of the area of young forest around the study area on EcM richness in HAs ($p=0.054$), whereas the area of fields around the study plot had a significant positive effect on EcM richness in SBs ($p=0.017$).

In contrast to OTU richness, tree species had a significant impact only on the relative abundance of plant pathogens ($p=0.043$). EcM relative abundance was positively affected by stand density ($p=0.006$) and negatively by shrub diversity ($p=0.033$). We found no significant predictors for the relative abundance of saprotrophic fungi. The results for the separate analysis of birch and hybrid aspen datasets are given in Supplementary Table S4.

Environmental variables

Although the average stand density was considerably lower in HAs than in SBs, the basal area of the tree layer was similar for both tree species (Table 3). Shrub layer diversity was also similar in SBs and HAs, although a significantly higher amount of canopy transmitted direct and diffuse solar radiation reached the understory in HAs. The amount of leaf litter was on average $2.6\times$ higher and the amount of branch litter $3.0\times$ higher in SBs than in HAs. Soil properties were similar for both tree species, except for soil N that was considerably higher in the 10–20 cm mineral layer of the soil in SBs. SBs and HAs were surrounded by a similar landscape matrix, except for the area covered by young forest, which was significantly higher around HAs.

Above- and below-ground species composition

The results of PERMANOVA indicated a similar herb layer composition among SBs and HAs, whereas all other species groups showed compositional differences (Table 4). Moreover, the compositional variability associated with tree species was more pronounced in epiphytic communities ($R^2=0.49$ for epiphytic lichens, 0.57 for epiphytic bryophytes and 0.58 for epiphytic forest species) than in ground-dwelling species assemblages ($R^2=0.12$ for the bryophyte layer and 0.15 for ground-dwelling forest species) and below-ground species assemblages (R^2 varying between 0.17 to 0.24 for soil fungal groups).

The effect of tree species on bryophyte, lichen and forest species assemblages was also evident based on NMDS ordination as SBs and HAs were clearly separated in the ordination space (Fig. 4b–d, Table 5). Based on indicator species analysis, both SBs and HAs hosted characteristic species. Herbaceous species *Agrostis capillaris*, bryophytes *Dicranum scoparium*, *Hypnum cupressiforme*, *Lophocolea heterophylla*, *Pleurozium schreberi*, *Ptilidium pulcherrimum* and lichens *Hypogymnia physodes* and *Lecanora pulicaris* were characteristic to SBs, while herbaceous species *Dryopteris carthusiana*, *Dryopteris filix-mas*, *Equisetum arvense*, *Hieracium umbellatum* and bryophytes *Amblystegium serpens*, *Eurhynchium angustirete*, *Lewinskia speciosa*, *Plagiomnium cuspidatum*, *Radula complanata* and lichens *Caloplaca cerina*, *Gyalolechia flavorubescens*, *Lecania naegelii*, *Lecanora argentata*, *Lecanora chlarotera*, *Physcia adscendens*, *Xanthoria parietina* and ten other lichen species were characteristic to HAs (Fig. 4b, c). Out

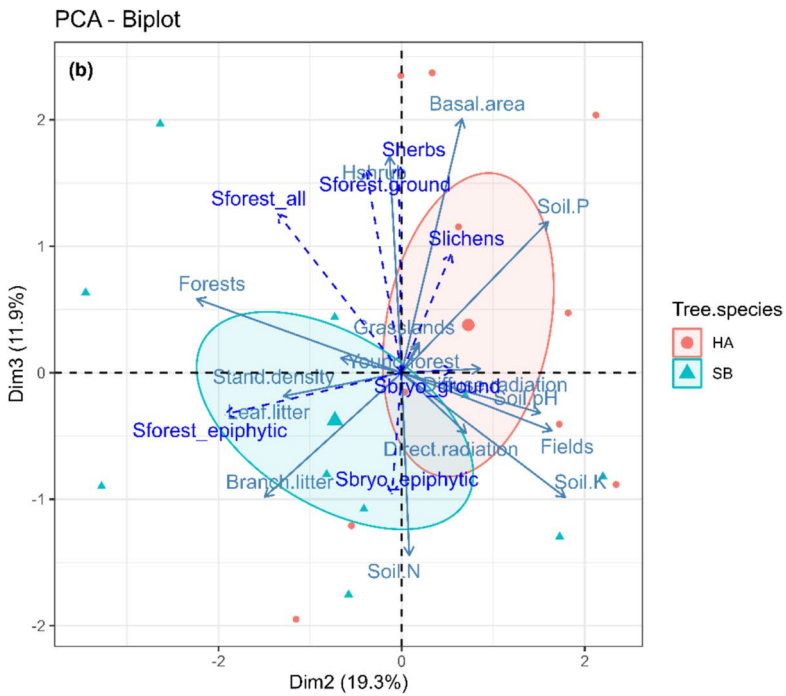
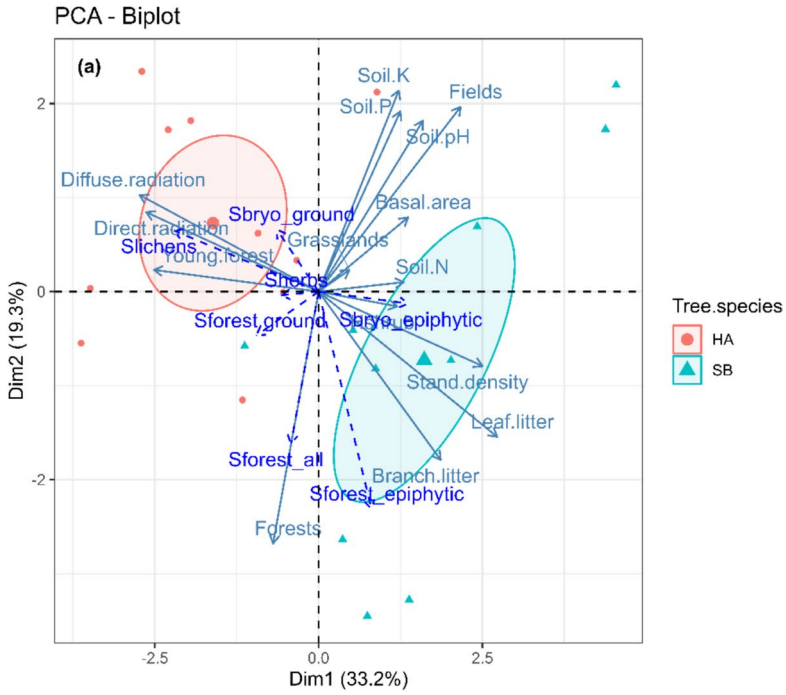


Table 2 Comparison of estimated marginal means of OTU richness and relative abundances of fungal guilds in silver birch and hybrid aspen plantations based on LM

Fungal group	Silver birch	Hybrid aspen	<i>p</i> -value
Richness of all fungi (OTU richness)	147	302	< 0.001
Richness of EcM fungi (OTU richness)	30	47	0.001
Richness of plant pathogens (OTU richness)	7	18	0.001
Richness of saprotrophic fungi (OTU richness)	40	90	< 0.001
Relative abundance of EcM fungi (%)	46.9	42.9	0.684
Relative abundance of plant pathogens (%)	2.1	3.4	0.043
Relative abundance of saprotrophic fungi (%)	29.2	28.3	0.949

Significant effects ($p < 0.05$) are presented in bold

Table 3 Differences among environmental variables (mean \pm standard error) between silver birch ($n = 10$) and hybrid aspen ($n = 10$) plantations

Environmental variable	Silver birch plantation	Hybrid aspen plantation	<i>p</i> -value
Stand density, (ha ⁻¹)	1381.0 \pm 97.6	787.0 \pm 80.5	< 0.001
Basal area, (m ² ha ⁻¹)	21.6 \pm 0.9	21.6 \pm 1.9	0.984
Direct radiation, (mol m ⁻² d ⁻¹)	2.3 \pm 0.3	3.4 \pm 0.4	0.033
Diffuse radiation, (mol m ⁻² d ⁻¹)	2.3 \pm 0.2	3.9 \pm 0.4	0.001
Leaf litter, (t ha ⁻¹)	6.6 \pm 0.7	2.5 \pm 0.3	< 0.001
Branch litter, (t ha ⁻¹)	2.7 \pm 0.6	0.9 \pm 0.5	0.029
Soil pH _{KCl} depth 0–10 cm	5.3 \pm 0.3	5.3 \pm 0.2	0.994
Soil N depth 0–10 cm, (%)	0.18 \pm 0.01	0.15 \pm 0.01	0.085
Soil P depth 0–10 cm, (mg kg ⁻¹)	121.1 \pm 31.7	126.8 \pm 24.3	0.888
Soil K depth 0–10 cm, (mg kg ⁻¹)	171.9 \pm 27.7	155.7 \pm 13.0	0.602
Soil pH _{KCl} depth 10–20 cm	5.3 \pm 0.3	5.1 \pm 0.2	0.665
Soil N depth 10–20 cm, (%)	0.14 \pm 0.01	0.10 \pm 0.01	0.025
Soil P depth 10–20 cm, (mg kg ⁻¹)	102.8 \pm 32.8	107.0 \pm 25.1	0.920
Soil K depth 10–20 cm, (mg kg ⁻¹)	105.7 \pm 18.8	103.1 \pm 11.6	0.908
Diversity of shrub layer	1.6 \pm 0.1	1.5 \pm 0.2	0.846
Area of forest around study plot, (%)	35.5 \pm 6.9	25.8 \pm 6.8	0.333
Area of young forest around study plot, (%)	9.5 \pm 2.2	39.7 \pm 5.6	< 0.001
Area of fields around study plot, (%)	40.1 \pm 8.3	25.4 \pm 6.0	0.169
Area of grasslands around study plot, (%)	6.8 \pm 2.0	3.3 \pm 1.4	0.171

P-values indicate the results of t tests. Significant effects ($p < 0.05$) are presented in bold

of them, *Dryopteris carthusiana*, *D. filix-mas*, *Eurhynchium angustirete*, *Lophocolea heterophylla*, *Ptilidium pulcherrimum* and *Lecanora argentata* are considered closed forest species. In addition to tree species, the assemblages of closed forest species were affected by surrounding landscape (the area of young forests, forests and grasslands in the vicinity of the study plots), the amount of diffuse solar radiation, leaf litter, soil potassium content and stand density. In accordance with the results of PERMANOVA, the herb layer assemblages of SBs and HAs were not clearly distinguished in the

Table 4 Comparison of assemblages of different species groups between silver birch and hybrid aspen plantations according to PERMANOVA

Species group	R^2	F	p -value
Herb layer species	0.07	1.44	0.090
Bryophyte layer species	0.12	2.51	0.012
Epiphytic bryophyte species	0.57	24.04	0.001
Epiphytic lichen species	0.49	17.03	0.001
Ground-dwelling forest species	0.15	2.84	0.017
Epiphytic forest species	0.58	24.43	0.001
All above-ground forest species	0.36	10.33	0.001
All fungi	0.22	4.98	0.001
EcM fungi	0.17	3.63	0.001
Fungal plant pathogens	0.17	3.25	0.001
Saprotrophic fungi	0.24	5.77	0.001

Significant effects ($p < 0.05$) are presented in bold

ordination space (Fig. 4a), and instead of tree species the herb layer responded to soil conditions (soil pH and potassium content) and landscape level variables (Table 5).

Regarding soil fungal communities, we found a significant effect of tree species on the assemblages of all fungi, ectomycorrhizal fungi, saprotrophic fungi, and plant pathogenic fungi based on NMDS ordination as SBs and HAs were clearly separated in the ordination space (Fig. 5b–d, Table 6). The compositions of all four groups of fungal taxa were significantly affected by tree species, stand density, leaf litter, and area of young forest around the study plot. Additionally, the assemblages of all fungi and plant pathogenic fungi were affected by diffuse radiation, whereas plant pathogens were also affected by direct radiation, and ectomycorrhizal fungi by branch litter.

Discussion

Hybrid aspen and silver birch are two tree species widely planted on former agricultural land in Northern and Eastern Europe, however, so far it is not clear whether they provide similar habitat for various groups of organisms. We hypothesized that the diversity of ground-dwelling herbs and bryophytes is similar between hybrid aspen and silver birch plantations, while epiphytic communities of bryophytes and lichens differ considerably between plantation types. Regarding ground-dwelling species results partially confirmed our expectations as SBs and HAs hosted similar diversity of herbs but showed differences in bryophyte assemblages. Regarding epiphytic communities our hypothesis was confirmed as we observed significant differences in the richness and composition of epiphytic bryophytes and lichens between HAs and SBs. The communities of closed forest species also varied considerably between HAs and SBs. We identified some differences in environmental variables between SBs and HAs that were linked to differences in vegetation characteristics.

Resulting from the lower initial planting density, the number of trees was considerably lower in HAs than in SBs. Lower stand density affected the light conditions and litter characteristics (Supplementary Table S2) as more light reached the understory of HAs where the amount of litter was considerably lower. Joncak et al. (2023) also observed a correlation between stand density and litter production, although the main

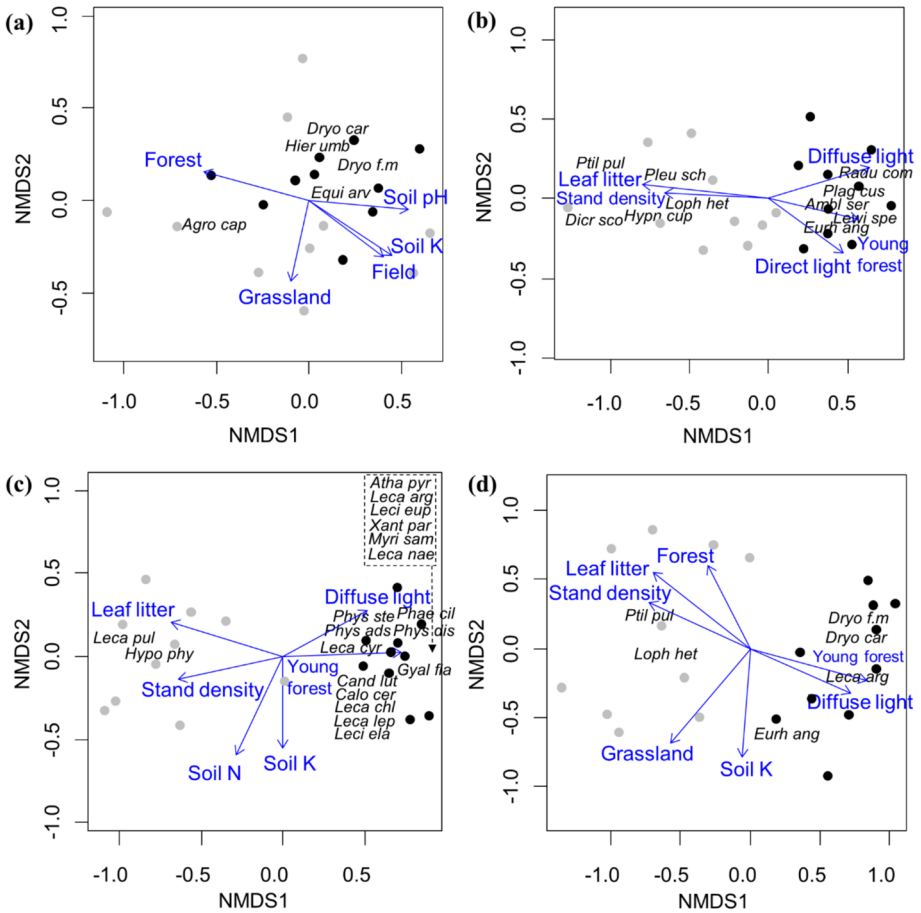


Fig. 4 NMDS ordination of herb (a, stress 0.19), bryophyte (b, stress 0.13), lichen (c, stress 0.08) and closed forest species (d, stress 0.11) assemblages in silver birch (grey dots) and hybrid aspen (black dots) plantations. Indicator species for both plantation types are shown on the plot and indicator species for silver birch are underlined. Abbreviations: *Agro car*—*Agrostis capillaris*, *Dryo car*—*Dryopteris carthusiana*, *Dryo f.m*—*Dryopteris filix-mas*, *Equi arv*—*Equisetum arvense*, *Hier umb*—*Hieracium umbellatum*, *Ambl ser*—*Amblystegium serpens*, *Dicr sco*—*Dicranum scoparium*, *Eurh ang*—*Eurhynchium angustirete*, *Hypn cup*—*Hypnum cupressiforme*, *Lewi spe*—*Lewinskya speciosa*, *Loph het*—*Lophocolea heterophylla*, *Plag cus*—*Plagiommium cuspidatum*, *Pleu sch*—*Pleurozium schreberi*, *Ptil pul*—*Ptilidium pulcherrimum*, *Radu com*—*Radula complanata*, *Atha pyr*—*Athallia pyracea*, *Calo cer*—*Caloptaca cerina*, *Cand lut*—*Candelariella lutella*, *Gyal fla*—*Gyalolechia flavorubescens*, *Hypo phy*—*Hypogymnia physodes*, *Leca pyr*—*Lecania cyrtella*, *Leca nae*—*Lecania naegelii*, *Leca arg*—*Lecanora argentata*, *Leca chl*—*Lecanora chlorotera*, *Leca lep*—*Lecanora leptyroides*, *Leca pul*—*Lecanora pulicaris*, *Leci ela*—*Lecidella elaeochroma*, *Leci eup*—*Lecidella euphoria*, *Myri sam*—*Myriolecis sambuci*, *Phae cil*—*Phaeophyscia ciliata*, *Phys ads*—*Physcia adscendens*, *Phys ste*—*Physcia stellaris*, *Phys dis*—*Physconia distorta*, *Xant par*—*Xanthoria parietina*

driver of litter production was stand age. In addition to stand density, light conditions are affected by stand structure. Martiník et al. (2024) compared the structure of silver birch and European aspen (*Populus tremula*) stands and concluded that although birch and aspen are both pioneer tree species, they exhibit different behaviour in monoculture

Table 5 Associations between different species groups (herbs, bryophytes, lichens, closed forest species) and environmental variables (NMDS ordination, Fig. 4)

Environmental variable	Herbs		Bryophytes		Lichens		Closed forest species	
	<i>R</i> ²	<i>p</i> -value	<i>R</i> ²	<i>p</i> -value	<i>R</i> ²	<i>p</i> -value	<i>R</i> ²	<i>p</i> -value
Tree species	0.06	0.305	0.56	0.001	0.80	0.001	0.57	0.001
Stand density	0.01	0.953	0.40	0.013	0.44	0.011	0.39	0.013
Basal area	<0.01	0.984	0.03	0.761	0.01	0.920	0.06	0.587
Direct radiation	0.04	0.717	0.31	0.045	0.19	0.167	0.19	0.152
Diffuse radiation	0.03	0.812	0.41	0.006	0.35	0.031	0.37	0.021
Leaf litter	0.02	0.860	0.59	0.001	0.53	0.002	0.47	0.003
Branch litter	0.16	0.240	0.20	0.158	0.13	0.326	0.19	0.166
Soil pH _{KCl}	0.52	0.003	0.19	0.176	0.24	0.082	0.17	0.204
Soil P	0.17	0.225	<0.01	0.970	0.08	0.485	0.06	0.620
Soil K	0.51	0.001	0.22	0.139	0.32	0.049	0.37	0.022
Soil N	0.13	0.313	0.06	0.589	0.45	0.005	0.17	0.210
Diversity of shrub layer	0.16	0.261	0.07	0.508	0.24	0.103	0.08	0.489
Area of forest around study plot	0.62	0.001	0.28	0.058	0.22	0.117	0.28	0.050
Area of young forest around study plot	0.20	0.147	0.31	0.042	0.54	0.003	0.45	0.004
Area of fields around study plot	0.45	0.006	0.02	0.831	0.22	0.103	0.06	0.599
Area of grasslands around study plot	0.36	0.032	0.06	0.567	0.04	0.709	0.47	0.004

Significant effects (*p* < 0.05) are presented in bold

stands as aspen grows faster and shows higher mortality than birch, indicating lower self-tolerance and higher self-thinning. The different crown architecture of birch and aspen may be another reason behind the differences in light conditions. For instance, Nelson et al. (2014) found that aspen species (*Populus tremuloides* and *P. grandidentata*) had considerably less leaf area per tree size unit than birch species (*Betula papyifera*, *B. populifolia*).

Based on PCA and NMDS, light conditions were associated with the richness of lichens and affected the composition of lichens, bryophytes, closed forest species and soil fungi. In general, low light availability limits lichen growth, whereas excessive light can cause photoinhibition and contribute to the dehydration of thalli (Green et al. 2008). Community level studies indicate that higher light availability favours higher lichen species richness (Fritz and Brunet 2009) and cover (Jüriado et al. 2009) in deciduous forests. Our results are in accordance with these findings as hybrid aspen plantations with lower stand density and a significantly higher amount of canopy-transmitted solar radiation hosted higher richness of lichens than plantations of silver birch with higher stand density and less light.

The richness of ground-dwelling bryophytes was higher in HAs, likely indicating the inhibitory effect of litter on ground-dwelling bryophytes described by several studies in deciduous stands (Márialigeti et al. 2009; Bartels and Chen 2013; Jean 2017; Ilić et al. 2023). Another factor that affects ground-dwelling bryophytes is light (Tinya et al. 2009). In our study the light indicator value of ground-dwelling bryophytes varied from four to eight (van Zuijlen et al. 2023), indicating a preference for moderate to

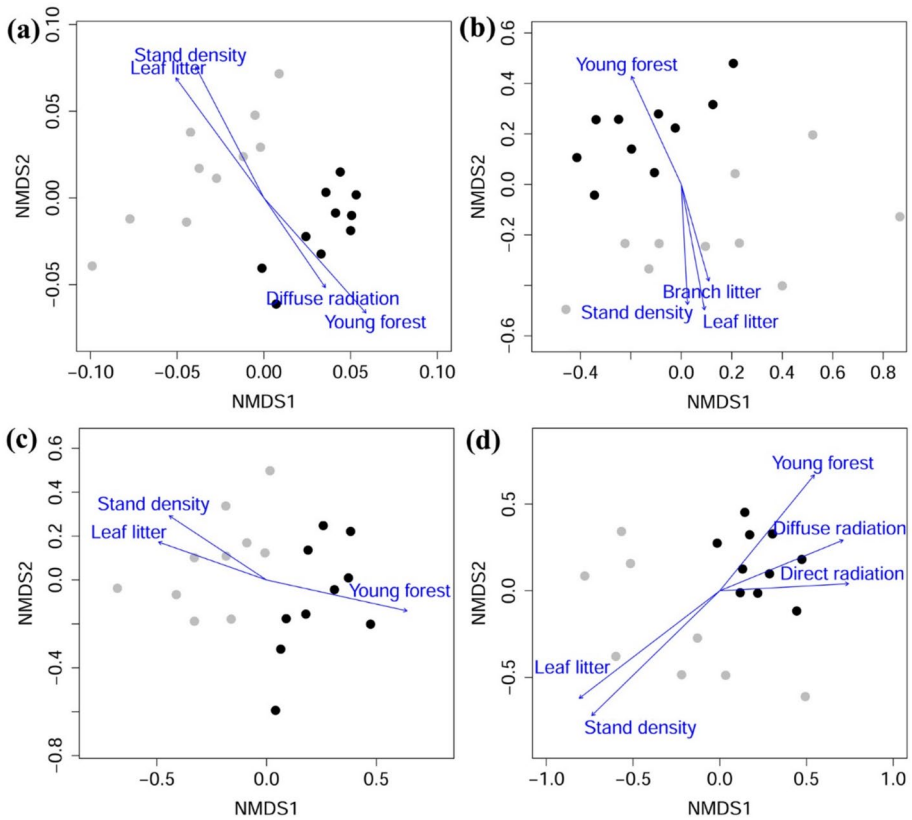


Fig. 5 NMDS ordination of all (a, stress 0.14), ectomycorrhizal (b, stress 0.19), saprotrophic (c, stress 0.19) and plant pathogenic fungal species (d, stress 0.18) assemblages in silver birch and hybrid aspen plantations. Birch plantations—grey dots, hybrid aspen plantations—black dots

high amounts of light. In addition, the bryophyte assemblages contained several light-loving species (e.g., *Brachythecium erythrorrhizon* and *Calliergonella cuspidata*) and the higher amount of light reaching the understory of HAs was likely beneficial to them.

The overall richness of closed forest species was similar in SBs and HAs, while the proportion of closed forest species formed only 11% of the recorded species. As the studied stands were younger than 25 years this result was not surprising. Numerous studies have concluded that the recovery of biodiversity typical to closed forests on former agricultural land is a long process that depends on many factors, including type and duration of previous agricultural activities, soil conditions, stand structure and landscape-related variables (Honnay et al. 2002; Hermy and Verheyen 2007; Bergès and Dupouey 2019). Based on our results, the richness of closed forest species increased in correlation with the area of older forests around the plantations that is in accordance with studies emphasizing the importance of proximity to old forests (Naaf and Kolk 2015; Brunet et al. 2021). Higher stand basal area was also positively correlated with the richness of ground-dwelling forest species. The identified association between stand characteristics and the number of forest species is in line with Brunet et al. (2011), who suggested that forest specialist species can be promoted by maintaining a shrub layer and canopy cover of 70–80%.

Table 6 Associations between different fungal species groups (all, ectomycorrhizal, saprotrophic, plant pathogenic) and environmental variables (NMDS ordination, Fig. 5)

Environmental variable	All fungi		Ectomycorrhiza		Saprotroph		Plant pathogen	
	R^2	p -value	R^2	p -value	R^2	p -value	R^2	p -value
Tree species	0.92	0.001	0.79	0.001	0.78	0.001	0.80	0.001
Stand density	0.59	0.001	0.48	0.006	0.31	0.046	0.71	0.001
Basal area	0.05	0.651	0.04	0.709	0.09	0.424	0.03	0.776
Direct radiation	0.16	0.213	0.11	0.345	0.05	0.663	0.37	0.038
Diffuse radiation	0.32	0.033	0.25	0.079	0.20	0.155	0.39	0.027
Leaf litter	0.60	0.002	0.54	0.001	0.30	0.047	0.69	0.001
Branch litter	0.13	0.293	0.33	0.034	0.09	0.468	0.18	0.233
Soil pH _{KCl}	0.00	0.963	0.03	0.838	0.00	0.967	0.03	0.781
Soil P	0.09	0.448	0.05	0.655	0.04	0.706	0.02	0.848
Soil K	0.16	0.236	0.10	0.391	0.12	0.334	0.06	0.650
Soil N	0.25	0.083	0.25	0.102	0.23	0.109	0.29	0.065
Diversity of shrub layer	0.03	0.812	0.01	0.891	0.12	0.362	0.00	0.989
Area of forest around study plot	0.23	0.120	0.15	0.228	0.27	0.068	0.13	0.367
Area of young forest around study plot	0.64	0.002	0.47	0.006	0.48	0.003	0.49	0.006
Area of fields around study plot	0.24	0.113	0.17	0.198	0.07	0.516	0.17	0.245
Area of grasslands around study plot	0.14	0.283	0.16	0.226	0.25	0.092	0.02	0.851

Significant effects ($p < 0.05$) are presented in bold

Although the overall richness of closed forest species was similar, we identified compositional differences in the assemblages of forest species between HAs and SBs. Furthermore, we found opposite responses of ground-dwelling and epiphytic forest species, as the richness of ground-dwelling species was higher in HAs and the richness of epiphytic species in SBs. This leads us to conclude that the impact of hybrid aspen and silver birch on the recovery of closed forest species is somewhat different and neither species is superior in this regard.

Regarding below-ground diversity we hypothesized that HAs and SBs do not exhibit large differences. However, this hypothesis was not confirmed as we found that the richness of all fungi, EcM, saprotrophic fungi and plant pathogens was considerably higher in HAs compared to SBs. Moreover, the compositional patterns of soil fungi in HAs and SBs showed distinct differences which were also confirmed by PERMANOVA. Based on NMDS, the fungal assemblages were affected by stand density, leaf litter, solar radiation, area of young forests around the study plots and tree species. Overall, the remarkable differences in fungal richness and community composition between HAs and SBs was rather unexpected. Contradicting our results, a study in Sweden describing wood-inhabiting fungi in the dead wood of aspen, birch, oak and spruce, found that species occurring on birch and aspen were highly similar, while aspen-oak similarity was approximately two times lower (Lindhe et al. 2004). One factor that might have affected our results was the usage of two different primers on birch and aspen soil samples. Therefore, the results regarding lower fungal richness in SBs should be considered with caution. Notably, the proportions of studied fungal groups in HAs and SBs were

similar with the exception of AM fungi, which were potentially underestimated in birch plantations due to the used primer.

The found positive correlation between the area of fields around the study plot and the richness of pathogenic fungi in HAs was expected, since these areas host different herbaceous pathogens that could spread to plantations, resulting in higher plant pathogen richness. The negative impact of surrounding older forest area on the richness of all fungi across the whole dataset (HAs and SBs) may be associated with the lower stand density of older forests. Liang et al. (2021) found that plant pathogen abundance around tree roots increases with higher stand density, while Yin et al. (2023) reported lower proportions of pathogenic fungi in higher density stands of *Tilia amurensis* and *Fraxinus mandshurica* seedlings. In contrast, the latter study showed that EcM proportions were higher in high-density conditions.

While higher amount of sun exposure had a positive impact on lichen species richness, it had a negative impact on total fungal richness in birch plantations in our study. Available light is known to have an effect on ectomycorrhizal fungi, which prefer lower light availability (Yin et al. 2023). Cogliati (2022) showed that ultraviolet radiation has a negative impact on yeast and mould fungi, leading to decreased growth. However, this study is not sufficient to generalize these results to major functional guilds of soil fungi. Overall, the impact of sun exposure on soil fungi has not been studied thoroughly, in contrast to spore dispersal (Langomarsino Oneto et al. 2020) and pathogens (Liu et al. 2017).

We found that the richness of all fungi and saprotrophs decreased with increasing soil N %. Previous studies have also found that an increase in mineral N is associated with a decline in saprotroph and EcM richness (Buée et al. 2011; Maaroufi et al. 2019). Furthermore, a study in beech forest found that EcM sporocarps almost ceased after N-addition (Rühling and Tyler 1991).

In terms of species composition, we found that all groups other than herbaceous vascular plants showed compositional differences between HAs and SBs. Instead of tree species, the composition of herbs responded to soil characteristics and landscape level variables, highlighting the importance of surrounding landscape as seed sources for the herb layer that is in accordance with the findings of Márialigeti et al. (2016). Baum et al. (2009) also showed that the herb layer of plantations reflects the characteristics of the surrounding landscape matrix.

Differences in species assemblages between SBs and HAs were especially pronounced for epiphytic communities. Species richness of lichens was nearly two times higher in aspen plantations than in silver birch plantations (Fig. 2d). The identity of phorophyte species is an important factor determining the richness and composition of epiphytic lichens due to the specific chemical and physical characteristics of the bark (Jüriado et al. 2009; Ellis 2012; Király et al. 2013) and the ability to form variable microhabitats (Wierzcholska et al. 2024). European aspen (*Populus tremula*) is frequently highlighted as a suitable substrate for a great number of epiphytic lichens, housing more host-tree-specific lichens than any other boreal tree species (Jüriado et al. 2003; Hedenås and Ericson 2004) if the phorophyte grows in late-successional forest stands (Ellis and Ellis 2013). Birch, on the contrary, is known to be a poor host for epiphytes due to low bark pH and poor physical trunk conditions (Coppins 1984; Thor et al. 2010). Our results in nearly rotation-age plantations also demonstrated that epiphytic lichen communities in hybrid aspen and silver birch stands differed considerably (having only 33% of species in common). Furthermore, indicator species analysis revealed two lichens characteristic of birch and 17 lichen species characteristic of aspen. Majority of the latter taxa were sexually reproducing crustose species which are considered early colonists (Ellis and Ellis 2013; Randle et al. 2017) preferring

subneutral bark reaction and tolerating moderate to strong eutrophication (Wirth 2010). *Hypogymnia physodes* and *Lecanora pulicaris*, the two species characteristic of birch, had different qualities, clearly preferring rather acid bark and weak to rather weak eutrophication (Wirth 2010).

We conclude that on the landscape scale plantations of both silver birch and hybrid aspen should be established for afforestation (and ecological restoration) of abandoned agricultural lands as they support different and ecologically complementary compositions of bryophytes, lichens, soil fungi and forest species. Further studies are needed to clarify the effect of short-rotation plantations on biodiversity and forest species after the first harvest and during later rotations when the presence of retention trees and coarse dead wood may be important factors that contribute to the biodiversity value of short-rotation broad-leaf plantations.

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Availability of data and materials The datasets generated and/or analysed during the current study are available from the corresponding author upon reasonable request.

Declarations

Competing interests The authors declare no competing interests.

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