

# Diversity of lichens and bryophytes in hybrid aspen plantations in Estonia depends on landscape structure

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**Abstract:** The importance of single-species forest plantations in sustaining biodiversity could be bigger than expected. We described the diversity of lichens and bryophytes in 15 midterm (16- to 17-year-old) hybrid aspen (*Populus tremula* × *Populus tremuloides*) plantations in Estonia. Species richness and composition data were linked with environmental and landscape-scale variables. Altogether, 44 lichen and 37 bryophyte species were recorded from plantations; richnesses of bryophytes and lichens were positively correlated. Lichen species composition was significantly affected by landscape-scale parameters (distance to the nearest present forest, distance to the nearest forest continuously occurring in the same place since the 1930s, and forest area in the study plot vicinity in the 1930s). Bryophyte species composition was affected mainly by light conditions and forest area in the 1930s. Among lichens, the sexual crustose species functional group dominated in midterm plantations; appearance of asexual lichens of different growth forms is expected during the next years. Our results indicate the importance of long-term availability of good-quality forests as sources of propagules. Short-rotation hybrid aspen plantations can provide temporary habitats for forest species and thus in part contribute to preserving landscape-scale biodiversity, if they are close to possible colonization sources. Green-tree retention in plantations will probably raise the biodiversity value of those short-term communities.

**Key words:** bryophytes, forest continuity, forest plantations, hybrid aspen, lichens.

**Résumé :** L'importance des plantations forestières monospécifiques pour le maintien de la biodiversité pourrait être plus grande que prévu. Nous décrivons la diversité des lichens et des bryophytes dans 15 plantations d'âge intermédiaire (16–17 ans) de peuplier hybride (*Populus tremula* × *Populus tremuloides*) en Estonie. Les données de richesse et de composition en espèces ont été reliées aux variables environnementales et à celles du paysage. Globalement, 44 espèces de lichens et 37 espèces de bryophytes ont été notées dans les plantations. La richesse des bryophytes et celle des lichens étaient positivement corrélées. La composition en espèces de lichens était significativement influencée par les paramètres du paysage (distance de la forêt actuelle la plus proche, distance de la plus proche forêt continuellement présente au même endroit depuis les années 1930, et superficie de la forêt à proximité des places échantillons dans les années 1930. La composition en espèces de bryophytes était surtout influencée par les conditions de luminosité et la superficie de la forêt dans les années 1930. Parmi les lichens, le groupe fonctionnel des espèces sexuées croûteuses dominait dans les plantations d'âge intermédiaire; on s'attend à voir apparaître des lichens asexués aux formes variées de croissance au cours des prochaines années. Nos résultats montrent l'importance de la disponibilité à long terme de forêts de bonne qualité comme sources de propagules. Les plantations de peuplier hybride à courte rotation peuvent fournir des habitats temporaires pour les espèces forestières et contribuent par conséquent en partie à préserver la biodiversité à l'échelle du paysage si elles sont situées près de sources potentielles de colonisation. La coupe avec réserve dans les plantations augmentera probablement la valeur de ces communautés temporaires en termes de biodiversité. [Traduit par la Rédaction]

**Mots-clés :** bryophytes, continuité de la forêt, plantations forestières, peuplier hybride, lichens.

## 1. Introduction

Forests are among the most important repositories of terrestrial biodiversity offering diverse habitats for various groups of organisms. In northern Eurasia and North America, the proportion of landscape covered by forests is currently (1990–2015) considered stable or even expanding (Keenan et al. 2015), while the effects of intensive forest management are still accompanied by a significant loss of forest biodiversity at all levels, exhibiting decreases of genetic diversity, species richness, and ecosystem variability (Bernes et al. 2015). It has been suggested that some negative impact of forest management on the biodiversity can be reduced by

harvesting timber not from natural forests but from plantations of woody plants, considering that the sites chosen for plantations are not habitats crucial to biodiversity (Hartmann et al. 2010).

Hybrid aspen (*Populus tremula* L. × *Populus tremuloides* Michx.) is one of the fastest growing trees in northern Europe suitable for the production of pulp and energy wood (Tullus et al. 2012a). This artificial cross is capable of growing faster and therefore shows higher biomass productivity than its parent species during the first 20–30 years (Yu 2001), which is the recommended rotation period for this tree in northern Europe (Tullus et al. 2012a). Both parent species are widely distributed in the world, *P. tremula* in Eurasia and *P. tremuloides* in North America. Currently, the area of

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hybrid aspen plantations in Nordic and Baltic countries is estimated to cover ca. 9000 ha (Tullus et al. 2015), and most of the plantations are established on abandoned agricultural lands (Soo et al. 2009a). Studies about the nutritional status of soil in first-generation hybrid aspen plantations on former agricultural fields revealed the decrease of soil reaction (pH) but did not show significant depletion of primary macronutrients (N, P, K) and soil organic carbon (Lutter et al. 2016).

Forest plantations, especially single-species plantations, have earned a reputation of being “green deserts” due to unsuitable conditions for several species (Bremer and Farley 2010). However, recent studies addressing biodiversity issues in relation to forest plantations reveal controversial results, depending on the taxonomic group considered and characteristics of studied plantations such as age of trees, light conditions, or previous agricultural land use (Felton et al. 2010). In general, biodiversity is frequently found to be higher within tree plantations compared with agricultural croplands but clearly lower than that on native forest land (Stephens and Wagner 2007).

In hybrid aspen or other *Populus* plantations, biodiversity studies have dealt with understorey vegetation of vascular plants and bryophytes (Weih et al. 2003; Soo et al. 2009a, 2009b; Tullus et al. 2012b, 2015). Previously, it has been shown that both vascular plant and bryophyte diversity increased with increasing age of plantations, and a slow succession towards a shade-tolerant understorey occurs in midterm plantations. However, the number of species that appeared characteristic of natural forests growing on similar soil types was low (Tullus et al. 2015). The parent species of hybrid aspen (*P. tremula* and *P. tremuloides*) support diverse epiphytic bryophyte communities, especially at an older age (Kuusinen 1996; Boudreault et al. 2000), while data about epiphytic bryophytes in hybrid aspen plantations are scarce; e.g., nine bryophyte species have earlier been recorded as growing only on hybrid aspen trunks (in addition to 19 species that inhabited both ground and tree bases or trunks) (Tullus et al. 2015).

Lichen-forming fungi, another group of spore-producing organisms aside from bryophytes, also form a species-rich component of the forest biota (Will-Wolf et al. 2002). European aspen (*Populus tremula*) is frequently pointed out as a special 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). The epiphytic lichen communities on aspen differ significantly between early- and late-successional forest stands and reach highest species richness values at the tree age of 80–100 years, while on younger trees, the richness values are clearly lower (Ellis and Ellis 2013); in late successions, a large number of cyanolichens characteristically occur on the basal trunks of aspens (Kuusinen 1994; Hedenås and Ericson 2000). In addition to the specific cyanobacterial lichens, the presence of *P. tremula* individuals in forests supports a multitude of common species and can remarkably increase the lichen diversity of a stand (Jüriado et al. 2003). For example, 273 lichen species were recorded as aspen epiphytes in Scotland (Ellis and Ellis 2013); 27 threatened (categories CR, EN, VU, and NT of the national red list according to Randlane et al. (2008)) and altogether 120 lichen species were listed as growing on aspen in Estonia (Marmor et al. 2017). Considerably less lichenized taxa (from 23 to 75) have been reported growing on trembling aspen (*Populus tremuloides*) in different regions of North America (Sheard and Jonescu 1974; Case 1977; Boudreault et al. 2000; Rogers and Ryel 2008). However, all of these data about aspen lichens are based on the studies performed in medium-aged or old natural stands of hybrid aspen parent species (*P. tremula* and *P. tremuloides*), while plantations of their hybrid have not been investigated in regard to lichen-forming fungi.

In general, epiphytic lichen diversity is influenced by tree-level, stand-level, and large-scale (e.g., climate, air pollution, landscape structure) effects. At the tree level, occurrence of lichen species

depends mainly on the physical (e.g., roughness, hardness, and water-holding capacity) and chemical (acidity) properties of the bark, while forest tree species composition, moisture regime, and habitat light availability (tree density and canopy cover) are considered the most influential factors for epiphytes at the stand level (Jüriado et al. 2009; Ellis 2012). In addition, landscape-scale factors such as forest history, extent of woodlands, habitat fragmentation, or connectivity have been used to explain the epiphytic biodiversity (e.g., Fritz et al. 2009; Marmor et al. 2010; Ellis 2012). These factors influence the community composition and richness mainly through the dispersal properties of lichens and bryophytes (Ellis 2012), and in single-species plantations, where tree- and stand-level factors vary little, they should play an important role in shaping the epiphytic communities.

Species responses to the changes in their ecosystems are currently often studied using a functional-trait-based approach (see review in Hevia et al. 2017). Species respond to environmental conditions individually, using species' adaptive traits; however, the response of many individual species comprising a community is scaled up to a complex shift in compositional structure of the community. Understanding the community response to environmental or habitat change may be simplified through the search for trait-based rules structuring community composition (Ellis and Coppins 2007a). Among functional traits controlling successional trends of lichens, characters related to thallus gross morphology, reproductive strategy, and lichen compounds have been mentioned. The generally accepted succession of epiphytic lichens, considering functional traits, starts with pioneer species, which tend to be smaller and reproduce sexually by small ascospores, while late-successional competitive species tend to be larger, with a greater investment in large vegetative diaspores and local establishment (Ellis 2012). Such a trait-based approach is considered useful not only for describing and understanding community responses, but also for conservation practices (e.g., Leppik et al. 2015) and predicting changes in communities (Ellis and Coppins 2007a).

Improved knowledge about species diversity and succession of communities in single-species forest plantations might help to understand the possible importance of these plantations in sustaining landscape-scale biodiversity. We aim to investigate the lichen biota and bryophyte flora in the first-generation midterm hybrid aspen plantations and answer the following questions:

1. Do midterm hybrid aspen plantations support low or high species diversity of lichen-forming fungi and bryophytes?
2. Which functional species groups dominate among lichens and bryophytes inhabiting hybrid aspen plantations?
3. Which environmental and landscape factors influence the richness and composition of lichens and bryophytes in hybrid aspen plantations?

## 2. Material and methods

### 2.1. Study sites

This study was carried out in Estonia, which is situated in northern Europe on the eastern shores of the Baltic Sea, lying in the moderate climate zone and in the hemiboreal forest zone, a transitional zone between the boreal coniferous and temperate deciduous forests. The 15 study sites were located in southern Estonia (57.752°N–58.590°N, 25.247°E–27.405°E) (Fig. 1). The studied hybrid aspen plantations were established in 1999 and 2000 on previous mineral agricultural soil using 1-year-old clonal micropropagated plants originating from Finland (Tullus et al. 2007). For site preparation, whole-area or strip ploughing had been carried out before planting the trees to reduce competition between young seedlings and the field layer. The size of plantations varied from 0.7 to 32 ha, and the average planting density was 1300 trees per hectare. Permanent circular experimental plots, with an area of 0.1 ha and an average of 106 aspens per plot, were established in 2003 and 2004

**Fig. 1.** Location of the studied hybrid aspen plantations (indicated with grey circles) in southern Estonia.



in hybrid aspen plantations to monitor aboveground growth development and productivity of the trees (Tullus et al. 2007).

## 2.2. Data collection

Lichen and bryophyte data were collected during 2015 from 15 midterm (16- to 17-year-old) hybrid aspen plantations, within 10 × 10 m squares (one square in each plantation; squares located in the centre of the above-mentioned permanent experimental plots). Squares were located in a typical part of the microrelief in the plantation, surrounded by a buffer plantation zone of at least 15 m to avoid the edge effect. The presence of all bryophyte and lichenized species was recorded on all possible substrates within the established squares — on the bark of hybrid aspens (141 trees altogether in all studied plantations) and a few other young trees (*Betula* sp. and *Salix* sp., occurring only rarely within the squares, with maximum height of 2 m), on deadwood (mainly on fallen twigs, but also on a dead standing hybrid aspen tree in one square), and on the ground. In every square, the abundance of each species was estimated visually using a classical cover-abundance scale of (+)1–5 as follows: +, one to two specimens recorded, with a small cover area; 1, few specimens, with cover up to 5%; 2, any number, with cover 6%–20%; 3, any number, with cover 21%–50%; 4, any number, with cover 51%–75%; and 5, any number, with cover 76%–100%. Specimens that were difficult to identify in the field were collected for later determination. A stereomicroscope and light microscope were used for the identification of taxa in the laboratory. In a few cases, standardized thin-layer chromatography (Orange et al. 2001) was applied to identify secondary compounds in lichens. Nomenclature of lichenized taxa follows Randle et al. (2016). Data on lichen species frequency in Estonia were derived from Randle and Saag (1999), the eSEIS database of Estonian lichens (<http://www.eseis.ut.ee>, accessed 12 December 2016), and the eBiodiversity database (<http://elurikkus.ut.ee/>, accessed 12 December 2016). Lichenized taxa were grouped according to the ecological indicator values of species by Wirth (2010). Nomenclature and frequency data of bryophytes are according to Vellak et al. (2015). Bryophyte species were classified into life strategy categories based on Dierssen (2001) and into groups according to the ecological indicator values of taxa as specified by Düll (1991). The voucher specimens of lichens are

deposited in the lichenological herbarium of the Natural History Museum at the University of Tartu (TU).

Different environmental characteristics were gathered from the permanent experimental plots: soil properties during 2013–2014 according to the methods described in Lutter et al. (2016) and light data and measures of hybrid aspen trees in 2015, in the middle of the growing season, according to Tullus et al. (2015). Additionally, for each studied site, we estimated landscape-scale factors: (a) distance to the nearest currently present natural forest; (b) distance to the nearest natural forest that has continuously occurred in the same locality for at least 75–80 years, and (c) historical (1930s) and current (2000) forest cover in the surrounding landscape. Distances to natural forests were estimated by using recent (2015) aerial photos of Estonia, provided by the Estonian Land Board. Forest continuity was estimated by using historical topographic maps (1:50 000) of the Estonian Land Board from 1935–1939 and 1969. Historical and current forest cover was estimated by calculating the percent forest cover in a 500 m radius of around the study plots for the 1930s and in 2000, respectively. Habitat availability within a radius of 500 m has been found to describe local lichen and bryophyte diversity better than smaller or larger scales (Löbel et al. 2006). All observed characteristics are listed in Table 1.

## 2.3. Statistical analyses

Pearson correlation was used to link species richness of lichens and bryophytes. To visualize the result, we used type II (major axis) regression (R package “lmodel2”, function “lmodel2”; Legendre 2014) for obtaining the trend line. Type II regression is not dependent on the selection of  $x$  and  $y$  axes and can visualize correlative relationships.

For investigating the effect of environmental and landscape-scale factors (listed in Table 1) on diversity of lichens and bryophytes, we used linear regression models (R function “lm”; R Core Team 2016). As several variables were highly correlated (Table A1) and could not be included in a single model, we used the information-theoretic approach by weighting models according to Akaike information criterion adjusted for small sample size (AICc; Burnham and Anderson 2002). We used R package “MuMIn” (Barton 2016) and function “dredge”, as well as option “subset”, which included, in a single model, only dependent variables that were not strongly correlated ( $|r| < 0.3$ ). From all possible models, we considered these for which  $\Delta AICc < 2$ , which is generally considered as equally supported. We checked the spatial pattern of model residuals according to Moran’s  $I$  (R package “ape”, function “Moran.I”; Paradis et al. 2004). No significant spatial autocorrelation was detected. We also separately analysed diversity of sexual and vegetative lichen groups.

To test which environmental and landscape-scale variables influence the species composition of lichens and bryophytes in aspen plantations, nonmetric multidimensional scaling (NMDS) ordination was applied. We used R package “vegan” (Oksanen et al. 2013), function “metaMDS”, and Bray–Curtis dissimilarities based on the species abundance data. The significance of  $r^2$  of the regression model describing the relationship between the given environmental or landscape-scale factor and the two NMDS ordination axes scores was tested with a random permutation test (999 permutations), using the function “envfit”.

All variables were ln-transformed (except pH, which is already in log scale) prior analyses, and all percentages or proportions were logit-transformed.

## 3. Results

### 3.1. Diversity of lichens

Altogether, 44 species of lichenized fungi were found in 15 hybrid aspen plantations. The majority of them were common taxa frequently recorded in Estonia, with the exception of *Arthonia*

**Table 1.** Main characteristics of the study plots in midterm hybrid aspen plantations.

Characteristic	Abbreviation	Mean ± SE	Minimum	Maximum
<b>Tree-layer and environmental variables</b>				
Tree height (m)	H	18.9±0.8	11.3	22.2
Tree diameter at breast height (cm)	DBH	14.9±0.7	7.9	18.4
Density of trees (trees·ha <sup>-1</sup> )	Den_T	940±51.5	600.0	1300.0
Basal area of trees (m <sup>2</sup> ·ha <sup>-1</sup> )	BA	18.2±2.0	5.8	33.4
Soil pH <sub>KCl</sub>	S_pH	5.4±0.2	4.1	6.8
Soil P (mg·kg <sup>-1</sup> )	S_P	101.2±13.0	36.0	203.0
Soil K (mg·kg <sup>-1</sup> )	S_K	110.5±14.2	44.0	211.0
Soil organic C (%)	S_C	1.2±0.2	0.5	2.7
Soil N (%)	S_N	0.1±0.007	0.1	0.2
Canopy openness (%)	Can_O	16.1±1.7	8.4	28.2
Transmitted total radiation (mol·m <sup>-2</sup> ·day <sup>-1</sup> )	Tr_TR	6.2±0.7	3.3	10.8
<b>Landscape-scale variables</b>				
Distance from continuous forest, growing since 1935–1939 (m)	Dis_O	314.3±45.0	70.0	670.0
Distance from forest in 2015 (m)	Dis_C	211±46.1	35.0	670.0
Forest area in the radius of 500 m around the study plot in 1930s (ha)	For_O	8.3±2.8	0.1	0.25
Forest area in the radius of 500 m around the study plot in 2000 (ha)	For_C	35.3±7.04	36.5	78

*patellulata*, *Athallia cerinella*, *Diplotomma pharcidium*, and *Leptorhaphis tremulae*, which are known in less than 10 localities in Estonia to date (Table 2). One species, *Candelariella lutella*, was recorded for the first time nationally in 13 separate study plots of this research (Oja et al. 2016). The number of lichenized taxa in study plots varied from 14 to 32, and the mean number of lichen species per plot was 25. The most frequent species were *Caloplaca cerina*, *Lecania naegelii*, *Lecanora chlorotera*, and *Xanthoria parietina* (present in all plots) and *Candelariella lutella*, *Gyalolechia flavorubescens*, *Lecania cyrtella*, *Lecanora sambuci*, *L. symmicta*, *Lecidella euphorea*, *Phaeophyscia ciliata*, *Physcia adscendens*, *P. stellaris*, and *P. tenella* (present in >80% of plots) (Table 2).

According to the substrate, 43 of the recorded species grew on trunks and branches of trees, and one species, *Peltigera rufescens*, inhabited soil. Among the epiphytes, almost all species were recorded on hybrid aspen, with the exception of *Scoliciosporum sarothamni*, which was found only on a young *Betula* spp. Some species, e.g., *Lecanora carpinea*, *L. symmicta*, *Melanohalea olivacea*, and few others, were additionally recorded from *Betula* spp. and *Salix* spp. (Table 2).

Evaluation of recorded taxa according to the characteristic traits of species revealed some traits that were dominating. According to the growth form of the thallus, the species were divided between three main morphologies: species with crustose thalli (59%), foliose thalli (34%), or fruticose thalli (7%) (Table 2). In almost all recorded taxa, photobiont belonged to the group of coccoid green alga; lichens with cyanobacteria as photobiont were not found; two fungi, *Leptorhaphis tremula* and *Mycocomrothelia wallrothii*, are considered to be not lichenized (Smith et al. 2009). Among all recorded taxa, the majority of the species (75%) shared the strategy of reproducing sexually; of them, the two nonlichenized species, *L. tremula* and *M. wallrothii*, had perithecia, while all of the other species had apothecia as fruiting bodies. All vegetatively reproducing species had soredia as vegetative diaspores (Table 2); no taxa with isidia, phylloidia, or other attached vegetative propagules were found.

According to the ecological indicator values attributed to lichenized taxa (Wirth 2010), the recorded species can be characterized by the following features: generally preferring light, tolerating low or medium moisture, various values of substrate pH (between 4.1–4.8 and 6.6–7.5), and eutrophication (Table 2; Fig. 2).

### 3.2. Diversity of bryophytes

Altogether, 37 bryophyte species were found in hybrid aspen plantations. In addition, few specimens were identified at the genus level (*Pellia* spp. and *Pohlia* spp.). The majority of the recorded taxa belonged to common species, with the exception of

*Leskea polycarpa*, *Plagiomnium medium*, and *Tortula truncate*, which are sporadically found in Estonia (Table 3). The number of bryophyte species per study plot varied from 8 to 19, and the mean number of bryophyte species was 13. The most frequent species were *Amblystegium serpens*, *Brachythecium rutabulum*, and *Oxyrrhynchium hians* (in 100% of plots) and *Brachythecium salebrosum*, *Plagiomnium cuspidatum*, and *Sciuro-hypnum curtum* (present in >80% of plots).

According to the substrate, 21 species inhabited only the ground, 13 species were recorded growing on the ground and on the trunks and (or) tree bases of hybrid aspens, and three species (*Leskea polycarpa*, *Orthotrichum speciosum*, and *Pylaisia polyantha*) were found only on trunks (Table 3). Seven bryophyte species were recorded, besides on the ground and tree trunks, growing also on deadwood.

On the basis of life strategy categories according to Dierssen (2001), the bryophyte flora of hybrid aspen plantations was dominated by competitive perennials (38%), followed by perennial stayers (24%), and stress-tolerant perennials (14%), while the share of short-living bryophyte species was small (Table 3).

According to the ecological indicator values attributed to bryophyte species (Düll 1991), the recorded species can be characterized as generally preferring moderate to high light and humidity levels and moderately acid pH of substrate (Fig. 2).

Between the total species richnesses of bryophytes and lichens, a significant positive correlation ( $r = 0.56$ ,  $p = 0.03$ ) was revealed (Fig. 3).

### 3.3. The effect of environmental and landscape-scale variables on lichen and bryophyte biota in hybrid aspen plantations

Species richnesses of lichens and bryophytes in hybrid aspen plantations increased with historical forest cover around the study plot in the 1930s, and bryophyte richness additionally increased with the density of trees in the study plot (Table 4; Fig. 4). The positive effect of historical forest cover was significant for diversity of both sexual and vegetative lichens ( $t = 2.6$ ,  $p = 0.02$ , and  $t = 2.2$ ,  $p = 0.04$ , respectively).

The effects of environmental and landscape-scale variables on species composition of lichens and bryophytes were studied using NMDS ordination. Lichen species composition was significantly and strongly influenced by landscape-scale variables: distance from currently present nearest forest, distance from continuously occurring forest, and historical forest cover in the surroundings. At the same time, variables linked with soil and light conditions or tree characteristics did not significantly influence the variation of lichen species composition (Table 5; Fig. 5). Bryophyte species

**Table 2.** List of recorded lichen species, their frequency (percentage of occurrences) and substrate in the study plots ( $n = 15$ ) of midterm hybrid aspen plantations, frequency class in Estonia, functional groups, type of reproductive diaspores, and ecological indicator values.

Species	Species abbreviation (on Fig. 5)	Frequency (%)	Substrate <sup>a</sup>	Frequency class <sup>b</sup>	Functional group <sup>c</sup>	Reproductive diaspore <sup>d</sup>	Ecological indicator value <sup>e</sup>				
							L	T	F	R	N
<i>Arthonia mediella</i> Nyl.	Arth.med	13	P	st fq	sex cru	ap					
<i>Arthonia patellulata</i> Nyl.	Arth.pat	67	P	st r	sex cru	ap					
<i>Athallia cerinella</i> (Nyl.) Arup et al.	Calo.cla	53	P	r	sex cru	ap	7	6	3	7	6
<i>Athallia pyracea</i> (Ach.) Arup et al.	Calo.pyr	100	P, S	fq	sex cru	ap	7	x	3	7	5
<i>Caloplaca cerina</i> (Ehrh. ex Hedw.) Th. Fr.	Calo.cna	100	P	fqq	sex cru	ap	7	x	5	7	5
<i>Candelariella lutella</i> (Vain.) Räsänen	Cand.lut	87	B, P	st fq	sex cru	ap					
<i>Diplotomma pharcidium</i> (Ach.) M. Choisy	Dipl.pha	7	P	st r	sex cru	ap					
<i>Evernia prunastri</i> (L.) Ach.	Ever.pru	47	P	fqq	veg fru	sor	7	5	4	3	4
<i>Gyalolechia flavorubescens</i> (Huds.) Søchting et al.	Calo fla	87	P	fqq	sex cru	ap					
<i>Hypogymnia physodes</i> (L.) Nyl.	Hypo.phy	47	P	fqq	veg fol	sor	7	x	3	3	3
<i>Hypogymnia tubulosa</i> (Schaer.) Hav.	Hypo.tub	7	P	fqq	veg fol	sor	7	5	3	5	4
<i>Lecania cyrtella</i> (Ach.) Th. Fr.	Lia.cyr	93	P	fq	sex cru	ap	7	5	3	7	6
<i>Lecania naegelii</i> (Hepp) Diederich & Van den Boom	Lia.nae	100	P	fq	sex cru	ap	6	5	3	7	7
<i>Lecanora argentata</i> (Ach.) Malme	Leca.arg	40	B, P	fqq	sex cru	ap	5	5	4	5	3
<i>Lecanora carpinea</i> (L.) Vain.	Lec.car	73	B, P	fqq	sex cru	ap	6	5	3	5	4
<i>Lecanora chlarotera</i> Nyl.	Leca.chl	100	P	fqq	sex cru	ap	6	5	3	6	5
<i>Lecanora leptyroides</i> (Nyl.) Degel.	Leca.lep	80	P, S	fqq	sex cru	ap					
<i>Lecanora populicola</i> (DC.) Duby	Leca.pop	67	P	fq	sex cru	ap					
<i>Lecanora pulicaris</i> (Pers.) Ach.	Leca.pul	7	P	fqq	sex cru	ap	7	4	3	3	4
<i>Lecanora sambuci</i> (Pers.) Nyl.	Leca.sam	87	P	st fq	sex cru	ap	7	6	3	7	6
<i>Lecanora symmicta</i> (Ach.) Ach.	Leca.sym	87	B, P	fqq	sex cru	ap	7	4	5	5	4
<i>Lecidella elaeochroma</i> (Ach.) M. Choisy	Leci.ela	67	P	fqq	sex cru	ap	6	5	3	6	5
<i>Lecidella euphorea</i> (Flörke) Hertel	Leci.eup	87	P	fqq	sex cru	ap					
<i>Leptorhaphis tremulae</i> Körb.		7	P	r	sex cru	per					
<i>Melanelixia subaurifera</i> (Nyl.) O. Blanco et al.	Mela.sub	60	P	fqq	veg fol	sor	6	5	5	6	5
<i>Melanohalea olivacea</i> (L.) O. Blanco et al.	Mela.oli	40	B, P	fqq	sex fol	ap					
<i>Mycomicrothelia wallrothii</i> (Hepp) D. Hawksw.	Myco.wal	13	P	st fq	sex cru	per					
<i>Parmelia sulcata</i> Taylor	Parm.sul	67	P	fqq	veg fol	sor	7	x	3	5	7
<i>Peltigera rufescens</i> (Weiss) Humb.		7	G	fqq	sex fol	ap	8	x	3	8	5
<i>Phaeophyscia ciliata</i> (Hoffm.) Moberg	Phae.cil	87	P	fq	sex fol	ap					
<i>Phaeophyscia orbicularis</i> (Neck.) Moberg	Phae.orb	7	P	fqq	veg fol	sor	7	x	x	7	9
<i>Physcia adscendens</i> (Fr.) H. Olivier	Phys.ads	93	P	fqq	veg fol	sor	7	x	3	7	8
<i>Physcia aipolia</i> (Ehrh. ex Humb.) Fűrnr.	Phys.aip	7	P	fqq	sex fol	ap	7	x	3	7	5
<i>Physcia stellaris</i> (L.) Nyl.	Phys.ste	93	P	fqq	sex fol	ap	7	4	3	6	6
<i>Physcia tenella</i> (Scop.) DC.	Phys.ten	87	P	fqq	veg fol	sor	7	x	3	6	7
<i>Physconia distorta</i> (With.) J.R. Laundon	Phys.dis	47	P	fqq	sex fol	ap	7	5	5	7	6
<i>Ramalina farinacea</i> (L.) Ach.	Ram.far	80	B, P	fqq	veg fru	sor	6	5	4	5	4
<i>Rinodina exigua</i> Gray	Rino.exi	27	B, P	fq	sex cru	ap	7	5	3	7	7
<i>Rinodina pyrina</i> (Ach.) Arnold	Rino.pyr	60	P	fq	sex cru	ap	7	4	5	7	3
<i>Scoliosporum chlorococcum</i> (Stenh.) Vězda	Scol.chl	7	B	fq	sex cru	ap	6	5	3	3	6
<i>Scoliosporum sarothamni</i> (Vain.) Vězda	Scol.sar	47	B, P	st fq	veg cru	sor					
<i>Tuckermannopsis chlorophylla</i> (Willd.) Hale	Tuck.chl	7	P	fqq	veg fru	sor	6	4	6	3	3
<i>Xanthoria parietina</i> (L.) Th. Fr.	Xant.par	100	P	fqq	sex fol	ap	7	x	3	7	8
<i>Xanthoria polycarpa</i> (Hoffm.) Th. Fr. ex Rieber	Xant.pol	73	B, P	fqq	sex fol	ap	7	x	3	7	8

<sup>a</sup>B, *Betula* spp.; G, ground; P, *P. tremula* × *P. tremuloides*; S, *Salix* spp.

<sup>b</sup>fqq, very frequent, 51 or more localities; fq, frequent, 21–50 localities; st fq, rather frequent, 11–20 localities; st r, rather rare, 6–10 localities; r, rare, 3–5 localities (according to Randlane and Saag 1999).

<sup>c</sup>sex cru, sexually reproducing crustose species; sex fol, sexually reproducing foliose species; veg cru, vegetatively reproducing crustose species; veg fol, vegetatively reproducing foliose species; veg fru, vegetatively reproducing fruticose species (traits based on Smith et al. 2009).

<sup>d</sup>ap, species with apothecia; per, species with perithecia; sor, species dispersing with soredia.

<sup>e</sup>L, light value (5, sites in half-shade; 6, intermediate value between 5 and 7; 7, sites in half-light; 8, sites in light); T, temperature value (3, cool areas; 4, intermediate value between 3 and 5; 5, moderately cool to moderately warm areas; 6, mostly mild areas); F, moisture value (3, dry habitats tolerated but often also in moist habitats; 4, also in dry habitats but only at high air moisture; 5, dry habitats usually avoided, precipitation mainly over 700 mm·year<sup>-1</sup>; 6, precipitation usually over 800 mm·year<sup>-1</sup>); R, reaction (acidity) value (3, rather acid, pH 4.1–4.8; 5, moderate acid, pH 4.5–5.6; 6, weakly acid, pH 5.3–6.1; 7, subneutral, pH 5.7–6.5; 8, neutral, pH 6.6–7.5); N, eutrophication value (3–4, weak to rather weak eutrophication; 5–6, moderate to clear eutrophication; 7, rather strong eutrophication; 8, strong eutrophication; 9, very strong eutrophication) according to Wirth (2010); x, the value is determined as “of broad amplitude” by Wirth (2010).

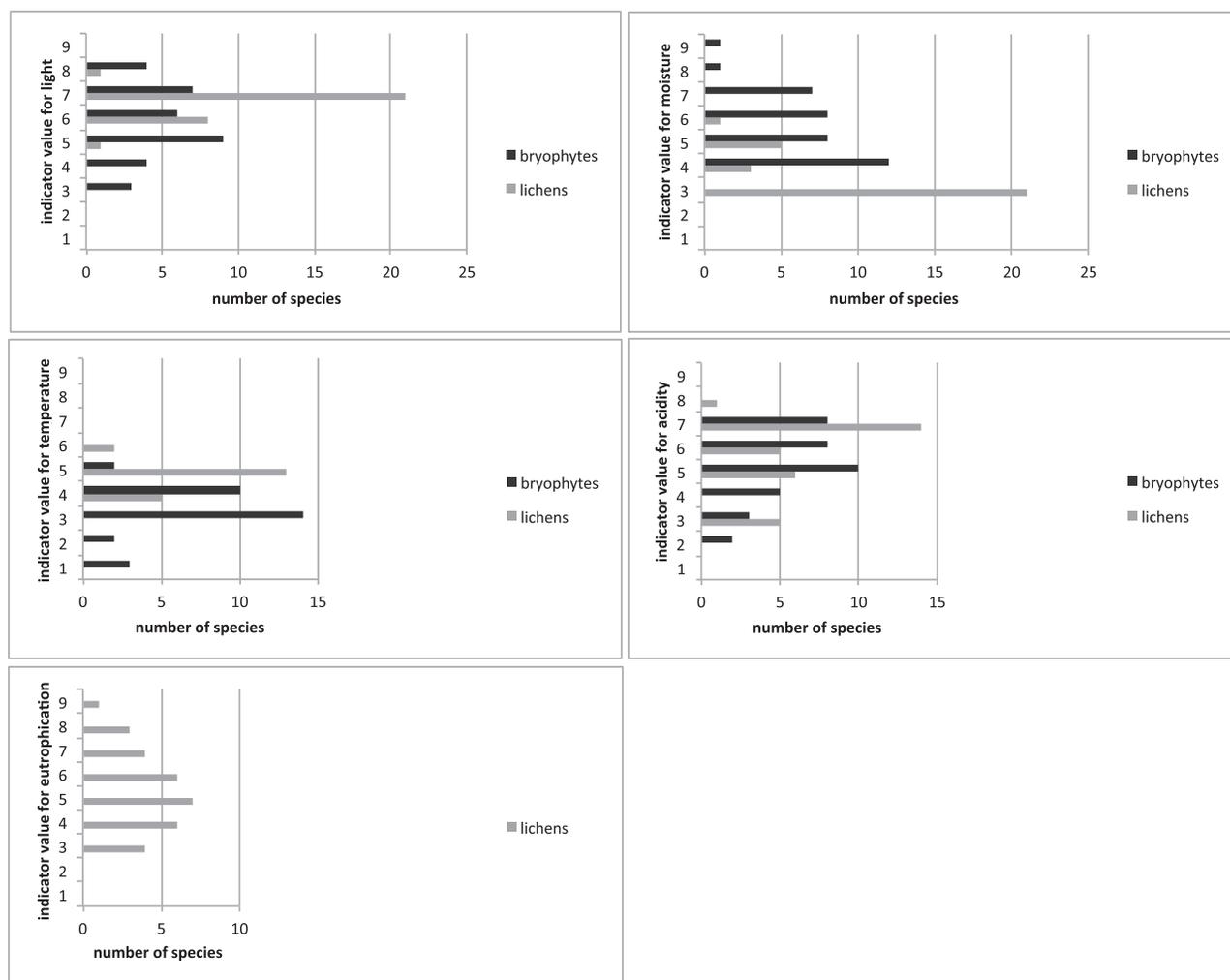
composition was significantly affected by the phosphorus content in soil, by canopy openness, and by the amount of canopy-transmitted solar radiation (Table 5; Fig. 6). Similarly to lichens, historical (in the 1930s) forest cover in the surrounding landscape had a significant effect on the variation of bryophyte species composition.

## 4. Discussion

### 4.1. Species diversity of lichens and bryophytes in midterm hybrid aspen plantations

Single-species forest plantations are generally considered habitats with a low number of inhabiting species (Bremer and Farley

**Fig. 2.** Distribution of recorded lichen and bryophyte species in groups according to ecological indicator values of lichens (based on Wirth 2010) and bryophytes (based on Düll 1991).



2010). We detected 44 lichen and 37 bryophyte species in 15 studied hybrid aspen plantations, with an average of 25 species of lichens and 13 bryophytes per 100 m<sup>2</sup> plot (Tables 2 and 3). One of the parent species of hybrid aspen, *P. tremula*, is widely known to support high diversity of epiphytes at the medium tree age, e.g., Ellis and Ellis (2013) recorded 139 lichen species from 40 aspen trees varying in age from 27 to 165 years, with a mean of 80 years. However, stands of young (less than 20 years) aspens have only rarely been investigated in regard to lichen-forming fungi. Davies et al. (2014) reported 23 epiphytic lichen species and three bryophytes on 15-year-old aspens grown at two experimental sites in Scotland. Compared with these data, the species richness of lichens and mosses in midterm (16- to 17-year-old) plantations of hybrid aspen was remarkable.

Strong positive correlation between lichen and bryophyte species richnesses (Fig. 3) indicates that the diversity of the two groups is influenced by similar factors. An opposite relationship, the negative association between the species numbers of lichens and mosses growing on the same substrate, has been earlier demonstrated in epiphytic communities (e.g., Löbel et al. 2006; Degtjarenko et al. 2016). In our study, almost all lichens (except one, *Peltigera rufescens*) inhabited trunks and branches of aspens and a few other young trees (mainly *Betula* spp.) while a majority of bryophytes (34 species out of 37) were recorded growing on the ground. The lack of lichens on the ground in hybrid aspen plantations is probably due to the absence of the available free sub-

strate as ground lichens are generally poor competitors with faster growing ground-dwelling vascular plants and the more vigorous bryophytes (Gilbert 1993). The lack of mosses on trees could be connected with time factor and also with the current light and moisture conditions on the trunks of young aspens as epiphytic lichens generally dominate over mosses in drier and lighter niches on trees (Sales et al. 2016). The other potential substrates for these groups of organisms were limited as the amount of deadwood was small in the studied stands and any kind of rocks or boulders were not available because the plantations had been established on abandoned agricultural lands, crop fields, or grassland (Tullus et al. 2007) where erratic boulders and other stones were obviously cleared on purpose.

The majority of both lichens and bryophytes recorded in studied plantations were common species (Tables 2 and 3). Although one lichenized fungus, *Candelariella lutella*, was recorded for the first time nationally, it is probably not rare in Estonia but has been overlooked due to its very small size (Oja et al. 2016). In general, aspen epiphytes include only a small number of specialist lichen species (e.g., *Arthonia patellulata* and *Lecanora populicola*), which are known only from aspen, in addition to numerous common species associated with more nutrient-rich bark conditions (Lewis and Ellis 2010). Our results are in accordance with these findings (Table 2). The so-called nationally valuable species, i.e., protected, threatened, or rare species with up to 10 localities in Estonia, were not recorded among bryophytes,

**Table 3.** List of recorded bryophyte species, their frequency (percentage of occurrences) and substrate in the study plots ( $n = 15$ ) of midterm hybrid aspen plantations, frequency class in Estonia, life strategy categories, and ecological indicator values.

Species	Species abbreviation (on Fig. 6)	Frequency (%)	Substrate <sup>a</sup>	Frequency class <sup>b</sup>	Life strategy category <sup>c</sup>	Ecological indicator values <sup>d</sup>			
						L	T	F	R
<i>Amblystegium serpens</i> (Hedw.) Schimp.	AmbI.ser	100	G, P, W	fq	p	5	4	6	
<i>Atrichum undulatum</i> (Hedw.) P. Beauv.	Atri.und	33	G	fq	s	6		6	4
<i>Brachytheciastrum velutinum</i> (Hedw.) Ignatov & Huttunen	Brac.vel	13	G	fq	p	5	3	4	6
<i>Brachythecium erythrorrhizon</i> Schimp.	Brac.ery	13	G	fq	p	8	1	7	6
<i>Brachythecium mildeanum</i> (Schimp.) Schimp.	Brac.mil	7	G	fq	p	8	4	7	6
<i>Brachythecium rivulare</i> Schimp.	Brac.riv	33	G	fq	pc		3	7	5
<i>Brachythecium rutabulum</i> (Hedw.) Schimp.	Brac.rut	100	G, P	fq	cp	5		4	
<i>Brachythecium salebrosum</i> (Hoffm. ex F. Weber & D. Mohr) Schimp.	Brac.sal	93	G, P, W	fq	cp	6	4	4	5
<i>Calliergonella cuspidata</i> (Hedw.) Loeske	Call.cus	40	G, P	fq	pc	8	3	7	7
<i>Campylidium sommerfeltii</i> (Myrin) Ochyra	Camp.som	47	G, P	fq	p	3	1	6	4
<i>Chiloscyphus pallescens</i> (Ehrh. ex Hoffm.) Dumort.	Chil.pal	7	G	fq	pc	5	3	8	7
<i>Chiloscyphus polyanthos</i> (L.) Corda	Chil.pol	13	G	fq	pc		4	9	2
<i>Cirriphyllum piliferum</i> (Hedw.) Grout	Cirr.pil	60	G, P	fq	pc	7	3	5	6
<i>Eurhynchiastrum pulchellum</i> (Hedw.) Ignatov & Huttunen	Eurh.pul	7	G	fq	ps	6	4	4	6
<i>Eurhynchium angustirete</i> (Broth.) T.J. Kop.	Eurh.ang	27	G, P	fq	p	5	4	4	7
<i>Hygroamblystegium varium</i> (Hedw.) Mönk.	Hygr.var	7	G	fq	p	5	5	5	6
<i>Hylocomium splendens</i> (Hedw.) Schimp.	Hylo.spl	13	G	fq	pc	6	3	4	5
<i>Hypnum cupressiforme</i> Hedw.	Hypn.cup	13	G, W	fq	ps	5		4	4
<i>Kindbergia praelonga</i> (Hedw.) Ochyra	Kind.pra	33	G, P	fq	p	6	4	6	5
<i>Leptobryum pyriforme</i> (Hedw.) Wilson	Lept.pyr	7	G	fq	f			6	7
<i>Leskea polycarpa</i> Hedw.	Lesk.pol	7	P	p	p	7	5	4	7
<i>Lophocolea heterophylla</i> (Schrad.) Dumort	Loph.het	47	G, P	fq	cp	4	3	4	3
<i>Orthotrichum speciosum</i> Nees	Orth.spe	47	P	fq	s	7	2	5	5
<i>Oxyrrhynchium hians</i> (Hedw.) Loeske	Oxyr.hia	100	G, P, W, S	fq	cp	7	4	5	7
<i>Pellia</i> sp.	Pell.sp	7	G						
<i>Plagiomnium affine</i> (Blandow ex Funck) T.J. Kop.	Plag.aff	33	G	fq	pc	5	4	5	5
<i>Plagiomnium cuspidatum</i> (Hedw.) T.J. Kop.	Plag.cus	87	G, P, W	fq	pc	4	3	5	7
<i>Plagiomnium medium</i> (Bruch & Schimp.) T.J. Kop.	Plag.med	7	G	p	pc	5	1	7	5
<i>Plagiomnium undulatum</i> (Hedw.) T.J. Kop.	Plag.und	7	G	fq	pc	4	3	6	6
<i>Pleurozium schreberi</i> (Willd. ex Brid.) Mitt.	Pleu.sch	20	G	fq	pc	6	3	4	2
<i>Pohlia</i> sp.	Pohl.sp	13	G						
<i>Pylaisia polyantha</i> (Hedw.) Schimp.	Pyla.pol	73	P	fq	ps	8	3	5	7
<i>Rhizomnium punctatum</i> (Hedw.) T.J. Kop.	Rhiz.pun	7	G	fq	l	3	3	6	4
<i>Rhytidiadelphus squarrosus</i> (Hedw.) Warnst.	Rhyt.squ	13	G	fq	pc	7	3	6	5
<i>Rhytidiadelphus triquetrus</i> (Hedw.) Warnst.	Rhyt.tri	13	G	fq	pc	7	3	4	5
<i>Sanionia uncinata</i> (Hedw.) Loeske	Sani.unc	13	G, P	fq	ps			7	3
<i>Sciuro-hypnum curtum</i> (Lindb.) Ignatov	Schy.cur	87	G, P, W	fq	pc	3	4	6	3
<i>Sciuro-hypnum reflexum</i> (Starke) Ignatov & Huttunen	Schy.ref	13	G, W	fq	ps	4	2	5	4
<i>Tortula truncata</i> (Hedw.) Mitt.	Tort.tru	7	G	p	a	7	4	7	5

<sup>a</sup>G, ground; P, *P. tremula* × *P. tremuloides*; S, *Salix* spp.; W, deadwood.

<sup>b</sup>fq, frequent, 31 or more localities; p, sporadically, 8–30 localities (according to Vellak et al. 2015).

<sup>c</sup>s, short-lived shuttle; a, annual shuttle; cp, pioneer colonists; f, fugitives; l, long-lived shuttle; p, perennials; pc, competitive perennials; ps, stress tolerant perennials (according to Dierssen 2001).

<sup>d</sup>L, light value (3, shade species; 4, intermediate value between 3 and 5; 5, half-shade species; 6, intermediate value between 5 and 7; 7, half-light species; 8, light species); T, temperature value (1, cold areas; 2, intermediate value between 1 and 3; 3, cool areas; 4, intermediate value between 3 and 5; 5, moderately warm areas); F, moisture value (4, intermediate value between 3 (dry habitats) and 5; 5, moderately moist habitats; 6, intermediate value between 5 and 7; 7, moist habitats; 8, intermediate value between 7 and 9; 9, temporarily water-logged habitats); and R, reaction (acidity) value (2, intermediate value between 1 (strongly acid) and 3; 3, acid, pH < 5; 4, intermediate value between 3 and 5; 5, moderately acid, pH 5.0–6.0; 6, intermediate value between 5 and 7; 7, weakly acid to weakly neutral, pH 6.0–6.9); x, species with “broad amplitude” (according to Düll 1991).

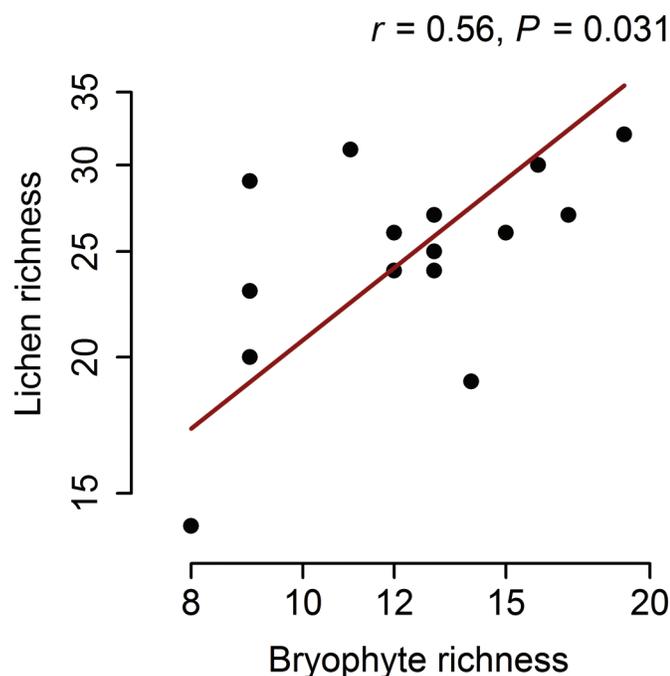
while a few species belonging currently to the rare taxa were found among lichens.

#### 4.2. Functional species groups among lichens and bryophytes in studied plantations

We used the functional trait based approach of species' groups to describe the current stage of lichen successions in midterm hybrid aspen plantations; functional groups related to thallus gross morphology and reproductive strategy (Ellis and Coppins 2007a) were applied. Among lichens, the functional group of sexually reproducing crustose species formed the most numerous

group (25 taxa; Table 2); such species (e.g., *Athallia pyracea*, *Lecania naegelii*, *Lecanora carpinea*, *L. chlarotera*, *L. populicola*, *Lecidella elaeochroma*, etc.) are considered early colonists of aspen bark, becoming less abundant as the tree ages, and are replaced progressively by asexually reproducing crustose lichens, foliose lichens, and bryophytes on middle-aged trees (Ellis and Ellis 2013). Higher frequencies of crustose lichens on younger trees are considered indicative of an open bark community, characterized by lower levels of competition for space and light (Ellis and Coppins 2006). In addition, we recorded one vegetatively reproducing crus-

**Fig. 3.** Correlation between total species richness of lichens and bryophytes in 10 × 10 m study plots (axes are in log scale; type II regression line is used to depict the linear relationship between significantly correlated variables).



tose lichen, *Scoliosporum sarothammi*, 15 foliose species, both sexually and asexually reproducing, and three asexual fruticose species in studied midterm plantations (Table 2). We also found 16 bryophyte species growing on the trees, but only three of them explicitly inhabited tree trunks. Among all recorded bryophytes, species with different life strategies were present, but perennials, including competitive and stress-tolerant perennials, dominated (Table 3). These data indicate that hybrid aspens growing in midterm plantations provide substrate to lichen species from other functional groups besides pioneers — sexual crustose taxa — and also to some bryophytes already at the tree age of 16–17 years.

According to the ecological indicator values that are ascribed to lichen (Wirth 2010) and bryophyte (Düll 1991) species, the two groups of spore-producing organisms found in hybrid aspen plantations showed some differences: compared with bryophytes, lichen species preferred stronger light, lower humidity, and higher temperature levels (Fig. 2). Both groups tolerated various values of substrate pH, and lichens also tolerated various eutrophication levels (data for bryophytes not available). These differences in ecological preferences of the two groups are explained by the fact that they generally inhabited different substrates in studied plantations — recorded lichen species were mostly epiphytic (with one exception), and bryophytes were mainly epigeic, growing on the ground (Tables 2 and 3) where light was evidently less and moisture more available than on aspen trunks.

#### 4.3. Factors affecting species diversity of lichens and bryophytes

We used linear modeling and NMDS ordination to study the effects of several environmental and landscape variables on lichen and bryophyte species richnesses and compositions in hybrid aspen plantations. None of the studied environmental factors had a significant effect on lichen diversity measures. Richness of bryophytes was positively correlated with tree density on the study plot (Fig. 4), and bryophyte species composition was significantly affected by the environmental parameters connected to the light conditions — the amount of canopy-transmitted solar radiation and canopy openness (Table 5; Fig. 6). Although bryo-

phytes are generally regarded as shade plants, there is a wide range in the light responses of different bryophyte species (Marshall and Proctor 2004). The bryoflora of the current study also contained species with variable light preferences, ranging from shade-tolerant species (with a light index of 3) to light-demanding species (with a light index of 8) (Fig. 2). As in young (7- to 8-year-old) hybrid aspen plantations (Tullus et al. 2012b), the share of light-preferring species, typical of open grassland communities, was continuously high in midterm plantations as the species with light indices of 5–7 formed the most numerous group (Fig. 2).

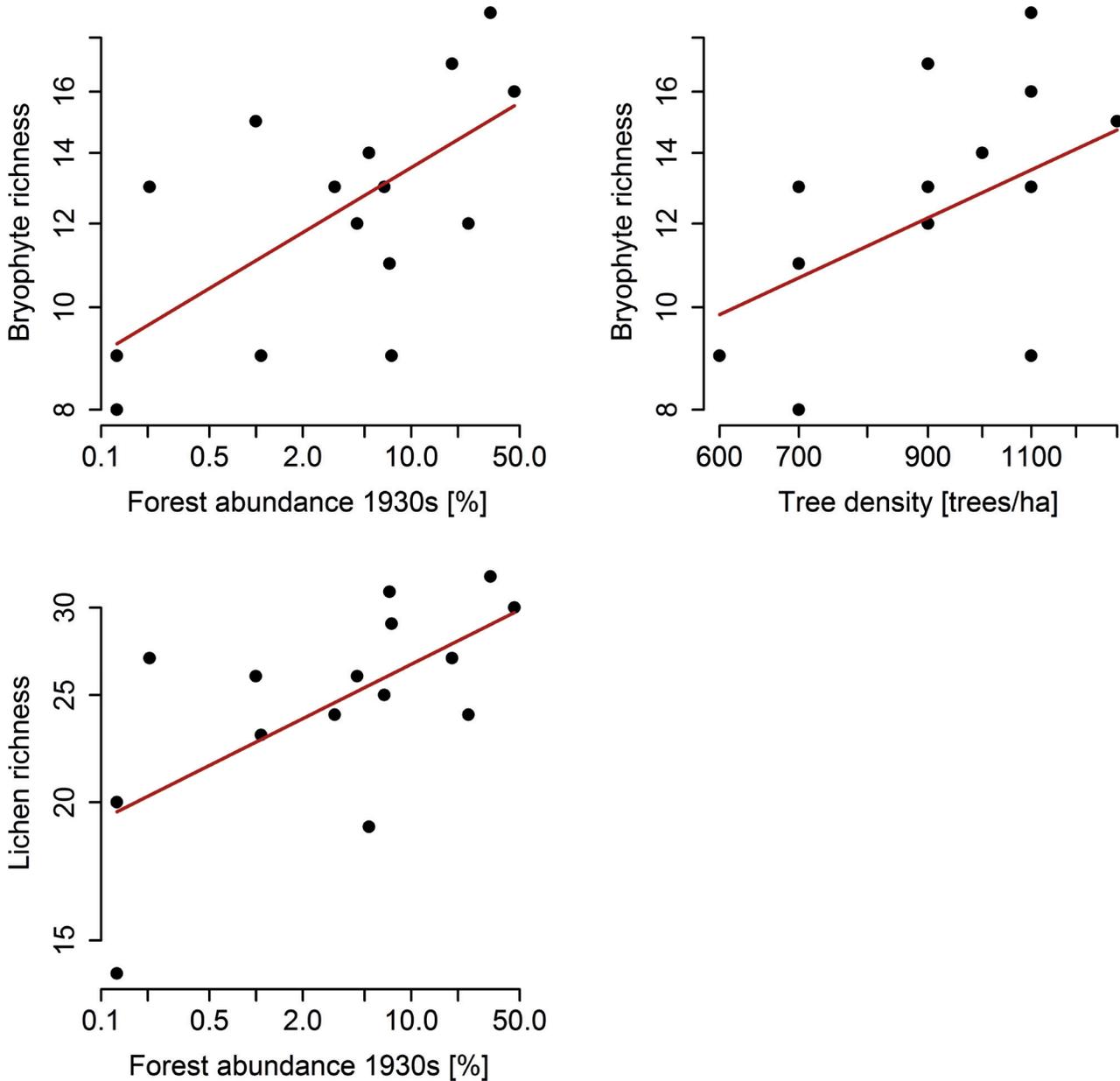
Most tested landscape-scale factors strongly influenced the richness and composition of lichens and bryophytes. Only current forest cover in the plot surroundings did not have any effect on studied biodiversity elements. Forest cover in the surroundings of the study plot in the 1930s strongly determined the richness of both bryophytes and lichens (Fig. 4), including the richness of sexual and vegetative lichen taxa. The distance from the study plot to the nearest contemporary forest and the distance from the study plot to the nearest continuously occurring forest significantly affected the variation of lichen species composition (Table 5; Fig. 5). These results indicate the importance of landscape structure and quality on species colonization patterns. First colonizers among epiphytes, sexual crustose lichens, are characterized by long-range dispersal via ascospores, while both vegetative propagules of lichens (Dettki and Esseen 2003) and a large fraction of bryophyte diaspores (Sundberg 2005) are suitable for short-distance dispersal. This is explained by the fact that sexual diaspores are commonly distinctly smaller than asexual diaspores and thus seem to fit to a ruderal strategy of dispersal over longer distances, including between unoccupied patches (Calviño-Cancela et al. 2013). In our study, the distances from the study plot to the closest forest remained between 35 and 670 m (Table 1). Various values of the effective dispersal distance for asexual lichens are suggested, but generally they remain within a few hundreds of metres (Walser 2004). For example, for an epiphytic foliose lichen *Lobaria pulmonaria*, the maximum dispersal ranges from 30 to 75 m for vegetative propagation by isidioid soredia and thallus fragments have been reported (Öckinger et al. 2005; Jüriado et al. 2011). However, it is commonly accepted that extreme events such as wind storms or long-distance vectors such as birds may carry not only the light sexual propagules, but also the heavier vegetative propagules of lichens, several hundreds of metres (Walser 2004). Therefore it is not impossible that asexual lichen species would colonize the trees in plantations located farther from the closest forest than the generally accepted effective dispersal distance of these species, but the process may need time. Bryophytes, in general, are considered to have high potential for generative and vegetative propagation, being able to disperse long distances (Frahm 2008). Though, on a smaller spatial scale, many bryophyte species may be dispersal-limited (Snäll et al. 2003; Kimmerer 2005), emphasizing the importance of vicinity to propagule sources. Adjacent land use and high structural connectivity of landscape has been shown to be highly important in determining the community development in young or restored forests (Crouzeilles and Curran 2016).

Furthermore, our results demonstrated that distance from the closest forest was vital for the dispersal of lichens and bryophytes, as was forest quality, i.e., its area and ecological continuity. A study by Marmor et al. (2011) in the coniferous forests in Estonia revealed that forest continuity was the most important variable explaining the number of epiphytic lichen species at the forest-stand scale. The significant effect of forest continuity on the lichen species richness has been related to both the low dispersal capacity and the specific microhabitat or substrate preferences of several species. Similarly to our results, the strong effect of forest history on lichen biota has been described by Ellis and Coppins (2007b), who showed that species richness was better explained by historic woodland structure compared with the present one.

**Table 4.** Best models (with  $\Delta\text{AICc} < 2$ ) describing lichen and bryophyte species richnesses in hybrid aspen plantations.

Species richness	$\Delta\text{AICc}$	$R^2_{\text{adj}}$	Independent variable	Estimate	SE	$t$	$p$
Lichen	0	0.36	Forest area in 1930s	0.07	0.02	3.0	0.011
	1.05	0.42	Soil K	0.14	0.09	1.6	0.145
			Forest area in 1930s	0.07	0.02	2.9	0.014
Bryophyte	0	0.58	Forest area in 1930s	0.09	0.02	3.9	0.002
			Density of trees	0.59	0.20	3.0	0.012

**Fig. 4.** Effect of environmental and landscape-scale parameters on species richness estimates for lichens and bryophytes within  $10 \times 10$  m study plots (axes are in log scale). Only variables included to the best models (Table 4) are shown.



Effect of historical forest cover on current species richness indicates possible time lags in the landscape (Kuussaari et al. 2009). Species extinctions take time, and historically, larger and better connected forests still likely have higher richnesses of lichens and bryophytes in the remaining habitat patches, thus also influencing the colonization patterns of nearby plantations. Epiphytic lichens and bryophytes can have considerably delayed responses

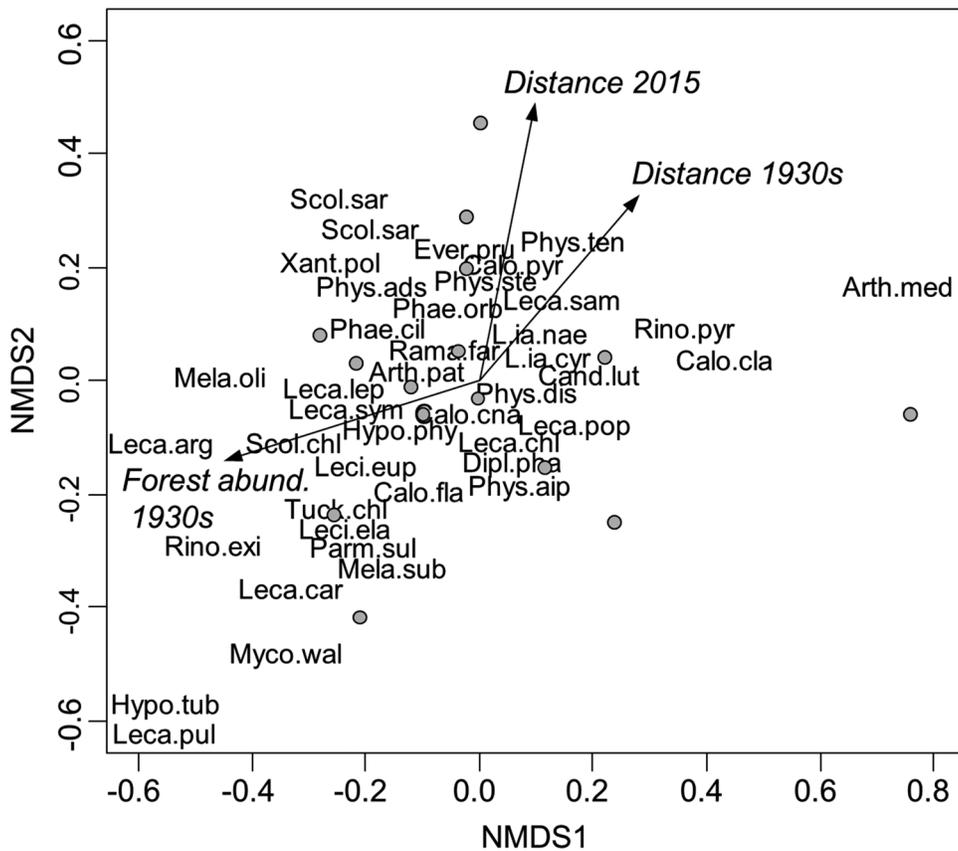
to changes in environmental conditions or landscape structure due to low rates of extinction (Snäll et al. 2004; Johansson et al. 2013a). For example, Johansson et al. (2013b) showed that habitat connectivity (density of oak trees) of almost 180 years ago determined the current occurrence of epiphytic lichens in Swedish landscapes. It is additionally possible that in continuously occurring and historically larger forests, extant lichen and bryophyte

**Table 5.** Relationships between lichen/bryophyte species compositions (NMDS ordinations; Figs. 5 and 6, accordingly) and environmental variables in midterm hybrid aspen plantations.

Environmental or landscape factor	Lichens		Bryophytes	
	$r^2$	$p$ value	$r^2$	$p$ value
Tree height	0.15	0.358	0.13	0.441
Diameter at breast height	0.17	0.291	0.24	0.198
Tree density	0.13	0.439	0.04	0.78
Basal area	0.03	0.844	0.08	0.612
Soil pH	0.15	0.373	0.02	0.899
Soil P	0.01	0.936	0.49	<b>0.022</b>
Soil K	0.19	0.268	0.03	0.84
Soil organic C	0.07	0.623	0.02	0.895
Soil N	0.2	0.228	0.24	0.19
Canopy openness	0.02	0.88	0.51	<b>0.025</b>
Transmitted total radiation	0.04	0.78	0.52	<b>0.023</b>
Distance from continuous (since the 1930s) forest	0.47	<b>0.015</b>	0.27	0.165
Distance from forest in 2015	0.62	<b>0.004</b>	0.02	0.906
Forest area in the vicinity in the 1930s	0.56	<b>0.004</b>	0.42	<b>0.042</b>
Forest area in the vicinity in 2000	0.31	0.13	0.23	0.218

**Note:** The  $r^2$  values indicate the strength of correlation between respective environmental or landscape-scale factor and the NMDS ordination axes scores;  $p$  values are based on random permutations of the data; significant ( $p < 0.05$ ) relationships are indicated in bold.

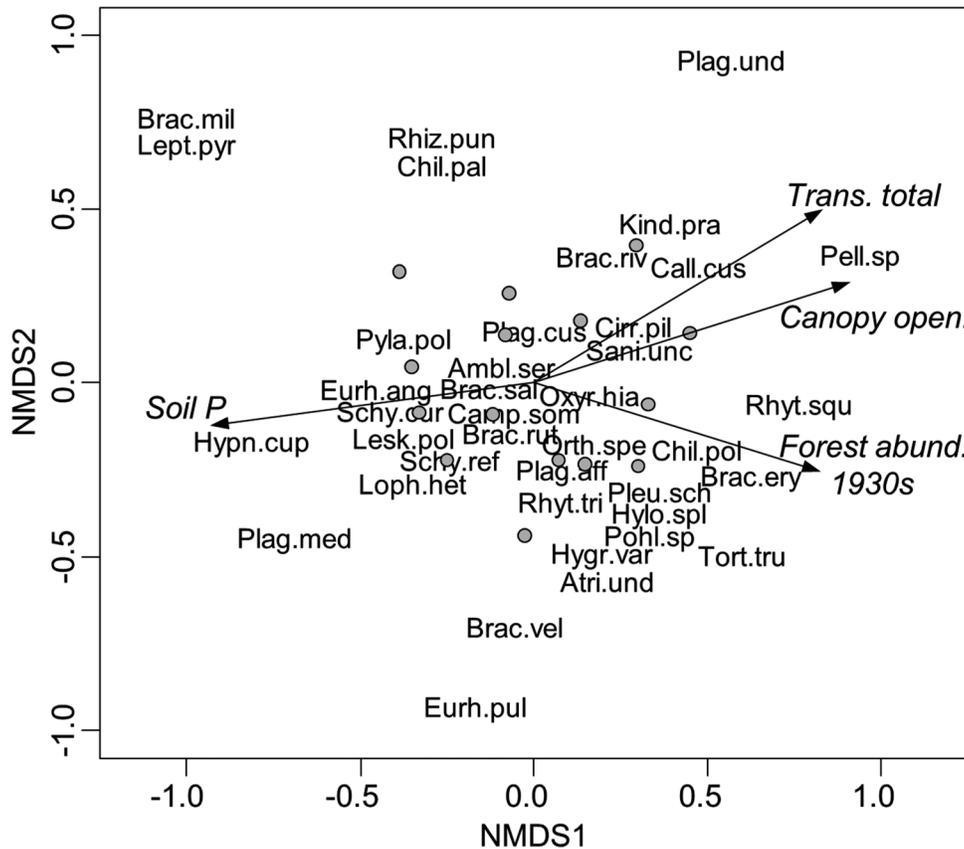
**Fig. 5.** NMDS ordination of study plots and lichen species (stress 0.12). The arrows indicate the direction and strength of correlation ( $r^2$ ) for environmental vectors that were significantly ( $p < 0.05$ ) related to ordination (see also Table 5). Study plots are indicated with grey circles. Forest abund. 1930s, forest area in the vicinity of study plot in the 1930s; Distance 2015, distance from study plot to natural forest in 2015; Distance 1930s, distance from study plot to continuous (since the 1930s) forest. For abbreviations of species names, see Table 2.



populations are still larger, genetically more diverse, and more viable, providing also more propagules for establishing new populations (Jüriado et al. 2011). Such time lags can also provide conservation opportunity: in landscapes where historically large forest habitats have harboured high diversity of lichens and bryophytes, increases in forest cover can help to avoid possible future

extinctions by enhancing functional connectivity between populations and increasing metapopulation size (Johansson et al. 2013a). Our results show that even short-rotation hybrid aspen plantations can in part contribute to mitigating the effects of habitat loss and fragmentation, but only if they are close to possible colonization sources.

**Fig. 6.** NMDS ordination of study plots and bryophyte species (stress 0.19). The arrows indicate the direction and strength of correlation ( $r^2$ ) for environmental vectors that were significantly ( $p < 0.05$ ) related to ordination (see also Table 5). Study plots are indicated with grey circles. Forest abund. 1930s, forest area in the vicinity of study plot in the 1930s; Soil P, concentration of available P in soil A horizon; Canopy open., canopy openness; Trans. total, transmitted total radiation. For abbreviations of species names, see Table 3.



To conclude, hybrid aspen plantations support remarkable species diversity of lichen-forming fungi and bryophytes already at such a young age as 16–17 years. The predicted felling age of hybrid aspen is less than 30 years (Tullus et al. 2012a); thus, an increase in species richness of both studied groups can be expected during the next dozen or more years, considering that the increasing diameter of tree stems and stumps left after harvest will provide new habitats for bryophytes and lichens (Tullus et al. 2012b). This assumption is in accordance with a recently described unimodal trend in species richness on European aspen revealing the addition of species to a lichen community during an earlier phase of tree growth (20–80 years), with a peak (80–100 years) and subsequent loss of species from a community during a later phase of tree growth (>100 years) (Ellis and Ellis 2013). It can also be assumed that the current successional stage of epiphytic lichen communities in studied plantations, composed mainly of sexual crustose species, will change during the following years and more asexual species (crustose, foliose, and fruticose) will inhabit the trees as greater competitive ability of asexual lichens in establishment within more crowded microhabitats has been suggested (Ellis and Coppins 2007a). Similar results were received in the eucalypt plantations of different ages in Spain where crustose lichens with sexual reproduction were especially linked to young and intermediate stages, whereas asexual lichens were more frequently recorded in later stages (Calviño-Cancela et al. 2013). However, in contrast to eucalypt plantations, where lichen species richness and abundance remained low also in mature stands, hybrid aspen plantations may achieve some ecological value at their later ages. In regions where historical forests areas are present and nearby, hybrid aspen plantations can increase functional con-

nectivity for a number of lichen and bryophyte species and provide support for preservation of landscape-scale biodiversity. To additionally increase the effectiveness of hybrid aspen plantations, green-tree retention in hybrid aspen plantations should be considered as recommended for native aspen forests (Hazell and Gustafsson 1999; Rosenvald and Lõhmus 2008). In the case of leaving retention trees in plantations, the planted stands may act not only as sink habitats that the species can colonize 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. Green-tree retention in hybrid aspen plantations will probably raise the overall biodiversity value of these short-term plantations. However, it is not currently known which lichen and bryophyte species really are able to colonize the hybrid aspens by their felling age, and thus further studies of epiphytic communities in hybrid aspen plantations should be performed before their clearcut.

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## Appendix A

**Table A1.** Correlation matrix of studied environmental and landscape-scale variables and species richnesses of bryophytes (Bry\_R) and lichens (Lic\_R) in mid-term hybrid aspen plantations.

	H	DBH	Den_T	BA	S_pH	S_P	S_K	S_C	S_N	Can_O	Tr_TR	Dis_O	Dis_C	Lic_R	Bry_R
H	1														
DBH	0.93	1													
Den_T	0.31	0.15	1												
BA	0.89	0.86	0.62	1											
S_pH	-0.14	-0.21	0.23	-0.08	1										
S_P	0.28	0.41	0.01	0.34	-0.01	1									
S_K	-0.08	-0.08	0.09	-0.06	0.61	-0.04	1								
S_C	0.05	0.09	0.62	0.39	0.11	-0.05	0.08	1							
S_N	-0.24	-0.32	0.42	-0.03	0.14	-0.47	0.17	0.65	1						
Can_O	-0.27	-0.44	-0.24	-0.43	-0.18	-0.49	-0.18	-0.21	0.2	1					
Tr_TR	-0.23	-0.37	-0.25	-0.39	-0.13	-0.48	-0.24	-0.18	0.18	0.98	1				
Dis_O	-0.37	-0.5	-0.09	-0.42	0.1	-0.2	0.14	-0.22	0.23	0.48	0.41	1			
Dis_C	-0.11	-0.24	-0.02	-0.18	0.14	-0.35	-0.32	0.19	0.43	0.38	0.42	0.34	1		
Lic_R	-0.33	-0.32	0.11	-0.23	0.05	-0.31	0.4	0.1	0.28	0.18	0.08	0.64	0.02	1	
Bry_R	-0.03	-0.2	0.45	0.06	0.08	-0.19	-0.04	0.08	0.18	0.17	0.12	0.62	0.37	0.56	1

Note: For abbreviations of variables, see Table 1.