



Mature hybrid aspen plantations on former agricultural land can enhance landscape connectivity for forest species

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ABSTRACT

Fast-growing hybrid aspen has been widely planted on former agricultural lands in Northern and Eastern Europe to produce pulpwood and sequester carbon into woody biomass. The biodiversity of mature hybrid aspen plantations has so far been rarely analysed. Moreover, the potential of hybrid aspen plantations to host flora typical of European aspen stands – recognised as biodiversity hotspots in Eurasian boreal forests – has not been evaluated. This study focused on two organism groups with contrasting habitat preferences – ground-dwelling herbs and epiphytic lichens. We sought to clarify how environmental and landscape factors influenced the diversity of herbs, lichens, and species characteristic of European aspen stands (EA species). Data were collected across 42 study plots within 20 hybrid aspen plantations in Estonia. Altogether, 162 herb species and 65 lichens were recorded, including 92 species also found in European aspen stands. The proportion of EA species was higher among lichens (86.2 %) than among herbs (22.2 %), reflecting a stronger legacy effect of former agricultural land-use on ground-dwelling species than on epiphytes. Responses of herb and lichen diversity to environmental variables differed. Richness of herbs was related to litter and stand characteristics. Compositional analyses also highlighted the role of soil-litter variables and stand structure in herb composition. Lichens responded to landscape-related variables. A greater extent of older forests around the study plots increased the richness of EA species. In conclusion, mature hybrid aspen plantations are relatively species-rich and can enhance landscape connectivity for forest species, particularly epiphytes, in agricultural landscapes.

1. Introduction

Plantation forests play an important role in global wood production (Mishra et al., 2021), contributing significantly to the supply of industrial roundwood (FAO, 2022). In 2020, the worldwide area of intensively managed plantation forests was 158 million ha (FAO, 2025). To meet the future demand for wood products, the area of plantations is expected to increase by 20–40 million ha by 2050 (FAO, 2022). While the importance of plantations in timber production is immense (McEwan et al., 2020), intensively managed plantation forests are less appreciated as habitats for forest flora (Brockerhoff et al., 2008), especially when plantations comprise exotic species (Stephens and Wagner, 2007; Bremer and Farley, 2010; Wang et al., 2021). Although the overall species richness of plantations may be quite high (Carnus et al., 2006;

Randrimananjara et al., 2025), they often host generalist and ruderal species and lack forest specialists (Archaux et al., 2010; Rédei et al., 2020). The low number of forest specialists in plantations may be related to land-use history, e.g., when trees are planted on former agricultural land, the formation of the forest understorey is hampered by the legacy effects of previous land use (Randrimananjara et al., 2023), expressed in altered soil conditions (Blondeel et al., 2019; Manpoong et al., 2025) and dispersal and recruitment limitations (Bergès and Dupouey, 2019). Other contributing factors may include competition from more vigorously growing, light-demanding species (Randrimananjara et al., 2025), and the uniform structure of plantations (Pedersen et al., 2025), as forest specialists benefit from the heterogeneous forest structure (Smyčková et al., 2024). Forest species in plantations are also affected by management practices (Spake et al., 2019) and plantation age (Wang et al.,

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2021). Thinnings promote light-demanding generalist species over specialist species (Haughian and Frego, 2016; Haughian, 2018), and the compositional similarity to natural forests increases when plantations mature (Tudge et al., 2023), with forest species becoming more abundant, especially in the proximity to old woodlands (Coote et al., 2013).

Hybrid aspen (*Populus tremula* L. × *P. tremuloides* Michx. = *P. × wettsteinii* Hämet-Ahti), an artificial cross between two phylogenetically close species (Cervera et al., 2005) – European aspen (*P. tremula*) and quaking aspen (*P. tremuloides*), has been extensively planted on former agricultural lands in Northern and Eastern Europe to produce pulpwood, logs, and energy wood in short rotations (Jansons et al., 2017; Hytönen, 2018; Fahlvik et al., 2021). At the age of 20–30 years, mature hybrid aspen plantations are clear-cut. After this, hybrid aspens regenerate vegetatively from stumps and root sprouts, and second-generation plantations can be managed either with very short rotations (< 5 years) or longer rotations (25 years) (Tullus et al., 2012; Hepner et al., 2021). As the initial planting density of hybrid aspen is quite low (1100–1600 trees ha⁻¹) and thinning practices are usually carried out in midterm plantations (Tullus et al., 2012), the amount of understorey reaching sunlight is high even in mature (age > 20 years) first-generation plantations (Tullus et al., 2025). Therefore, it may be expected that light-demanding herbs persist in the understorey of mature hybrid aspen plantations, and a tendency observed in the herb layer of young and mid-term plantations, where species typical to open communities prevailed and the proportion of forest species was low, continues (Weih et al., 2003; Soo et al., 2009; Tullus et al., 2015). Regarding epiphytic biodiversity, a study compiled in 16–17-year-old hybrid aspen plantations (Randlane et al., 2017) concluded that depending on the landscape structure, hybrid aspen trees may host a significant number of lichen-forming fungi consisting mainly of light-preferring sexually reproducing crustose species. At the same time, the diversity of herbs and lichens in plantations is associated with various environmental factors. In addition to light conditions and landscape structure, soil and litter conditions, stand attributes, and microhabitat availability also play an important role in shaping herb and lichen communities (Coote et al., 2008; Berg et al., 2013; Norden et al., 2021; Tullus et al., 2022a; Randriamananjara et al., 2023; Corli et al., 2025). However, herbs are mainly ground-dwelling, while lichens inhabiting the ground are out-competed by more vigorously growing vascular plants and bryophytes; for that reason, they can be found mainly on trunks and branches of trees in plantations (Randriamananjara et al., 2023; Randlane et al., 2017). Therefore, the diversity of herbs and lichens in plantations may be related to different environmental factors.

So far, biodiversity studies in mature first-generation hybrid aspen plantations have been scarce (Tullus et al., 2025), and no study has evaluated whether these plantations offer habitat for herb and lichen species characteristic of European aspen forests. In general, European aspen stands are considered biodiversity hotspots in Eurasian boreal forests, harbouring a high number of understorey and epiphytic species, including numerous aspen-associated species (Kivinen et al., 2020; Rogers et al., 2020). If hybrid aspen plantations provide habitat for the flora typical of European aspen stands, they could enhance landscape connectivity between forest patches and thereby foster aspen-associated biodiversity. Although the role of tree plantations in harbouring native forest flora has been repeatedly evaluated before (e.g., Coote et al., 2012; Calviño-Cancela et al., 2013), these studies have not included hybrid aspen plantations, with the exception of one study on soil fungi (Rähn et al., 2024).

This study focused on ground-dwelling herbs and epiphytic lichens in mature hybrid aspen plantations on former agricultural land, being the first to analyse such plantations in terms of fostering aspen-associated biodiversity and enhancing landscape connectivity. We aimed to 1. identify the main environmental and landscape factors that affect the diversity of herbs and lichens in mature plantations, and 2. evaluate the potential of hybrid aspen plantations to host species typical of European aspen stands. We hypothesised firstly that the responses of ground-

dwelling herbs and epiphytic lichens to environmental variables were somewhat different, i.e., the diversity of herbs was related to soil and litter conditions while the diversity of lichens was associated with the surrounding landscape, and both organism groups responded to stand structural attributes. Secondly, we expected to see that the diversity of species characteristic of European aspen stands was higher in plantations that were located in the proximity of existing older forest patches. We also hypothesised that lichen communities in hybrid aspen plantations hosted more species characteristic of European aspen stands than herb communities because understorey communities bear a strong imprint of agricultural land use, which is less evident in epiphytic communities.

2. Materials and methods

2.1. Study area

The study area comprised 20 hybrid aspen plantations, established in 1999 and 2000 with one-year-old micropropagated plants on former agricultural land in the continental part of Estonia (Fig. 1). The size of plantations varied from 1 to 34 ha. Study sites, each 0.1 ha in size, were established in each plantation between 2003 and 2004 to monitor tree growth and assess the effects of short-rotation forestry on soil properties (Tullus et al., 2007). As microrelief and soil types vary within larger plantations, sometimes divided into scattered parts by small roads, 2 to 5 study sites were established within larger plantations. In total, 42 study sites in mature (age 22–26 years) hybrid aspen plantations were monitored for the current study.

2.2. Data collection

A 10 × 10 m study plot was established in the centre of each study site. Data on woody and herbaceous vascular plants and epiphytic lichens from tree trunks up to 2 m from the ground were collected on these plots ($n = 42$). The lists of vascular plants and lichens were compiled for every plot, and the abundance of each species was visually estimated, following a scale of 1–5 (1 – 1–5 % cover, 2 – 6–20 % cover, 3 – 21–50 % cover, 4 – 51–75 % cover, 5 – 76–100 % cover). For species covering less than 1 %, an estimate of 0.5 was applied. Vascular plant inventories were conducted in the middle of the vegetation period from 2021 to 2023, while lichen inventories were carried out in autumn and spring from 2021 to 2024. Vascular plant nomenclature follows Leht (2010), and lichen nomenclature follows Randlane et al. (2024b). Species categorised as near-threatened, vulnerable, and endangered according to the IUCN Red List of Estonia (Kull et al., 2018; Randlane et al., 2024a), protected species (Decree of the Estonian Government no. 195, 2004; Decree of the Estonian Minister of Environment no. 51, 2004), and indicator species of woodland key habitats (Decree of the Estonian Minister of Environment no. 36, 2017) were considered conservationally valuable in the study.

Soil samples were collected from a depth of 0–10 cm and from eight different locations at each study plot. The samples were analysed at the Centre of Estonian Rural Research and Knowledge for pH_{KCl} from a 1 M KCl suspension, available potassium (K, mg kg⁻¹), and phosphorus (P, mg kg⁻¹) using the Mehlich III method. Total nitrogen (N, %, Kjeldahl method) of soil samples was determined at the Laboratory of the Department of Soil Sciences and Agrochemistry of the Estonian University of Life Sciences. Litter samples (including leaves and branches) were collected by hand from the same locations as soil samples, using a 20 × 20 cm metal frame, dried at 70 °C to constant weight, weighed, and converted to the hectare scale (t ha⁻¹). Hemispherical photos were taken from four different locations 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 6D Mark II digital camera. Canopy-transmitted solar radiation (mol m⁻² d⁻¹) was analysed from the hemispherical photos using Gap Light Analyzer 2.0 (Frazer et al., 1999). The growing season was

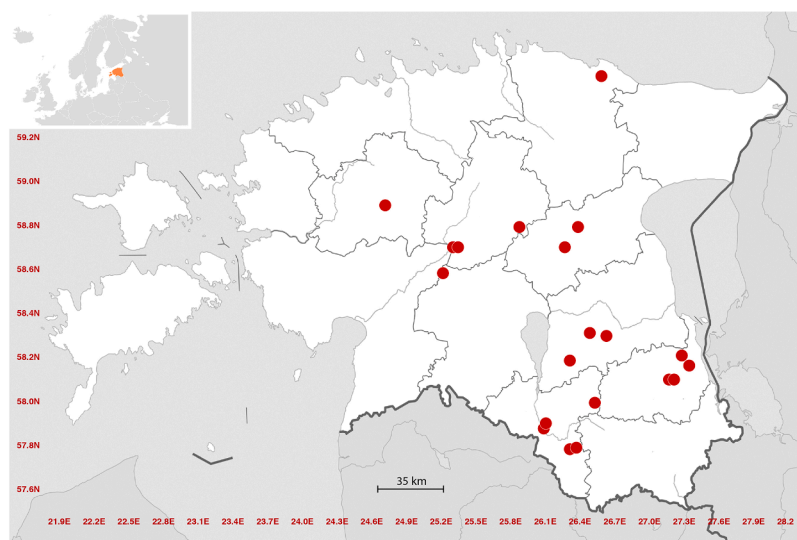


Fig. 1. Locations of hybrid aspen plantations.

defined from April 22 to October 28, based on the long-term monitoring (Kollo et al., 2023). Soil, litter, and light condition data were collected simultaneously with the vascular plant inventories. Averaged values of soil and litter samples and hemispherical photos were used for further data analysis.

Tree layer characteristics (number of trees, stem diameter at breast height) were measured on a 0.1 ha plot surrounding the 100 m² study plot in each plantation in 2021. Basal area of hybrid aspen (m² ha⁻¹) was estimated as the sum of the basal areas of individual trees growing on a 0.1 ha plot multiplied by 10. If other tree species besides hybrid aspen (birch, spruce, alder, pine, lime, willow with diameter ≥ 5 cm) were present on a plot, the basal area of other tree species (m² ha⁻¹) was calculated as well.

To characterise the surrounding landscape around study plots, orthophotos and spatial data from the Geoport of the Land Board and the National Forest Register were used. The percentage of area covered by fields, grasslands, and forests was estimated within a radius of 300 m around each study plot following Márialigeti et al. (2016). A similar spatial scale has been found to be appropriate when analysing plant diversity in heterogeneous landscapes (Kumar et al., 2006; Liccari et al., 2022). Fields and grasslands were combined into the category „agricultural land-use“. Forests were categorised based on stand age into two groups: young forests (age ≤ 20 years) and older forests (age > 20 years).

2.3. Data analysis

To determine the herb species characteristic of European aspen stands, a species list of herbaceous vascular plants from hybrid aspen plantations was compared to a species list from a study compiled in 20 European aspen stands in southeastern Estonia, following similar inventory methods as the current study (Tullus et al., 2022b). Additionally, the list of European forest species (Heineken et al., 2022) was checked, and if a hybrid aspen plantation hosted a forest specialist species restricted to closed forests, it was also marked. To determine lichen species characteristic of European aspen stands, the following publications were used: Tullus et al. (2022b) and Jüriado et al. (2003). If a species found in hybrid aspen plantations was not listed in these publications, lichen samples from the PlutoF database (plutof.ut.ee) were checked, and species recorded on European aspen were determined. The schematic overview of species classification is presented in Supplementary Fig. S1.

All statistical analyses were carried out with R version 4.5.1 (R Core

Team, 2025). To describe the diversity of woody species, herbs, lichens, and species typical of European aspen stands on study plots, Shannon diversity indices were calculated based on the abundance data using the „vegan“ package. As the majority of woody species grew in the shrub layer of the studied plantations, „the diversity of woody species“ is henceforth referred to as „the diversity of shrub layer“ and is used as a variable characterising stand structure in further data analysis.

The impact of environmental variables (amount of litter, soil pH, soil P, soil K, soil N, canopy transmitted solar radiation, basal area of hybrid aspen, basal area of other tree species, diversity of the shrub layer, area of agricultural land-use, and young and older forests) on the species richness and diversity of herbs, lichens, and aspen-associated species was evaluated with linear mixed models (LMM, function „lmer“). Plantation was added as a random factor in LMMs due to the hierarchical sampling design (2 to 5 study plots were monitored within larger plantations). The final models were created using backward stepwise model selection. The significance of the final LMMs was evaluated based on comparison with intercept-only models using the chi-square test. Possible multicollinearity among the predictor variables was checked based on the variance inflation factor (VIF). Estimates of species richness were square-root transformed, and values of litter, soil pH, soil P, soil K, soil N, canopy transmitted solar radiation, basal area of hybrid aspen, and basal area of other tree species were log-transformed before statistical analyses to meet the assumption of normality.

To analyse patterns in herb and lichen assemblages, Nonmetric Multidimensional Scaling (NMDS) was performed with the function „metaMDS“ from package „vegan“ using Bray-Curtis dissimilarity. Environmental variables were fitted onto ordination graphs using the function „envfit“.

To partition the variation in herb and lichen communities by environmental variables, the „varpart“ function in „vegan“ was applied, and redundancy analysis ordination was carried out. Three different explanatory matrices were used to describe the variation in the response table: 1. soil-litter matrix containing values of litter, soil pH, P, K, and N, 2. matrix consisting of stand structure variables (basal area of hybrid aspen, basal area of other tree species, diversity of the shrub layer, and canopy transmitted solar radiation), and 3. landscape-related matrix (including the percentage area of agricultural land-use and young and older forests around study plots and the geographic location of study plots expressed in X and Y coordinates).

3. Results

3.1. Environmental variables

Although the age of the tree layer was similar among hybrid aspen plantations, environmental variables varied considerably between study plots (Table 1). The median value for litter was 2.9 t/ha, while the maximum value of litter was four times higher. Soil pH ranged from strongly acidic (4.1) to alkaline (7.3) according to the Estonian pH_{KCl} scale for soils (Astover et al., 2012), and the amount of soil available phosphorus differed more than 30 times between study plots. Variables characterising stand structure (basal area of hybrid aspens, basal area of other tree species, canopy transmitted solar radiation, diversity of the shrub layer) and landscape structure (area of agricultural land-use and forests around study plots) also varied substantially (Table 1).

3.2. Species richness and diversity

3.2.1. Herbaceous species

Altogether, 162 herbaceous vascular plant species were recorded at 42 study plots (Supplementary Table S1). In addition, specimens from 12 genera were recorded at the genus level due to juvenility or vegetative state. The most frequent herb species in hybrid aspen plantations were *Dactylis glomerata* (present at 92.9 % of plots) and *Elymus repens* (88.1 %).

A total of 22.2 % of herbaceous species recorded in hybrid aspen plantations have also been found in European aspen stands, e.g. *Veronica chamaedrys* (present at 83.3 % of study plots in hybrid aspen plantations), *Dryopteris carthusiana* (57.1 %) and *Aegopodium podagraria* (52.4 %). Concerning conservationally valuable herb species, protected orchids (specimens of either genus *Dactylorhiza*, *Epipactis*, *Orchis*, or *Platanthera*) were recorded at 16 study plots, and *Gentiana cruciata* (an endangered species on the Red List) was found at one study plot. Out of these species, *Platanthera chlorantha* also grows in European aspen

Table 1
Characterisation of environmental variables at study plots ($n = 42$).

Environmental variable	Mean	Median	Minimum	Maximum	Std. dev.	Var. coef., %
Leaf and branch litter (t ha ⁻¹)	3.9	2.9	0.7	12.6	2.6	66.6
soil pH _{KCl}	5.6	5.5	4.1	7.3	0.9	15.2
soil P (mg kg ⁻¹)	96.7	77.0	7.3	254.0	63.3	65.5
soil K (mg kg ⁻¹)	148.4	131.5	66.5	534.2	77.6	52.3
soil N (%)	0.2	0.1	0.1	0.5	0.1	49.3
Basal area of hybrid aspen (m ² ha ⁻¹)	17.8	17.7	7.0	32.1	6.7	37.7
Basal area of other tree species (m ² ha ⁻¹)	0.7	0	0	7.1	1.5	205.8
Canopy transmitted total radiation (mol m ⁻² d ⁻¹)	7.6	7.2	2.9	16.5	3.3	43.6
Diversity of shrub layer	1.5	1.6	0	2.6	0.7	46.6
Area of agricultural land-use around study plot (%)	26.2	25.4	2.9	52.8	14.8	56.6
Area of young forests around study plot (%)	10.6	6.8	0	30.1	9.8	91.8
Area of older forests around study plot (%)	19.2	14.9	0	46.5	15.5	80.9

stands.

The species richness of herbs per study plot varied between 14 and 51 species, with an average of 29 species. Species richness and diversity of herbs responded to the diversity of the shrub layer (a positive correlation, see Table 2), as well as to the amount of litter and the basal area of hybrid aspen (both negative correlations).

3.2.2. Lichens

Altogether, 65 species of lichenised fungi were found at 42 study plots (Supplementary Table S1). Out of these species, 86.2 % of lichens have also been recorded as epiphytes on European aspen. The most frequent lichens at the study plots included *Physcia adscendens* (present at 100 % of study plots), *Xanthoria parietina* (100 %), *Lecania naegelii* (97.6 %), *Gyalolechia flavorubescens* (95.2 %), *Lecanora chlorotera* (95.2 %) and *Lecidella euphorea* (95.2 %), all of which also grow on European aspen. Conservationally valuable lichens were present at 34 study plots, namely *Acrocordia cavata* (recorded at 1 plot), *Arthonia apatetica* (4), *Melanelixia glabrata* (3), *Normandina agroglypta* (1), *Phaeophyscia ciliata* (31), and *Pseudosagedia aenea* (2). Of these, one lichen species, *Acrocordia cavata*, is an indicator of woodland key habitat, while the others represent near-threatened or vulnerable taxa in the national Red List. With the exception of *Pseudosagedia aenea*, the other five species have also been found on European aspen.

The species richness of lichens per study plot varied between 14 and 37 species, with an average value of 26 species. Lichen richness correlated positively with the area of older forests around study plots (see Table 2). A similar trend was observed also for the diversity index of lichens; however, this relationship was insignificant ($p = 0.058$).

3.2.3. Shared species of hybrid aspen plantations and European aspen stands

Altogether 92 species (56 lichens and 36 herbs) that grow in European aspen stands (EA species) were also found in hybrid aspen plantations (Supplementary Table S1, Supplementary Fig. S1). The richness and diversity of EA species were associated with the area of forests around the study plots (a positive effect was observed for the area of older forests and a negative effect for the area of young forests, Table 2).

3.3. Environmental variables shaping species composition

According to NMDS ordination, the main gradients shaping herb communities were canopy transmitted total radiation, diversity of shrub layer, amount of litter, and soil properties (Table 3, Fig. 2). On the ordination scheme, the vector indicating an increase in light pointed towards light-demanding grassland species (e.g., *Alopecurus pratensis*, *Deschampsia cespitosa*, and *Phalaris arundinacea*), while species typical of closed-canopy forests (e.g., *Athyrium filix-femina*, *Dryopteris filix-mas*, *Dryopteris carthusiana*, and *Pyrola minor*) were found on the opposite side of the ordination graph. The location of the study plot also affected the composition of herbs as in some cases study plots from the same plantation were situated in close proximity in the ordination space (e.g., study plots from Mooste, Maltsi, and Sikka plantations, Fig. 2b). A similar tendency was also observed for lichens, which responded to the location of the study plot as well as landscape variables such as the area of agricultural land-use and area of young forests around the study plots (Fig. 2c-d).

Variation partitioning also revealed the importance of landscape structure for lichens. Altogether, landscape, soil-litter, and stand variables explained approximately 20 % of the variation in lichen communities (Fig. 3b). Landscape variables explained 13.7 %, soil-litter variables 6.1 %, and their shared contribution accounted for 3.4 %. The unique contribution of stand-related variables remained less than 0. Meanwhile, soil-litter, stand, and landscape variables described 15 % of the total variation in herb communities (Fig. 3a). The unique contribution of soil-litter variables explained 4.5 % of the variation, followed by stand variables (3.0 %) and landscape variables (< 1 %). The

Table 2

The effects (standardised regression coefficients based on LMMs) of environmental variables on the richness (S) and diversity (H) of herbs, lichens, and species typical of European aspen stands (final models after backward selection of independent variables).

Environmental variable	S_herbs	H_herbs	S_lichens	H_lichens	S_aspen species	H_aspen species
Litter	-0.46**	-0.42**				
Basal area of hybrid aspen	-0.32*	-0.32*				
Diversity of shrub layer	0.69***	0.66***				
Young forests					-0.35*	-0.32*
Older forests			0.36*		0.45**	0.38*
Model significance	***	***	*	ns	**	*
Max VIF	1.3	1.3	-	-	1.0	1.0

ns - $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Table 3

Correlations between environmental variables and ordination scores of herbs and lichens (NMDS ordination, Fig. 2). P-values in bold are significant.

Environmental variable	Herbs		Lichens	
	r ²	p-value	r ²	p-value
Leaf and branch litter	0.16	0.036	0.06	0.273
soil pH _{KCl}	0.23	0.008	0.01	0.848
soil P content	0.15	0.043	0.09	0.173
soil K content	0.29	0.003	0.08	0.211
soil N content	0.53	0.001	0.06	0.289
Basal area of hybrid aspen	0.12	0.080	0.01	0.878
Basal area of other tree species	0.04	0.449	<0.01	0.963
Canopy transmitted total radiation	0.30	0.001	<0.01	0.927
Diversity of shrub layer	0.23	0.011	<0.01	0.940
Area of young forests around study plot	0.01	0.837	0.38	0.001
Area of older forests around study plot	0.06	0.285	0.12	0.068
Area of agricultural land-use around study plot	0.04	0.410	0.16	0.026
Location of study plot	0.77	0.001	0.71	0.001

remaining portion was explained by combinations of different components, for example, the shared fraction of soil-litter and landscape variables accounted for 5.8 %. A relatively high proportion of the variation remained unexplained for the herb (84.9 %) and lichen (79.3 %) communities.

4. Discussion

The present study reports, for the first time, the results of extensive biodiversity monitoring in mature hybrid aspen plantations in the hemiboreal region. Our results showed that herb and lichen communities of mature hybrid aspen plantations were relatively diverse, as we recorded a total of 162 herb species and 65 lichenised fungi species at 42 study plots (averaging 29 herbs and 26 lichens per plot). As herbs and lichens typically inhabit different growth substrates (ground vs. trees) in plantations, we hypothesised that their diversity responses to environmental variables may differ, and the results supported this expectation. Species richness and diversity of herbs in hybrid aspen plantations responded to the amount of litter on the ground and to stand characteristics (diversity of shrub layer and basal area of hybrid aspens), while the species richness of lichens was influenced by the area of older forests in the vicinity of study plots (Table 2). The positive effect of a diverse shrub layer on herb species richness has been observed previously (Bartels and Chen, 2013; Kermavnar et al., 2021), explained by tolerance or facilitation between shrub and herb layer species (Bartels and Chen, 2013), as well as by the structural heterogeneity created by shrubs (Koorem and Moora, 2010). This heterogeneity provides habitats for herb species with varying ecological requirements and supports diverse ecological niches (Tripathi et al., 2026). Additionally, we observed a negative effect of higher basal area on the understory vegetation diversity, as noted by Ampoorter et al. (2020). We also found a negative effect of litter on herb diversity, consistent with the findings of Wulf and Naaf (2009) in beech forests. In general, the effects of litter on herbs can

vary significantly depending on litter type, litter quantity (Xiong and Nilsson, 1999), and the rate of litter decomposition which is influenced by environmental and climatic conditions (Singh et al., 2025).

Contrary to our hypothesis, we did not observe the effect of soil properties on herb richness; however soil pH, P, K, and N influenced the compositional patterns of the herb layer, consistent with earlier studies (Härdtle et al., 2005; Wulf and Naaf, 2009; Kermavnar et al., 2021; Zarfos et al., 2019). In addition to soil properties, herb layer composition was influenced by the shrub layer and light conditions. This result was expected, as light availability is a significant determinant of herb species composition in forests (Márialigeti et al., 2016; Tinya and Ódor, 2016). The importance of soil-litter variables and stand structural attributes to the herb layer was also confirmed by variance partitioning analysis.

The only environmental variables that affected either the species richness or species composition of lichen communities were landscape-related variables and the location of study plots (Tables 2 and 3). In earlier studies, the impact of various tree-related variables such as phorophyte species, bark pH (Jüriado and Paal, 2019), bark structure (Ellis, 2012), and tree age (Jüriado et al., 2009; Tullus et al., 2022b) has been observed on epiphytic lichen communities. In our study, individual tree-related factors were not recorded, while the effect of attributes characterising stand structure (basal area of hybrid aspen and canopy transmitted total radiation) on lichen communities was not found. It can be speculated that the stand level attributes in mature plantations were also affected by thinning practices between midterm and mature age, and therefore, their effect on lichen diversity was not expressed. The positive effect of a larger area of older forests (here: age > 20 years) in the vicinity of study sites on the lichen species richness is reasonable, as nearby forests evidently act as a pool of lichen propagules. Low connectivity among fragmented forest stands is proposed as an essential limiting factor for cryptogamic epiphytes (Snäll et al., 2005).

Of the 227 species recorded in hybrid aspen plantations, 92 have also been found in European aspen stands. Lichens showed a much higher proportion of these species (86.2 %) compared to herbs (22.2 %), confirming our hypothesis that lichen communities in hybrid aspen plantations host more species characteristic of European aspen stands than herb communities. The hybrid aspen plantations in this study were established in 1999 or 2000 on agricultural sites that had been abandoned during the 1990s, using either whole-area plowing or strip-tillage for site preparation. Therefore, the colonisation period for forest species has spanned approximately 20–25 years, which is evidently too short a period for the recovery of the herb layer typical of natural forests on previous agricultural land (Naaf and Kolk, 2015; Berges and Dupouey, 2019; Brunet et al., 2021). Another factor influencing the recovery of forest species is thinning. It has been carried out in the majority of hybrid aspen plantations and tends to favor light-demanding ruderals or generalists over less competitive forest specialists (Haughian and Frego, 2016). The colonisation of epiphytic lichens in plantations, however, is not hindered by competitive species persisting from former agricultural land use. Dispersal and local establishment of lichens are generally limited by their symbiotic nature and depend on their reproduction strategy (Tripp et al., 2016; Trindade et al., 2021), as sexual species usually disperse over longer distances but depend on the availability of a

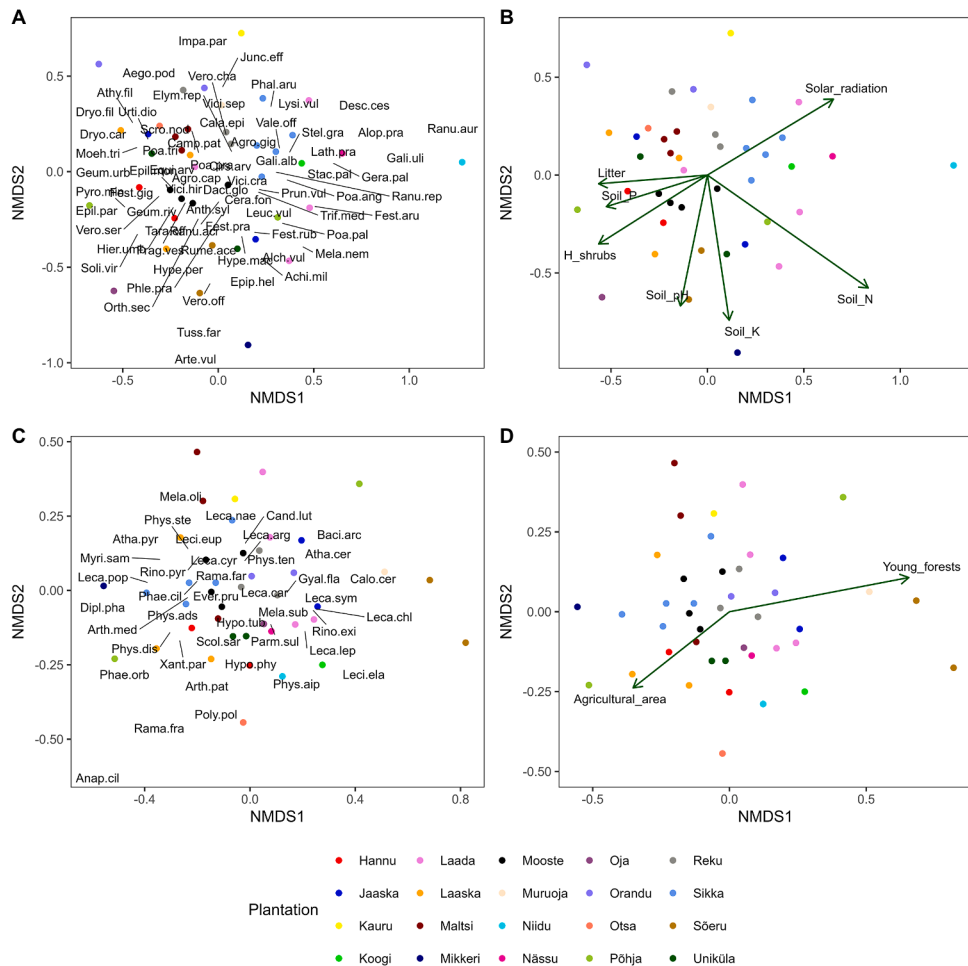


Fig. 2. NMDS ordination of herbs (A-B, stress 0.239) and lichens (C-D, stress, 0.211). Only species present in at least 10 % of the study plots are shown on graphs. Environmental variables that significantly ($p < 0.05$, Table 3) affect ordination scores are shown as vectors. Dots mark study plots and colours mark different plantations. Abbreviations of species names are presented in Supplementary Table S1.

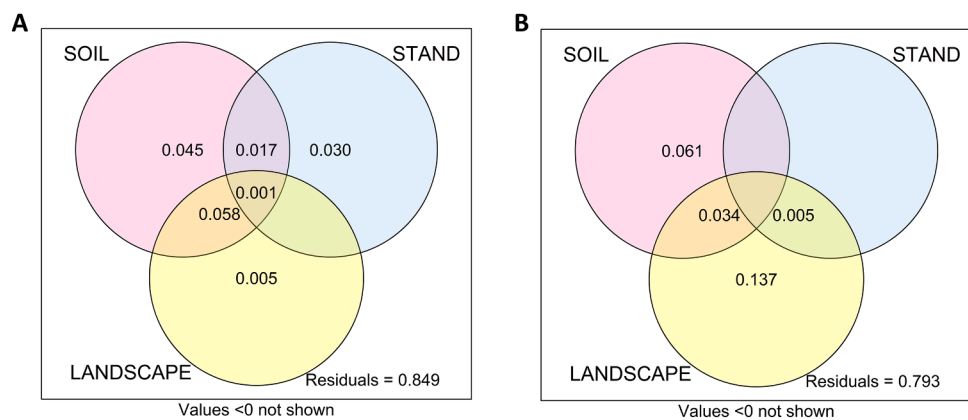


Fig. 3. Variation partitioning of herb (A) and lichen (B) communities based on three explanatory matrices: 1. soil-litter matrix (containing values of litter, soil pH, P, K, and N), 2. stand structure matrix (basal area of hybrid aspen, basal area of other tree species, diversity of shrub layer, and canopy transmitted solar radiation), and 3. landscape matrix (the percentage area of agricultural land-use and young and older forests around study plots and the geographic location of study plots). Values (adjusted R^2) represent unique and shared fractions of matrices in explained variance, residual variation is also presented.

suitable photobiont at the settled location to establish, whereas asexual species have usually heavier diaspores dispersing closer while they do not depend on such association (Yahr et al., 2006; Belinchón et al., 2015). The proportion of sexual lichen species has grown in mature hybrid aspen plantations (73.8 %; Supplementary Table S1) compared to

the mid-term plantations (56.8 %; Randlane et al., 2017), indicating that the lichen species richness is related to the presence of suitable lichen habitats in the surrounding areas of plantations, and that a longer period contributes to the establishment of a greater number of species. The richness and diversity of forest species increased along with the extent of

older forests near plantations. This finding aligns with previous research emphasising the importance of propagule sources and connectivity in restoring forest vegetation (De Frenne et al., 2011; Kolk et al., 2017; Brunet et al., 2021).

Only seven epiphytic lichen species found in hybrid aspen plantations have not been recorded on European aspen in Estonia so far (Supplementary Table S1). These species occurred in studied plantations rarely (in 1–4 study plots), with the only exception of *Scoliciosporum sarothamni* (recorded in 19 plots). The taxon is a sterile microlichen that may have been unrecorded in earlier studies.

We recorded conservationally valuable herbs, mainly orchids, on 38 % of the studied plots and conservationally valuable lichens on 81 % of the plots. Several earlier publications have reported occasional, and sometimes frequent, occurrences of orchids in hybrid aspen and poplar plantations (Adamowski and Conti, 1991; Tullus et al., 2015; Süveges et al., 2022). The high percentage of study plots with conservationally valuable lichens is due to the frequent occurrence of one lichen species, *Phaeophyscia ciliata*, which belongs to the alliance *Xanthorion parietinae* and exclusively inhabits aspen bark in hemiboreal forests. The species was not recorded in midterm hybrid aspen plantations (16- to 17-year-old) (Randlane et al., 2017); it has been categorised as being sensitive to the even-aged forest management (Löhmus and Löhmus, 2019), mainly recorded in older stands (Tullus et al., 2022b), and evaluated as near-threatened species in Estonia (Randlane et al., 2024a). Its occurrence in 31 study plots of mature (22- to 26-year-old) hybrid aspen plantations was surprising. Other lichens considered conservationally valuable were recorded infrequently, altogether in eleven study plots.

To conclude, mature hybrid aspen plantations are relatively species-rich and support taxa characteristic of European aspen stands, including conservationally valuable species, thereby enhancing connectivity and providing stepping-stones for forest species in agricultural landscapes. However, in the next few years, the planned clear-cutting of plantations is expected to strongly affect the observed biodiversity patterns. To preserve habitats for epiphytic lichens after clear-cutting, it is advisable to leave some mature trees for retention. In this case, the planted stands may act not only as sink habitats that the species can colonise and where they can survive until felling, but also as surviving points after cutting the majority of trees and from where the species can disperse further from the plantation area (Randlane et al., 2017). Lastly, although hybrid aspen plantations can enhance connectivity for forest species, they should be regarded as complementary, not as substitutes for the conservation of natural European aspen stands.

CRedit authorship contribution statement

Tea Tullus: Writing – review & editing, Writing – original draft, Validation, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Tiina Randlane:** Writing – review & editing, Writing – original draft, Data curation. **Andres Saag:** Writing – review & editing, Visualization, Data curation. **Reimo Lutter:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Arvo Tullus:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Conceptualization. **Mari-Liis Siller:** Writing – review & editing, Data curation. **Reeno Sopp:** Writing – review & editing, Data curation. **Kristjan Täll:** Writing – review & editing, Data curation. **Natalia Vysotska:** Writing – review & editing, Data curation. **Marju Kaivapalu-Kaasik:** Writing – review & editing, Data curation. **Katri Ots:** Writing – review & editing, Data curation. **Hardi Tullus:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.tfp.2026.101161.

Data availability

<https://doi.org/10.5281/zenodo.18095766> (Primary dataset is available at)

References

- Adamowski, W., Conti, F., 1991. Masowe występowanie storczyków na plantacjach topolowych pod czeremcha jako przykład apofityzmu. *Phytocoenosis* 3, 259–268. Polish with English summary.
- Ampoorter, E., Barbaro, L., Jactel, H., Baeten, L., Boberg, J., Carnol, M., Castagnyrol, B., Charbonnier, Y., Dawud, S.M., Deconchat, M., De Smedt, P., De Wandeler, H., Guyot, V., Hättenschwiler, S., Joly, F.-X., Koricheva, J., Milligan, H., Muys, B., Nguyen, D., Ratcliffe, S., Raulund-Rasmussen, K., Scherer-Lorenzen, M., van der Plas, F., Van Keer, J., Verheyen, K., Vesterdal, L., Allan, E., 2020. Tree diversity is key for promoting the diversity and abundance of forest-associated taxa in Europe. *Oikos* 129, 133–146.
- Archaux, F., Chevalier, R., Berthelot, A., 2010. Towards practices favourable to plant diversity in hybrid poplar plantations. *For. Ecol. Manag.* 259 (12), 2410–2417.
- Astover, A., Kölli, R., Roostalu, H., Reintam, E., Leedu, E., 2012. Mulliteadus. *Õpik kõrgkoolidele* (Soil science. Textbook for universities). Tartu. Estonian.
- Bartels, S.F., Chen, H.Y.H., 2013. Interactions between overstorey and understorey vegetation along an overstorey compositional gradient. *J. Veg. Sci.* 24, 543–552. <https://doi.org/10.1111/j.1654-1103.2012.01479.x>.
- Belinchón, R., Yahr, R., Ellis, C.J., 2015. Interactions among species with contrasting dispersal modes explain distributions for epiphytic lichens. *Ecography* 38, 762–768. <https://doi.org/10.1111/ecog.01258>.
- Berg, K., Hunt, S.L., Gordon, A.M., 2013. Epiphytic lichens in jack pine and black spruce plantations in northern Ontario, Canada: diversity and community patterns. *Bryologist* 116 (1), 65–77. <https://doi.org/10.1639/0007-2745-116.1.065>.
- Bergès, L., Dupouey, J.-L., 2019. Historical ecology and ancient forests: progress, conservation issues and scientific prospects, with some examples from the French case. *J. Ecol.* 32, e12846. <https://doi.org/10.1111/jvs.12846>.
- Blondeel, H., Perring, M.P., Bergès, L., Brunet, J., Decocq, G., Depauw, L., Diekmann, M., Landuyt, D., Liira, J., Maes, S.L., Vanhellemont, M., Wulf, M., Verheyen, K., 2019. Context-dependency of agricultural legacies in temperate forest soils. *Ecosystems* 22, 781–795. <https://doi.org/10.1007/s10021-018-0302-9>.
- Bremer, L.L., Farley, K.A., 2010. Does plantation forestry restore biodiversity or create green deserts? A synthesis of the effects of land-use transitions on plant species richness. *Biodivers. Conserv.* 19, 3893–3915. <https://doi.org/10.1007/s10531-010-9936-4>.
- Brockerhoff, E.G., Jactel, H., Parrotta, J.A., Quine, C.P., Sayer, J., 2008. Plantation forests and biodiversity: oxymoron or opportunity. *Biodivers. Conserv.* 17, 925–951. <https://doi.org/10.1007/s10531-008-9380-x>.
- Brunet, J., Hedwall, P.-O., Lindgren, J., Cousins, S.A., 2021. Immigration credit of temperate forest herbs in fragmented landscapes – Implications for restoration of habitat connectivity. *J. Appl. Ecol.* 58, 2195–2206. <https://doi.org/10.1111/1365-2664.13975>.
- Calviño-Cancela, M., López de Silanes, M.E., Rubido-Bará, M., Uribarri, J., 2013. The potential role of tree plantations in providing habitat for lichen epiphytes. *For. Ecol. Manag.* 291, 386–395.
- Carnus, J.-M., Parrotta, J., Brockerhoff, E.G., Arbez, M., Jactel, H., Kremer, A., Lamb, D., O'Hara, K., Walters, B., 2006. Planted forests and biodiversity. *J. For.* 104 (2), 65–77.
- Cervera, M.T., Storme, V., Soto, A., Ivens, B., Van Montagu, M., Rajora, O.P., Boerjan, W., 2005. Intraspecific and interspecific genetic and phylogenetic relationships in the genus *Populus* based on AFLP markers. *Theor. Appl. Genet.* 111, 1440–1456. <https://doi.org/10.1007/s00122-005-0076-2>.
- Coote, L., Dietzsh, A.C., Wilson, M.W., Graham, C.T., Fuller, L., Walsh, A.T., Irwin, S., Kelly, D.L., Fraser, J.G.M., Kelly, T.C., O'Halloran, J., 2013. Testing indicators of biodiversity for plantation forests. *Ecol. Indic.* 32, 107–115. <https://doi.org/10.1016/j.ecolind.2013.03.020>.

- Coote, L., French, L.J., Moore, K.M., Mitchell, F.J.G., Kelly, D.L., 2012. Can plantation forests support plant species and communities of semi-natural woodland? *For. Ecol. Manag.* 283 (1), 86–95.
- Coote, L., Smith, G.F., Kelly, D.L., O'Donoghue, S., Dowding, P., Iremonger, S., Mitchell, F.J.G., 2008. Epiphytes of Sitka spruce (*Picea sitchensis*) plantations in Ireland and the effects of open spaces. *Biodivers. Conserv.* 17, 953–968. <https://doi.org/10.1007/s10531-007-9302-3>.
- Corli, A., Vannucchi, F., Traversari, S., Orsenigo, S., Giovannelli, A., Chiarabaglio, P.M., Chianucci, F., Calfapietra, C., Scartazza, A., Mascherpa, M.C., Traversi, M.L., Cristaldi, L., Trentanovi, G., 2025. Drivers of vascular species diversity on floodplain poplar stands: an integrated approach for ecological and functional assessment. *For. Ecol. Manag.* 595, 123000.
- Decree of the Estonian Government no. 195. 20.05.2004. Riigi Teataja I 21.05.2004, 44: 313. (In Estonian).
- Decree of the Estonian Minister of Environment no. 36. 13.09.2017. Riigi Teataja I 15.09.2017, 5. (In Estonian).
- Decree of the Estonian Minister of Environment no. 51. 19.05.2004. Riigi Teataja Lisa 27.05.2004, 69: 1134. (In Estonian).
- De Frenne, P., Baeten, L., Graae, B.J., Brunet, J., Wulf, M., Orczewska, A., Kolb, A., Jansen, I., Jamoneau, A., Jacquemyn, H., Hermy, M., Diekmann, M., De Schrijver, A., De Sanctis, M., Decocq, G., Cousins, S.A.O., Verheyen, K., 2011. Interregional variation in the floristic recovery of post-agricultural forests. *J. Ecol.* 99, 600–609. <https://doi.org/10.1111/j.1365-2745.2010.01768.x>.
- Ellis, C.J., 2012. Lichen epiphyte diversity: a species, community and trait-based review. *Perspect. Plant Ecol., Evol. & System.* 14, 131–152.
- Fahlvik, N., Rytter, L., Stener, L.-G., 2021. Production of hybrid aspen on agricultural land during one rotation in southern Sweden. *J. For. Res.* 32 (1), 181–189. <https://doi.org/10.1007/s11676-019-01067-9>.
- FAO, 2025. Global Forest Resources Assessment 2025. Rome. <https://doi.org/10.4060/cd6709en>.
- FAO, 2022. Global Forest Sector Outlook 2050: Assessing future Demand and Sources of Timber For a Sustainable Economy – Background paper For The State of the World's Forests 2022. FAO Forestry Working Paper, No. 31, Rome. <https://doi.org/10.4060/cc2265en>.
- Frazier, G.W., Canham, C.D., Lertzman, K.P., 1999. Gap Light Analyzer (GLA), Version 2.0: Imaging software to Extract Canopy Structure and Gap Light Transmission Indices from True-Colour Fish-eye photographs, Users Manual and Program Documentation. Copyright © 1999: Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York.
- Haughian, S.R., 2018. Short-term effects of alternative thinning treatments on the richness, abundance and composition of epixylic bryophytes, lichens, and vascular plants in conifer plantations at microhabitat and stand scales. *For. Ecol. Manag.* 415–416, 106–117.
- Haughian, S.R., Frego, K.A., 2016. Short-term effects of three commercial thinning treatments on diversity of understory vascular plants in white spruce plantations of northern New Brunswick. *For. Ecol. Manag.* 370, 45–55.
- Heineken, T., Diekmann, M., Liira, J., Orczewska, A., Schmidt, M., Brunet, J., Chytrý, M., Chabrerie, O., Decocq, G., De Frenne, P., Dřevojan, P., Dzwonko, Z., Ewald, J., Feilberg, J., Graae, B.J., Grytnes, J.A., Hermy, M., Kriebitzsch, W.U., Laiviņš, M., Lenoir, J., Lindmo, S., Marage, D., Marozas, V., Niemeyer, T., Paal, J., Pyšek, P., Roosaluuste, E., Šádl, J., Schaminée, J.H.J., Tyler, T., Verheyen, K., Wulf, M., Vanneste, T., 2022. The European Forest Plant Species List (EuForPlant): concept and applications. *J. Veg. Sci.* 33, 1–16. <https://doi.org/10.1111/jvs.13132>.
- Hepner, H., Lukason, O., Lutter, R., Padari, A., Tullus, A., 2021. The value of hybrid aspen coppice investment under different discount rate, price and management scenarios: a case study of Estonia. *Forests* 12 (10), 1332.
- Hytönen, J., 2018. Biomass, nutrient content and energy yield of short-rotation hybrid aspen (*P. tremula* × *P. tremuloides*) coppice. *For. Ecol. Manag.* 413, 21–31.
- Härdtle, W., von Oheimb, G., Westphal, C., 2005. Relationships between the vegetation and soil conditions in beech and beech-oak forests of northern Germany. *Plant Ecol.* 177, 113–124. <https://doi.org/10.1007/s11258-005-2187-x>.
- Jansons, A., Rieksts-Riekstiņš, J., Senhofa, S., Katrevics, J., Lazdina, D., Sisenis, L., 2017. Above-ground biomass equations of Populus hybrids in Latvia. *Balt. For.* 23, 507–514.
- Jüriado, I., Liira, J., Paal, J., Suija, A., 2009. Tree and stand level variables influencing diversity of lichens on temperate broad-leaved trees in boreo-nemoral floodplain forests. *Biodivers. Conserv.* 18, 105–125.
- Jüriado, I., Paal, J., 2019. Epiphytic lichen synusia and functional trait groups in boreo-nemoral deciduous forests are influenced by host tree and environmental factors. *Nord. J. Bot.* 37, e01939. <https://doi.org/10.1111/njb.01939>.
- Jüriado, I., Paal, J., Liira, J., 2003. Epiphytic and epixylic lichen species diversity in Estonian natural forests. *Biodivers. Conserv.* 12, 1587–1607.
- Kermavnar, J., Kutnar, L., Marinšek, A., 2021. Disentangling the ecological determinants of species and functional trait diversity in herb-layer plant communities in European temperate forests. *Forests* 12, 552. <https://doi.org/10.3390/f12050552>.
- Kivinen, S., Koivisto, E., Keski-Saari, S., Poikolainen, L., Tanhuanpää, T., Kuzmin, A., Viinikka, A., Heikkinen, R.K., Pykälä, J., Virkkala, R., Vihervaara, P., Kumpula, T., 2020. A keystone species, European aspen (*Populus tremula* L.) in boreal forests: ecological role, knowledge needs and mapping using remote sensing. *For. Ecol. Manag.* 462, 118008.
- Kolk, J., Naaf, T., Wulf, M., 2017. Paying the colonization credit: converging plant species richness in ancient and post-agricultural forests in NE Germany over five decades. *Biodivers. Conserv.* 26, 735–755. <https://doi.org/10.1007/s10531-016-1271-y>.
- Kollo, J., Metslaid, S., Padari, A., Hordo, M., Kangur, A., Noe, S.M., 2023. Trends in thermal growing season length from years 1955–2020 – a case study in hemiboreal forest in Estonia. *Boreal. Environ. Res.* 28, 169–180.
- Koorem, K., Moora, M., 2010. Positive association between understory species richness and a dominant shrub species (*Corylus avellana*) in a boreonemoral spruce forest. *For. Ecol. Manag.* 260, 1407–1413.
- Kull, T., Kalamees, R., Kaljund, K., Kull, T., Leht, M., Luuk, O., Mesipuu, M., Mäemets, H., Pihu, S., Reier, Ü., Roosaluuste, E., Rünk, K., Saar, P., 2018. Kokkuvõte soontaimede ohustatuse hindamistulemustest 2017–2018. In: Liikide ohustatuse hindamine riigihanke 183098 osa nr 15 - Oistaimed (Anthophyta), okaspuutaimed (Coniferophyta), lehtsooneoistaimed (Monilophyta) ja pärisraigastaimed (Lycopodiophyta) vastavalt lepingule nr 7-27/17/59 (16. juuni 2017.a.). Lõpparuanne Keskkonnaametile. Eesti Maaülikool. Estonian.
- Kumar, S., Stohlgren, T.J., Chong, G.W., 2006. Spatial heterogeneity influences native and nonnative plant species richness. *Ecology* 87 (12), 3186–3199.
- Leht, M. (Ed.), 2010. Eesti Taimede Määraja (The Keybook of Estonian Vascular Plants). Eesti Loodusfoto, Tartu. Estonian.
- Liccardi, F., Boscutti, F., Bacaro, G., Sigura, M., 2022. Connectivity, landscape structure, and plant diversity across agricultural landscapes: novel insight into effective ecological network planning. *J. Environ. Manag.* 317, 115358.
- Lõhmus, P., Lõhmus, A., 2019. The potential of production forests for sustaining lichen diversity: a perspective on sustainable forest management. *Forests* 10 (12), 1063.
- Manpoong, C., Tripathi, S.K., Aravindakshan, S., Krupnik, T.J., 2025. Digging in: impact of land use changes on soil aggregation patterns and carbon stocks in the moist tropics of the Mizoram in the Indomalayan realm. *Total Environ. Adv.* 13, 200119.
- Márialigeti, S., Tinya, F., Bidló, A., Ódor, P., 2016. Environmental drivers of the composition and diversity of the herb layer in mixed temperate forests in Hungary. *Plant. Ecol.* 217, 549–556. <https://doi.org/10.1007/s11258-016-0599-4>.
- McEwan, A., Marchi, E., Spinelli, R., Brink, M., 2020. Past, present and future of industrial plantation forestry and implication on future timber harvesting technology. *J. For. Res.* 31 (2), 339–351.
- Mishra, A., Humpenöder, F., Dietrich, J.P., Bodirsky, B.L., Sohngen, B., Reyher, C.P.O., Lotze-Campen, H., Popp, A., 2021. Estimating global land system impacts of timber plantations using MAGPIE 4.3.5. *Geosci. Model Dev.* 14, 6467–6494.
- Naaf, T., Kolk, J., 2015. Colonization credit of post-agricultural forest patches in NE Germany remains 130–230 years after reforestation. *Biol. Conserv.* 182, 155–163. <https://doi.org/10.1016/j.biocon.2014.12.002>.
- Nordén, B., Olsen, S.L., Haug, S., Rusch, G., 2021. Recent forest on abandoned agricultural land in the boreonemoral zone – biodiversity of plants and fungi in relation to historical and present tree cover. *For. Ecol. Manag.* 489, 119045. <https://doi.org/10.1016/j.foreco.2021.119045>.
- Pedersen, N.K., Kephfer-Rojas, S., Riis-Nielsen, T., Johannsen, V.K., Schmidt, I.K., 2025. Natural colonization in abandoned agricultural fields benefits native, insect-pollinated and bird-dispersed woody species. *Trees, Forests and People*, 19, 100755.
- R Core Team, 2025. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Randlane, T., Jüriado, I., Mark, K., Marmor-Ohtla, L., Oja, E., Saag, A., Savchenko, A., Degtjarenko, P., 2024a. Steep increase in red-listed lichens of Estonia. *Lichenologist* 56 (6), 329–343.
- Randlane, T., Saag, A., Suija, A., 2024b. Lichenicolous and Allied Fungi of Estonia. <https://esamba.bo.bg.ut.ee/checklist/est/home.php>.
- Randlane, T., Tullus, T., Saag, A., Lutter, R., Tullus, A., Helm, A., Tullus, H., Pärtel, M., 2017. Diversity of lichens and bryophytes in hybrid aspen plantations in Estonia depends on landscape structure. *Can. J. For. Res.* 47, 1202–1214. <https://doi.org/10.1139/cjfr-2017-0080>.
- Randrimanajara, M.A., Fenton, N.J., DesRochers, A., 2025. Understory vegetation diversity and composition in intensively managed plantations compared to extensively managed forests. *New Forests* 56, 5. <https://doi.org/10.1007/s11056-024-10071-9>.
- Randrimanajara, M.A., Fenton, N.J., DesRochers, A., 2023. How does understory vegetation diversity and composition differ between monocultures and mixed plantations of hybrid poplar and spruce? *For. Ecol. Manag.* 549, 121434.
- Rédei, T., Csécséris, A., Lhotsky, B., Barabás, S., Kröel-Dulay, G., Ónodi, G., Botta-Dukát, Z., 2020. Plantation forests cannot support the richness of forest specialist plants in the forest-steppe zone. *For. Ecol. Manag.* 461, 117964.
- Rogers, P.C., Pinno, B.D., Šebesta, J., Albrechtsen, B.R., Li, G., Ivanova, N., Kusbach, A., Kuuluvainen, T., Landhäusser, S.M., Liu, H., Myking, T., Pulkkinen, P., Wen, Z., Kulakowski, D., 2020. A global view of aspen: conservation science for widespread keystone systems. *Glob. Ecol. Conserv.* 21, e00828.
- Rähn, E., Lutter, R., Riit, T., Tullus, T., Tullus, A., Tedersoo, L., Drenkhan, R., Tullus, H., 2024. Soil microbiomes in native European aspen forests and hybrid aspen plantations have a similar fungal richness but different compositions, mainly driven by edaphic and floristic factors. *Front. Microbiol.* 15. <https://doi.org/10.3389/fmicb.2024.1372938>.
- Smyčková, M., Koutecký, T., Ujházyová, M., Ujházy, K., Verheyen, K., Volařík, D., Šebesta, J., Friedl, M., Máliš, F., Hofmeister, J., 2024. Herb layer species richness declines with heterogeneity of the forest structure in primary beech-dominated forests while proportion of forest specialists increases. *For. Ecol. Manag.* 556, 121728.
- Singh, N.S., Brearley, F.Q., Tripathi, S.K., 2025. Climate control of litter decomposition and nutrient release in tropical and sub-tropical forest biomes of Northeast India. *Environ. Adv.* 20, 100634.
- Snäll, T., Pennanen, J., Kivistö, L., Hanski, I., 2005. Modelling epiphyte metapopulation dynamics in a dynamic forest landscape. *Oikos* 109, 209–222.

- Soo, T., Tullus, A., Tullus, H., Roosalu, E., 2009. Floristic diversity responses in young hybrid aspen plantations to land-use history and site preparation treatments. *For. Ecol. Manag.* 257, 858–867. <https://doi.org/10.1016/j.foreco.2008.10.018>.
- Spake, R., Yanou, S., Yamaura, Y., Kawamura, K., Kitayama, K., Doncaster, C.P., 2019. Meta-analysis of management effects on biodiversity in plantation and secondary forests of Japan. *Conserv. Sci. Pract.* 1, e14. <https://doi.org/10.1111/csp2.14>.
- Stephens, S.S., Wagner, M.R., 2007. Forest plantations and biodiversity: a fresh perspective. *J. For.* 105 (6), 307–313. <https://doi.org/10.1093/jof/105.6.307>.
- Süveges, K., Vincze, O., Löki, V., Lovas-Kiss, A., Takács, A., Fekete, R., Tüdösné Budai, J., Molnár, V.A., 2022. Native and alien poplar plantations are important habitats for terrestrial orchids. *Preslia* 94, 429–445.
- Tinya, F., Ódor, P., 2016. Congruence of the spatial pattern of light and understory vegetation in an old-growth, temperate mixed forest. *For. Ecol. Manag.* 381, 84–92.
- Trindade, D.P.F., Pärtel, M., Carmona, C.P., Randlane, T., Nascimbene, J., 2021. Integrating dark diversity and functional traits to enhance nature conservation of epiphytic lichens: a case study from Northern Italy. *Biodiv. Conserv.* 30, 2565–2579. <https://doi.org/10.1007/s10531-021-02211-w>.
- Tripathi, S.K., Chanda, R., Ao, A., Moirangthem, B., Chauhan, S., Mizo, L., Singh, S.S., Singh, N.S., Upadhyay, K.K., Vanlalakawma, D.C., Lalnunmawia, 2026. Elevation and management-induced vegetation and soil carbon shift in Eastern Himalayan forests: advancing nature-based sustainability solutions (NbS). *Environ. Sustain. Indic.* 29, 101082.
- Tripp, E.A., Lendemer, J.C., Barberán, A., Dunn, R.R., Fierer, N., 2016. Biodiversity gradients in obligate symbiotic organisms: exploring the diversity and traits of lichen propagules across the United States. *J. Biogeogr.* 43, 1667–1678. <https://doi.org/10.1111/jbi.12746>.
- Tudge, S.J., Harris, Z.M., Murphy, R.J., Purvis, A., De Palma, A., 2023. Global trends in biodiversity with tree plantation age. *Glob. Ecol. Conserv.* 48, e02751. <https://doi.org/10.1016/j.gecco.2023.e02751>.
- Tullus, A., Rytter, L., Tullus, T., Weih, M., Tullus, H., 2012. Short-rotation forestry with hybrid aspen (*Populus tremula* L. × *P. tremuloides* Michx.) in Northern Europe. *Scand. J. Forest Res.* 27, 10–29. <https://doi.org/10.1080/02827581.2011.628949>.
- Tullus, T., Lutter, R., Randlane, T., Saag, A., Tullus, A., Kaasik, A., Sopp, R., Ots, K., Kaivapalu, M., Pärtel, M., Tullus, H., 2022a. The biodiversity of birch stands in agricultural landscapes of Estonia is associated with past land use, restoration approach, site and landscape variables. *Appl. Veg. Sci.* 25, e12678. <https://doi.org/10.1111/avsc.12678>.
- Tullus, T., Lutter, R., Randlane, T., Saag, A., Tullus, A., Oja, E., Degtjarenko, P., Pärtel, M., Tullus, H., 2022b. The effect of stand age on biodiversity in a 130-year chronosequence of *Populus tremula* stands. *For. Ecol. Manag.* 504, 119833.
- Tullus, T., Tullus, A., Roosalu, E., Lutter, R., Tullus, H., 2015. Vascular plant and bryophyte flora in mid-term hybrid aspen plantations on abandoned agricultural land. *Can. J. For. Res.* 45, 1183–1191. <https://doi.org/10.1139/cjfr-2014-0464>.
- Tullus, A., Tullus, H., Vares, A., Kanal, A., 2007. Early growth of hybrid aspen (*Populus × wettsteinii* Hämet-Ahti) plantations on former agricultural lands in Estonia. *For. Ecol. Manag.* 245, 118–129.
- Tullus, T., Lutter, R., Randlane, T., Saag, A., Tullus, A., Rähn, E., Riit, T., Sopp, R., Siller, M.-L., Täll, K., Ots, K., Kaivapalu, M., Tullus, H., 2025. Do silver birch (*Betula pendula*) and hybrid aspen (*Populus tremula* × *P. tremuloides*) plantations on former agricultural land differ from the perspective of biodiversity? *New Forests* 56, 27. <https://doi.org/10.1007/s11056-025-10095-9>.
- Wang, C., Zhang, W., Li, X., Wu, J., 2021. A global meta-analysis of the impacts of tree plantations on biodiversity. *Global. Ecol. Biogeogr.* 31, 576–587. <https://doi.org/10.1111/geb.13440>.
- Weih, M., Karacic, A., Munkert, H., Verwijst, T., Diekmann, M., 2003. Influence of young poplar stands on floristic diversity in agricultural landscapes (Sweden). *Basic. Appl. Ecol.* 4 (2), 149–156. <https://doi.org/10.1078/1439-1791-00157>.
- Wulf, M., Naaf, T., 2009. Herb layer response to broadleaf tree species with different leaf litter quality and canopy structure in temperate forests. *J. Veg. Sci.* 20, 517–526.
- Xiong, S., Nilsson, C., 1999. The effects of plant litter on vegetation: a meta-analysis. *J. Ecol.* 87, 984–994.
- Yahr, R., Vilgalys, R., DePriest, P.T., 2006. Geographic variation in algal partners of *Cladonia subtenuis* (Cladoniaceae) highlights the dynamic nature of a lichen symbiosis. *New Phytol.* 171, 847–860. <https://doi.org/10.1111/j.1469-8137.2006.01792.x>.
- Zarfos, M.R., Dvociak, M., Lawrence, G.B., McDonnell, T.C., Sullivan, T.J., 2019. Plant richness and composition in hardwood forest understories vary along an acidic deposition and soil-chemical gradient in the northeastern United States. *Plant Soil* 438, 461–477. <https://doi.org/10.1007/s11104-019-04031-y>.