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The effect of stand age on biodiversity in a 130-year chronosequence of *Populus tremula* stands

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ABSTRACT

The effect of stand age on biodiversity in the stands of *Populus tremula*, a keystone tree species in boreal forests, has been insufficiently studied, although this knowledge is crucial for maintaining biodiversity in managed forests. We studied the assemblages of vascular plants, bryophytes and lichens from a chronosequence of aspen stands (n = 20) with an age from 8 to 131 years, aiming to identify the main patterns in species richness and composition.

Altogether, 72 vascular plant species were found in the field layer and 17 species in the shrub layer. The total numbers of bryophyte and lichen species were 92 and 104, respectively. Overall, 2 vascular plant, 12 bryophyte and 9 lichen species were the taxa with a high conservation value. Sixteen lichens were regarded as management-sensitive or focal species based on earlier studies, and 10 vascular plant species were hemeraphobic (severely disturbed by human activities).

The effect of stand age on average species richness estimates depended on the studied species groups. Stand age had a negative effect on the average number of vascular plants, field layer species, apophytic vascular plants and epixylic lichens and a positive effect on the number of lichens, the number of epiphytic bryophytes and lichens and on bryophytes and lichens with a high conservation value.

The compositional patterns of vascular plants, bryophytes and lichens strongly correlated with stand age. In addition, stand characteristics, soil properties and light conditions influenced the assemblages, although the direct effects were variable for different groups. The largest differences could be observed in vascular plant, bryophyte and lichen communities between young and old stands; for lichens, also mature and old stands differed significantly.

Our results indicate that more than 60 years are required for the recovery of some species groups after clear-cutting. At the same time, other species groups were either not negatively affected by clear-cutting or showed a higher richness in younger stands. Therefore, we conclude that the management of aspen stands should involve the combination of different management regimes on the landscape scale (variation from short to long rotations in different stands, maintaining retention trees and ceasing of clear-cutting in some stands). Our results also show that as second-storey *Tilia cordata* played an important role in maintaining biodiversity in the studied stands, this tree species needs to be preserved in forests where lime trees naturally grow as co-dominants.

1. Introduction

European aspen (*Populus tremula* L.) is a keystone tree species in boreal Europe (Kivinen et al., 2020; Rogers et al., 2020) and host numerous specialist species (Kuusinen, 1996; Kouki et al., 2004), including rare and red-listed bryophytes and lichens (Tikkanen et al., 2006; Mežaka et al., 2010; Tarasova et al., 2017). Aspen has more host-specific lichen species associated with it than any other boreal tree species (Hedenås and Ericson, 2000), and it is also considered as the best substitution offering a suitable substrate for the greatest part of threatened lichen species that are usually growing on temperate broadleaved trees in hemiboreal forests (Marmor et al., 2017).

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High diversity values and unique communities of bryophytes and lichens are usually found in old aspen stands as many aspen-associated species depend on the presence of large, old trees that may provide different and more diverse habitats than smaller trees (Hazell et al., 1998; Ellis et al., 2013), together with longer time periods for colonisation and growth (Ódor et al., 2013). Forest stand age is especially important when epiphytic communities are studied, and this characteristic has been pointed out as one of the most important factors affecting the species richness of epiphytes (Mežaka et al., 2010). However, the responses of different taxonomic groups may vary; e.g., Tarasova et al. (2017) observed an increase in the total number of lichens with increasing time-since-disturbance but an insignificant correlation in the case of bryophytes.

Epiphytic communities of aspen stands are also affected by forest stand structure, which determines light conditions (Gustafsson and Eriksson, 1995). Another important trait for epiphytic assemblages is the presence and composition of accompanying tree species (Ódor et al., 2013) because bryophyte and lichen species compositions on different tree species vary considerably (Hazell et al., 1998; Jüriado et al., 2003; Mežaka et al., 2008). In addition to the characteristics of the tree layer, the richness and composition of bryophyte and lichen communities in aspen stands are impacted by the amount and quality of deadwood, as many specialist species colonise dead aspen wood (Andersson and Hytteborn, 1991; Crites and Dale, 1998).

The successful regeneration and establishment of aspen as a light-demanding pioneer species usually depends on either natural disturbances (e.g., fires, storms) or forest logging (e.g., clear-cutting), which are followed by the rapid formation of a new stand mainly from root-suckers or, seldom, from seedlings (Worrell, 1995). Already young (16–17-year-old) aspen trees offer suitable habitat for several common epiphytic lichens, mainly from the functional group of sexually reproducing crustose species (Randlane et al., 2017). The value of aspen as a host tree in cutover sites can be retained by leaving retention trees (Kivinen et al., 2020; Rogers et al., 2020). Several studies have concluded that retained aspens function as lifeboats for old-forest bryophytes and lichens (Oldén et al., 2014; Lundström et al., 2013), although the life-boating success depends on the life-history traits of species (Oldén et al., 2014), and the epiphyte communities on retention trees change remarkably over time (Lõhmus and Lõhmus, 2010). At the same time, it is still unclear at what age the new tree regeneration starts to host rare or ecologically important epiphytic species.

The effects of clear-cutting on forest flora are long-lasting (Duffy and Meier, 1992). For example, Dynesius and Hylander (2007) pointed out that differences in bryophyte communities of boreal stream-side forests remained significant even 30–50 years after clear-cutting, including the reduced species richness of forest species and liverworts, of which the latter is considered especially vulnerable to harvest-induced changes (Dovčiak et al., 2006; Dynesius, 2015). Other taxonomic groups, such as vascular plants, are less sensitive to logging than bryophytes and lichens (Haeussler et al., 2002, Åström et al., 2005; Tonteri et al., 2016) but still may strongly be influenced by clear-cutting. The overall species richness of vascular plants often increases after clear-cutting due to the appearance of early successional species (Haeussler et al., 2002; Pykälä, 2004), but the richness and abundance of late successional old-forest species may decline drastically (Hannerz and Hånell, 1997; Tonteri et al., 2016). Concerns have been raised that if the rotation length is short, the populations of old-forest species do not have enough time to recover, resulting in long-term loss of biodiversity and impoverished flora (Halpern and Spies, 1995). Species severely disturbed by human activities (hemeraphobic species) (Trass et al., 1999) may be especially vulnerable to shortened rotation lengths. Due to the fast tree growth, the legitimate minimum felling age for aspen stands is quite low and varies between 30 and 50 years in commercial forests of the region (Anonymous, 2000, 2010, 2012, 2015, 2017a, 2020). Another reason behind the short rotation length is the aim to minimise the damages caused by the trunk rot fungus *Phellinus tremulae*, which are highly common in older stands (Tamm, 2000).

To date, the recovery of assemblages of different taxonomic groups in aspen stands throughout the full rotation period has been insufficiently studied, although this knowledge is crucial for maintaining biodiversity in managed forests. In the current study, we address the recovery process of vascular plant, bryophyte and lichen communities in aspen stands, where the second layer of lime (*Tilia cordata* Mill.) is also present, by using a chronosequence of stands (n = 20) with an age ranging from 8 to 131 years. The main aims of our research were as follows: (i) to study the impact of stand age on the species richness of vascular plants, bryophytes and lichens and, separately, on the richness of different species groups (shrub and field layer species, vascular plant groups with variable sensitivity to human impact, bryophyte and lichen communities on different substrate types and taxa with a high conservation value); (ii) to test the compositional differences in vascular plant, bryophyte and lichen communities among young (age < 30 years), mature (age 30–60 years) and old (age > 60 years) stands and analyse which stand and site characteristics (tree species composition, light and soil properties) influence the compositional patterns; (iii) to evaluate the role of second-layer lime trees in hosting the epiphytic biodiversity in comparison with overstorey aspens.

We expected to see 1) a negative impact of stand age on the overall species richness of vascular plants but an opposite trend for the richness of hemeraphobic vascular plants; 2) a positive impact of stand age on the overall species richness of bryophytes and lichens, especially on a) the richness of epiphytic and epixylic species and on b) the richness of taxa with a high conservation value. We hypothesised that 1) due to the differences in stand characteristics, the largest compositional differences can be observed between young and old stands, and 2) stand and site factors that govern compositional patterns are variable for different taxonomic groups. We predicted that lime trees host some unique epiphytic species in comparison with aspens and therefore contribute substantially to the diversity of epiphytic communities in the studied stands.

2. Materials and methods

2.1. Study area

The study was carried out in southeastern Estonia, located within the hemiboreal vegetation zone and the northern temperate climatic zone, with the long-term (1966–2010) mean annual temperature of 6.1 °C and a mean annual precipitation of 708 mm in the study region (Tarand et al., 2013). Data were collected from 20 European aspen-dominated stands (Fig. 1, Table 1), where *Tilia cordata* is a typical accompanying tree species in fertile sites. Stands were situated in the area of the Järvselja Training and Experimental Forestry District. All stands originated from natural regeneration, formed mainly after clear-cutting, and the ages of the stands ranged from 8 to 131 years, according to the Forest Register of Järvselja Forestry District (jarvselja.emu.ee). A few of the studied stands were thinned, however due to the risk of moose browsing, intermediate cuttings are seldom carried out in aspen stands in the study area. The stands were located on nutrient-rich mineral soils typical for this region, representing *Aegopodium* (12 stands), *Oxalis-Myrtillus* (4), *Oxalis* (2) or *Filipendula* (2) forest site types (Lõhmus, 1984).

2.2. Data collection

Data were collected in the summer of 2016. In each stand, a square plot with the size of 100 m^2 was established, with sides positioned parallel to the cardinal directions (Noreika et al., 2019), and species lists of vascular plants, bryophytes and lichens were compiled. The abundance of vascular plant and bryophyte species was estimated visually based on a 5-point cover-abundance scale (1 – cover 1–5%, 2 – cover 6–20%, 3 – cover 21–50%, 4 – cover 51–75%, 5 – cover 76–100%; for species covering less than 1%, the abundance value 0.5 was used). The

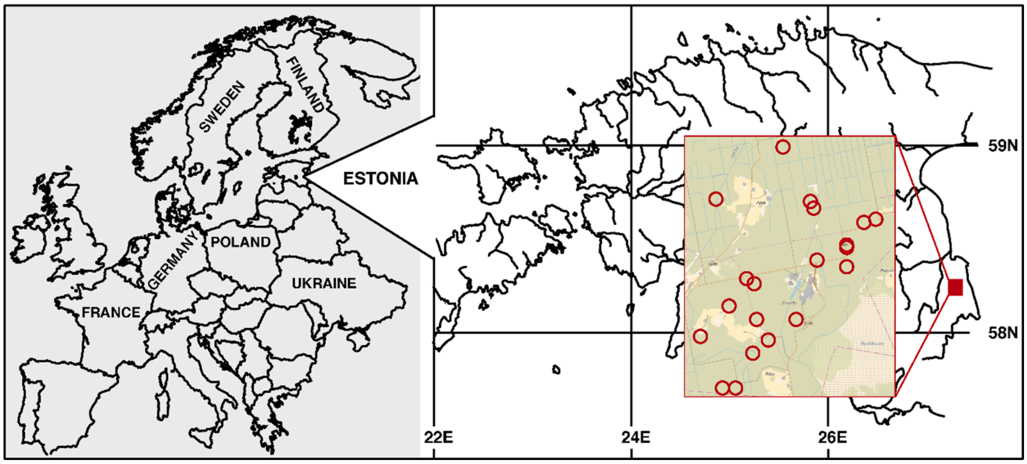

Fig. 1. Locations of the study sites (red circles). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Main characteristics of study sites. DBH – stem diameter at breast height, BA – basal area of stand. Age groups: Y – young, M – mature, O – old stands.

Stand code	Age (yrs)	Age group	1st storey *Populus tremula*			1st storey other species			2nd storey *Tilia cordata*			2nd storey other species		
			Height (m)	DBH (cm)	BA (m^2/ha)	Height (m)	DBH (cm)	BA (m^2/ha)	Height (m)	DBH (cm)	BA (m^2/ha)	Height (m)	DBH (cm)	BA (m^2/ha)
JS253-9	8	Y	11.1	6.9	9.3				2.0	1.5	1.8			
JS240-18	9	Y	11.1	8.2	15.4				10.1	11.5	5.8			
JS208-1	14	Y	12.7	7.8	11.8	15.0[a]	10.8[a]	2.8[a]	10.9	9.6	7.1	10.3[c]	7.6[c]	0.9[c]
JS243-10	15	Y	14.0	9.3	12.6				5.6	3.5	4.3			
JS305-6	24	Y	15.1	8.7	20.1				10.8	6.9	14.5			
JS267-1	28	Y	15.0	8.3	18.9	15.0[a]	8.0[a]	0.1[a]	13.9	10.5	3.5			
JS208-7	29	Y	23.6	20.1	39.8	24.7[b]	21.9[b]	11.4[b]	12.3	8.5	8.0			
JS203-2	30	M	25.1	14.2	37.3				15.7	9.6	10.3	13.2[d]	10.0[d]	3.5[d]
JS294-11	39	M	26.8	26.2	34.9	25.9[a]	17.7[a]	0.2[a]	12.6	10.1	7.3	12.3[e]	7.5[e]	1.3[e]
JS269-8	40	M	31.0	30.8	71.7				12.9	8.6	14.8			
JS283-2	41	M	30.6	26.2	27.0				16.6	9.5	9.5			
JS171-4	45	M	26.2	21.5	35.7				12.2	8.8	13.6			
JS260-7	55	M	31.6	35.9	46.1				19.7	13.1	9.7	19.4[b]	13.9[b]	0.1[b]
JS297-7	65	O	31.7	27.7	30.5				11.1	6.7	5.6	10.1[d]	9.3[d]	0.7[d]
JS228-10	70	O	35.2	31.4	39.3				12.2	9.3	2.6	12.8[c], 9.2[d]	8.0[c], 12.0[d]	1.6[c], 1.1[d]
JS253-2	70	O	37.3	33.3	53.4				22.1	16.1	8.3	12.0[d]	11.7[d]	1.1[d]
JS251-8	75	O	39.4	38.9	85.1				16.1	15.5	10.6			
JS243-6	95	O	40.0	49.5	77.8				22.0	14.9	10.9	7.6[d]	8.7[d]	2.0[d]
JS242-12	99	O	40.0	67.8	72.4				16.5	10.0	10.6			
JS272-17	131	O	37.9	63.9	64.1				13.3	11.7	16.0			

[a]*Betula* spp.; [b]*Alnus* spp.; [c]*Fraxinus excelsior*; [d]*Picea abies*; [e]*Acer platanoides*

cover of bryophyte species on other substrates but ground was estimated visually, taking into account the cover percentage on the available amount of the substrate type on the plot. In the case of vascular plants, separate lists were compiled for field layer (including ferns, grasses, sedges, herbs and dwarf-shrubs) and shrub layer (including shrubs and young trees and tree seedlings found growing in this layer with less than 25% from the first storey tree height). In the case of bryophytes and lichenised fungi, separate species lists were compiled for different substrate types within the plot, e.g., ground, trunks (up to 2 m), branches and bases of different tree species, deadwood. Specimens that were difficult to identify in the field were collected for further investigation under a stereo- or light microscope. Standardised thin-layer chromatography (TLC) using solvent system A (Orange et al. 2001) was performed to confirm the identification of several lichen specimens.

Tree measurements were carried out in the 10 × 10-m vegetation plots by separating aspens in the 1st layer and limes in the 2nd tree layer. All other species (*Betula* spp., *Alnus* spp., *Fraxinus excelsior*, *Picea abies* and *Acer platanoides*) were recorded for both tree layers, but their share was minor from the stand basal area (Table 1). In the 10 × 10-m plots, height (m) with a Vertex IV and stem diameter at breast height (cm) with a forest calliper were recorded for each individual tree. The plot-based diameters at breast height were summed for each tree species in the given tree layer and then transformed to the hectare scale (m^2 ha^{-1}) (Table 1).

Soil sampling was conducted in summer 2016, along with the vegetation surveys. Five subsamples were taken from the centre and from each corner of the 10 × 10-m sample plot and then mixed together to obtain a homogenous composite soil sample. Samples were taken from the 0–5-cm depth after the removal of the forest floor. Soil acidity (pH_{KCl}) was determined from the 1 M KCl suspension at a 10 g: 25 ml ratio; the concentration of total nitrogen (N, %) was determined via the Kjeldahl method, and organic matter (C_{org}, %) was measured with the loss on ignition method at 360 °C for two hours. The concentrations of available phosphorus (P, mg kg^{-1}) and potassium (K, mg kg^{-1}) were extracted with ammonium lactate solution and those of available calcium (Ca, mg kg^{-1}) and magnesium (Mg, mg kg^{-1}) were extracted with ammonium acetate solution (5 g in 100 ml ratio with shaking time of 90 min). All soil chemical analyses were carried out in the Laboratory of Plant Biochemistry at the Estonian University of Life Sciences.

Hemispherical photos were taken at the height of the field layer from five different positions (centre and corners of the plot) in each plot, using a Sigma 8-mm F3.5 EX DG Circular Fisheye lens attached to a Canon EOS 5D digital camera. The photos were analysed using the software Gap Light Analyzer 2.0 (Frazer et al., 1999) to estimate canopy openness and the amount of canopy-transmitted direct, diffuse and total solar radiation incident on a horizontal receiving surface. The averaged values of the five measurements were used for further data analyses.

2.3. Data analysis

Tree species diversity for each 10 × 10-m plot was characterised using the Simpson's diversity index (*D'*) (Eq. (1)):

$$Dtrees' = 1 - \sum_{i=1}^{n} p_i^2 \tag{1}$$

where p_i is the proportion (based on basal area) of first and second storey tree species and n is the number of first and second storey tree species in the given plot.

The nomenclature followed Leht (2010) for vascular plants, Vellak et al. (2015) for bryophytes and Randlane et al. (2019) for lichenised taxa. Species with a high conservation value were defined as protected, threatened or near-threatened species or indicator species of woodland key habitats. The conservation status of species was attributed according to the Estonian Nature Conservation Act (Anonymous, 2014), and the woodland key habitat species were determined according to the Estonian Forest Act (Anonymous, 2017b). The threat status of the recorded species, based on the IUCN system, was used/assigned from the latest revisions of the local Red Lists (Ingerpuu et al., 2018; Kull et al., 2018; Lõhmus et al., 2019). Sensitivity of vascular plants to human impact was determined based on Kukk (1999). Vascular plants were grouped into the following categories: hemerophobes (taxa severely disturbed by human activities), hemeradiaphors (taxa indifferent to a certain limit of human activities), apophytes (indigenous taxa preferring moderate to strong human impact) and anthropophytes (introduced taxa surviving in communities significantly changed by human activities). Sensitivity of lichens to forest management disturbances according to Lõhmus and Lõhmus (2019) was additionally highlighted, and the following categories were used: old-growth-dependent species (further: old-growth) – lichens having all or most of their populations in old-growth stands; management-sensitive species (further: sensitive) – lichens either having statistically significant preference to old stands, defined as sensitive to management stage modifications in even-aged management or infrequent substrate-specific species. Furthermore, the so-called 'focal species' determined in Lõhmus and Lõhmus (2019), i.e., taxa having different habitat requirements for forest landscapes and considered to be useful in managing biodiversity protection, were also pointed out.

The effect of stand age on the richness of vascular plants, bryophytes and lichens and on the richness of different species groups (shrub and field layer species, vascular plants with variable sensitivity to human impact, epigeic, epiphytic and epixylic non-vascular species and taxa with a high conservation value) was evaluated with a generalized linear model with a Poisson error distribution in the R Statistics software (R Core Team, 2021). Stand age values were log-transformed to improve the model fit. Normality of the residuals was checked from histograms.

Non-metric multidimensional scaling (NMDS) was used to explore assemblages of vascular plants, bryophytes and lichens, using the function "metaMDS", and Bray-Curtis dissimilarities, with the community ecology package "vegan" in R (Oksanen et al., 2013). The function "envfit" was applied to describe the relationship between the two NMDS ordination axis scores and site and stand characteristics. The assemblage of vascular plants included species from field and shrub layers.

The studied stands were divided into three age groups: young (age < 30 years, n = 7), mature (age 30–60 years, n = 6) and old (age > 60 years, n = 7), as all aspen stands belonged to quality class 1A (based on the site index), where rotation age is achieved at the age of 30 (Anonymus, 2017a). The linear correlation matrix of stand and site characteristics across all studied aspen stands was compiled. Differences among the groups in average stand and site characteristics were clarified according to the Tukey test after one-way ANOVA.

Compositional differences in vascular plant, bryophyte and lichen communities among age groups were tested with Multiresponse Permutation Procedures (MRPP), using the Bray-Curtis distance measure. To correct the p-values for multiple comparisons, Bonferroni correction was applied. Indicator Species Analysis (ISA) was performed to find vascular plant, bryophyte and lichen species characteristic for young, mature and old stands. The MRPP and ISA were carried out with PC-ORD Version 7 (McCune and Mefford, 2016). NMDS, MRPP, ISA were performed separately for vascular plants, bryophytes and lichens, using the species abundance data in the case of vascular plants and bryophytes and species presence-absence data in the case of lichens.

3. Results

3.1. Site and stand characteristics

Soil chemical properties (soil pH, N, P, K, Ca, Mg, organic matter content) were not affected by stand age (Supplementary Table S2). The characteristics of first-storey aspen and second-storey lime trees (tree height, diameter at breast height and basal area) correlated positively with ascending stand age. In comparison of stand age groups, the height and diameter of aspen trees differed significantly among young, mature and old stands, whereas for basal area, only young stands differed significantly from other age groups (Supplementary Table S3). In the case of second-storey lime characteristics, basal area was similar in all stand age groups, and height and diameter showed significant differences between young and old stands. The diversity of tree species in the first and second overstorey layers was highest in young stands and decreased along the age gradient with the growing size of aspens. Stand age had a negative impact on canopy openness, which also correlated with the basal area and height of lime trees and soil properties. At the same time, in comparison with stand age groups, the amount of canopy-transmitted light was similar in young, mature and old stands.

3.2. Species richness

Altogether, 72 vascular plant species were found in the field layer and 17 species in the shrub layer of the studied plots (Supplementary Table S1). The total numbers of bryophyte and lichen species were 92 (including 18 liverwort and 74 moss species) and 104, respectively. In addition, eight vascular plants, three bryophytes and five lichens were determined at genus level. Seventy-six taxa of bryophytes were found growing on dead-wood substrates (including 9 unique taxa recorded only on this substrate type), 68 on the ground (including 12 unique taxa), 59 on the base or trunks of aspen trees (including 2 unique taxa) and 48 on the base and trunks of lime trees (2 unique taxa) (Supplementary Table S1). Most lichens were recorded on aspen trees (68 taxa, including 11 unique taxa), followed by taxa recorded on lime trees (48 taxa, including 3 unique taxa). None of the lichen species were found growing on the ground.

The list of the most frequent species (present in the shrub and field layers of all plots) included the vascular plants *Aegopodium podagraria*, *Oxalis acetosella* and *Tilia cordata*, the bryophytes *Amblystegium serpens*, *Brachythecium rivulare*, *B. rutabulum*, *B. salebrosum*, *Eurhynchium angustirete*, *Lophocolea heterophylla*, *Plagiomnium cuspidatum*, *Sanionia uncinata*, *Sciuro-hypnum curtum*, *S. reflexum* and the lichens *Arthothelium ruanum* and *Graphis scripta*. Overall, 14 vascular plant species, 15 bryophyte species and 21 lichen species were present in one plot only. Most of the recorded species were common taxa; however, 2 vascular plant species, 12 bryophyte species and 9 lichen species were either protected, threatened/near-threatened species or indicator species of woodland key habitats. Furthermore, 16 lichens were considered either focal, old-growth or sensitive species. Based on the sensitivity to human impact, the majority of vascular plants were hemeradiaphors (61%), followed by apophytes (27%), hemerophobes (11%) and anthropophytes (1%).

3.3. Impact of stand age on the richness of different species groups

The effect of stand age on average species richness estimates depended on the studied species groups. The number of vascular plant taxa was negatively affected by ascending stand age (Table 2, Fig. 2), and the total number of vascular plant taxa was highest in young stands (88 taxa) in comparison with mature and old stands (66 and 63, respectively) (Supplementary Table S1). The negative effect of stand age was evident for the richness of field-layer species as well as for apophytic species, whereas the numbers of shrub-layer species, hemerophobes, hemeradiaphores and anthropophytes were unaffected by stand age (Table 2, Supplementary Table S4). In comparison with vascular plants, an opposite trend was revealed for lichens, as the richness of lichens was in strong positive correlation with stand age (Table 2, Fig. 3) and the total number of recorded lichen taxa was lowest in young stands (64 taxa) and highest in old stands (89 taxa) (Supplementary Table S1). The effect of stand age on the richness of bryophytes was less pronounced than in the case of lichens, as the effect of stand age on the overall number of bryophytes as well as on the number of epigeic and epixylic bryophytes remained insignificant (Table 2). However, similar to lichens, a strong positive correlation was revealed between stand age and 1) the number of epiphytic bryophytes (all epiphytes regardless of the host tree species as well as epiphytes on aspens and on limes) and 2) the number of bryophytes with a high conservation value (Fig. 2). At the same time, the individual responses of bryophyte and lichen species with a high conservation value or established management-sensitivity towards stand age were variable. Some species (e.g., *Lepidozia reptans*, *Syzygiella autumnalis*, *Buellia erubescens*, *Pertusaria leioplaca*) frequently occurred in recently clear-cut stands and *Zwackia viridis* was recorded only in 14- and 15-year-old stands (Supplementary Table S5), whereas species such as *Anomodon longifolius*, *Neckera pennata*, *Nowellia curvifolia*, *Bacidia rubella*, *Chaenotheca ferruginea* and *Usnea dasopoga* were not recorded in the stands younger than 55 years; and some species (e.g., *Alyxoria varia* and *Pertusaria albescens*) were found only from stands older than 90 years. At the same time, the liverwort species *Lejeunea cavifolia* (found uniquely on aspen trunks in this study) was recorded in the stands with variable age.

Table 2
Species richness of different species groups per plot and the effect of log(stand age) on it. Bold p-values indicate significant effects according to the Poisson regression models (the regression lines are shown in Figs. 2 and 3).

Response variable	Species richness			Effect of stand age
	min	max	mean	*p*-value
Vascular plants	23	54	35.9	**0.003**[a]
Shrub layer species	5	12	7.9	0.952[a]
Field layer species	18	45	28.1	**<0.001**[a]
Anthropophytes	0	1	0.1	0.231[a]
Apophytes	2	12	7	**0.001**[a]
Hemeradiaphors	17	34	23.6	0.105[a]
Hemerophobes	2	6	4.3	0.453
Vascular plants with a high conservation value	0	2	0.3	0.513[a]
Bryophytes	28	54	41.0	0.065
Epigeic bryophytes	9	27	17.8	0.479
Epiphytic bryophytes	9	36	25.1	**<0.001**
Epiphytic bryophytes on *Populus*	8	29	18.1	**<0.001**
Epiphytic bryophytes on *Tilia*	0	21	13	**<0.001**
Epixylic bryophytes	13	40	29.5	0.868[a]
Bryophytes with a high conservation value	0	7	2.3	**0.012**
Lichens	16	56	31.4	**<0.001**
Epiphytic lichens	8	43	25.6	**<0.001**
Epiphytic lichens on *Populus*	4	26	12.9	**<0.001**
Epiphytic lichens on *Tilia*	0	20	10.9	**<0.001**
Epixylic lichens	0	12	3.4	**<0.001**[a]
Lichens with a high conservation value	0	11	4.5	**<0.001**

[a] Stand age has a negative effect on the response variable.

3.4. Species composition

The compositional patterns of all studied taxonomic groups were influenced by stand age (Table 3, Fig. 4) and by the characteristics of aspen and (to lesser extent) lime trees. In addition, the composition of vascular plants and lichens was affected by soil properties. Soil pH and contents of Ca and Mg were important determinants for vascular plants and soil organic matter content and soil K determined lichens. Bryophytes and lichens responded to variations in canopy openness and to differences in the amount of canopy-transmitted light, and their composition was also associated with tree species diversity of the overstorey layers.

Similar to the NMDS, the results of MRPP also confirmed the importance of stand age in shaping vascular plant, bryophyte and lichen communities (Table 4). The largest differences could be observed in vascular plant, bryophyte and lichen communities between young and old stands. In the case of lichens, also mature and old stands differed significantly. The ISA pointed out 4 vascular plant, 2 bryophyte and 1 lichen species characteristic to young stands and 1 vascular plant, 2 bryophyte and 10 lichen species as indicator species of old stands (Fig. 3). The characteristic species of old stands included a protected bryophyte species *Neckera pennata*, a woodland key habitat indicative lichen species *Arthonia vinosa* and three other lichen species considered either management-sensitive (*Pertusaria leioplaca*, *Phaeophyscia ciliata*) or typical to old-growth stands (*Bacidia rubella*). None of the studied species was found to be characteristic to mature stands.

4. Discussion

In the current study, we analysed the patterns in species richness and species composition of vascular plants, bryophytes and lichens throughout a chronosequence of aspen stands with ages ranging from 8 to 131 years. The estimated life span of aspen in boreal forests usually varies between 100 and 200 years (Kivinen et al., 2020). However, old aspen stands are quite rare; for example, in 2019, only 1.4% of aspen-dominated stands in Estonia were > 100 years old (Valgepea et al., 2020).

As expected, the impact of aspen stand age on plant and lichen characteristics was evident; however, different species groups showed different responses towards the ascending stand age. The richness of vascular plants was higher in younger stands, which is in accordance with our hypothesis and with several earlier studies that have pointed out the increase in the richness of vascular plants after cutting (Pykälä, 2004; Tinya et al., 2019; Tullus et al., 2019). In our study, this was related to the higher number of apophytes in younger stands, including several species that are known to benefit from forest cutting (e.g., *Carex pallescens*, *Juncus effusus*, *Rubus idaeus*, *Solidago virgaurea*) (Götmark et al., 2005; Mayer et al., 2004). *Juncus effusus* and *Rubus idaeus* were

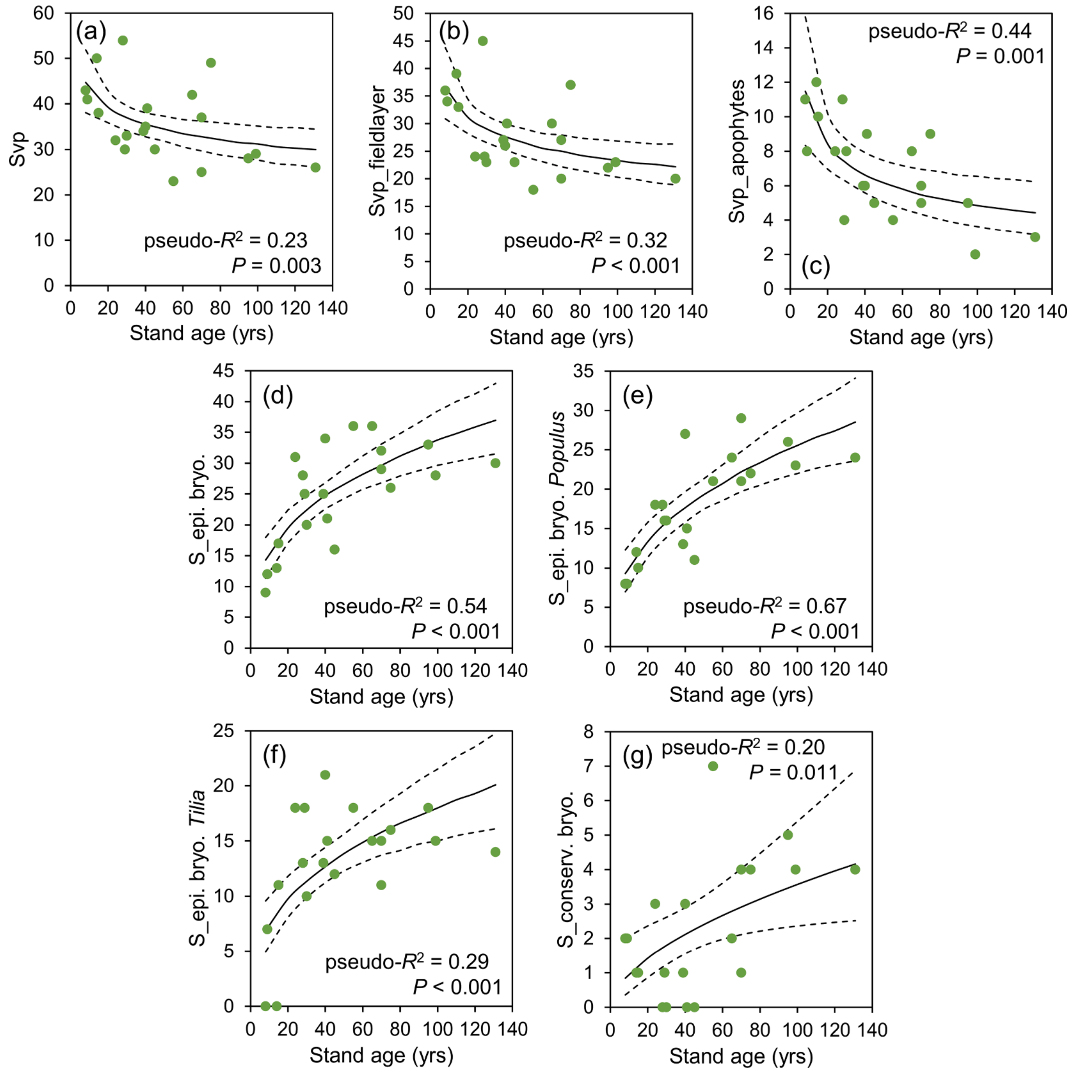

Fig. 2. Effect of stand age on the species richness of a) vascular plants (Svp), b) field layer species (Svp_fieldlayer), c) apophytic vascular plants (Svp_apophytes), d) epiphytic bryophytes (S_epi.bryo), e) epiphytic bryophytes on *Populus* (S_epi.bryo.*Populus*), f) epiphytic bryophytes on *Tilia* (S_epi.bryo.*Tilia*) and g) bryophyte species with a high conservation value (S_conserv_bryo). Solid lines depict regression lines between response variable and log(stand age), whereas dotted lines depict 95% confidence intervals.

pointed out as species characteristic to young stands; however, surprisingly, the list of indicator species of young stands also included the hemerophobe *Dryopteris expansa*. In addition, contrary to our expectations we did not observe a clear drop in the number of hemerophobes in young stands (Table 2, Supplementary Table S4), although these species are expected to be severely disturbed by management activities (Trass et al., 1999). This may refer to the high resilience of forest herb species to forest cuttings, which has been demonstrated in several studies (Götmark et al., 2005; Vanha-Majamaa et al., 2017).

Contrary to our hypothesis, stand age was not significantly correlated with species richness of bryophytes. A similar result, namely that bryophyte richness in harvested forests may be comparable to the richness of mature forests, has been observed in Estonian conifer stands after shelterwood cutting (Tullus et al., 2018). The also somewhat unexpected negligible effect of stand age on the richness of epixylic bryophyte species may indicate that the cutting residues and stumps provided the necessary growth substrate for epixylic bryophyte species in younger stands. However, as we did not evaluate the amount and quality of deadwood along the chronosequence, we cannot fully explain the reasons behind this tendency. Schmalholz and Hylander (2009) concluded that the recovery of epixylic bryophytes in clear-cut stands started before the accumulation of deadwood, indicating that a suitable microclimate may have a stronger impact than substrate availability on the recovery of epixylics. As the amount of canopy-transmitted solar radiation was similar in all stand age groups, this may be another explanation for our result for epixylic bryophytes. In the case of epiphytes and bryophytes with a high conservation value, the positive impact of ascending stand age on the richness of bryophyte groups was revealed, which is in accordance with our expectations and earlier studies (Mežaka et al., 2010; Kivinen et al., 2020).

In our study, the effect of stand age on the species richness of lichens was significant for this entire group as well as for all studied lichen subgroups (epiphytic lichens, epiphytic lichens on *Populus,* epiphytic lichens on *Tilia,* epixylic lichens and lichens with a high conservation value) (Table 2). This is in accordance with several earlier studies (Hedenås and Ericson, 2000; Ellis et al., 2013). In all lichen subgroups, species diversity responded positively to stand age, except in the subgroup of epixylic lichens, where the number of recorded species decreased in the mature and overmature stands compared to the young stands. As the studied stands mainly originated from clear-cutting, this result may refer to the importance of stumps in younger stands as a habitat for epixylic species. Altogether, 38 lichen taxa were found growing on deadwood in this study, including 18 taxa found on stumps. Stumps as suitable growth substrate for lichens were available only in

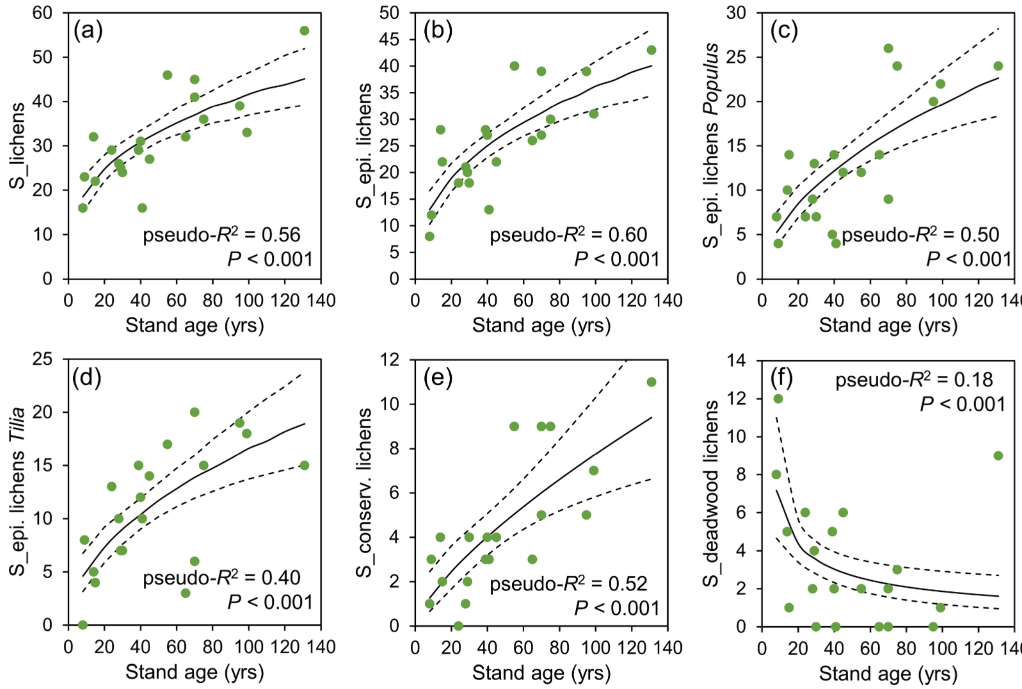

Fig. 3. Effect of stand age on the species richness of a) lichens (S_lichens), b) epiphytic lichens (S_epi.lichens), c) epiphytic lichens on *Populus* (S_epi.lichens*Populus*), d) epiphytic lichens on *Tilia* (S_epi.lichens*Tilia*), e) lichen species with a high conservation value (S_conserv.lichens) and f) epixylic lichens (S_deadwood lichens). Solid lines depict regression lines between response variable and log(stand age), whereas dotted lines depict 95% confidence intervals.

Table 3
Relationships among the species composition of vascular plants, bryophytes and lichens (NMDS ordinations, Fig. 4) and stand and site factors in an aspen chronosequence. *P*-values are based on random permutations of the data.

	Vascular plants		Bryophytes		Lichens	
	r^2	*p*-value	r^2	*p*-value	r^2	*p*-value
log(Stand age)	0.49	**0.002**	0.69	**0.001**	0.75	**0.001**
Height of aspens	0.50	**0.003**	0.58	**0.001**	0.74	**0.001**
Diameter of aspens	0.53	**0.003**	0.60	**0.001**	0.72	**0.001**
Basal area of aspens	0.39	**0.023**	0.41	**0.008**	0.57	**0.001**
Height of limes	0.43	**0.007**	0.46	**0.004**	0.63	**0.001**
Diameter of limes	0.22	0.126	0.33	**0.033**	0.58	**0.003**
Basal area of limes	0.22	0.133	0.37	**0.019**	0.23	0.101
Species diversity of tree layer	0.06	0.635	0.31	**0.043**	0.31	**0.048**
Canopy transmitted direct radiation	0.10	0.453	0.19	0.158	0.36	**0.027**
Canopy transmitted diffuse radiation	0.19	0.147	0.42	**0.002**	0.39	**0.022**
Canopy transmitted total radiation	0.15	0.243	0.33	**0.021**	0.40	**0.025**
Canopy openness	0.18	0.175	0.41	**0.003**	0.42	**0.020**
Soil pH	0.38	**0.015**	0.24	0.091	0.18	0.184
Soil N	0.13	0.306	0.02	0.876	0.29	0.051
Soil P	0.03	0.792	0.04	0.724	0.25	0.086
Soil K	0.07	0.545	0.12	0.345	0.35	**0.023**
Soil Ca	0.46	**0.004**	0.07	0.513	0.20	0.153
Soil Mg	0.47	**0.002**	0.05	0.624	0.16	0.230
Soil organic matter content	0.10	0.410	0.03	0.778	0.32	**0.033**

young stands (with ages of 8 to 28 years).

In accordance with our hypothesis, the largest compositional differences in vascular plant, bryophyte and lichen communities were observed between young and old stands, as the largest differences in tree layer characteristics (height and diameter of aspen and lime trees and basal area of aspens) could also be observed between young and old stands. Stand age was an important determinant of compositional variation for all studied species groups; however, other factors depended on the studied organism group. As for lichens, *Populus tremula* is inhabited by the greatest number of host-tree-specific species in boreal forests compared to other deciduous or coniferous trees (Hedenås and Ericson, 2000; Jüriado et al., 2003). Several of these lichen species (e.g., *Athallia cerinella, A. pyracea, Phaeophyscia ciliata, Physcia aipolia,* etc.) belonging to the alliance *Xanthorion parietinae* were recorded by us only in old stands. However, members of the other lichen community, which is considered characteristic of the old aspen forests, the alliance *Lobarion pulmonariae,* were not found in our study, not even in the old aspen stands with ages of 65–131 years. The causes for the total absence of these species are probably related to some environmental factors, for example, moisture. The cyanobacterial lichens of this alliance are confined to late-successional stands (Hedenås and Ericson, 2000), whereas other characteristics in habitat quality, e.g., the presence of conifers in older aspen stands, seem to be involved as well (Hedenås and Ericson, 2004). In all our study plots, coniferous trees were absent in the 1st storey, while *Picea abies* was present in the 2nd storey of some plots of old stands (Table 1). It may be that mixed forests have higher moisture levels than stands with only deciduous trees, offering more suitable environment for cyanolichens. The distributional and re-establishment aspects of lichens are crucial as well. For example, in the case of spore-dispersed cyanolichens, the occurence of the suitable photobiont in the surroundings is considered a fundamental prerequisite for successful establishment (Rikkinen et al., 2002; Hedenås et al., 2007). Furthermore, forest cover and historical continuity could also be important factors for cyanolichens (Jüriado et al., 2011).

Our results also show that second-storey lime trees played an important role in the studied aspen stands as they affected the light conditions (Supplementary Table S2) and, therefore, also the composition of bryophytes and lichens (Table 3). In addition, altogether, 96 bryophyte and lichen taxa were found growing on lime trees, and 3 out of 5 bryophyte and lichen taxa recorded only on lime trees had a high conservation value or were management-sensitive (*Ulota crispa*, *Lecanora albella* and *Pertusaria pupillaris*), confirming our expectation that lime trees contribute substantially to the diversity of epiphytic communities in the studied stands.

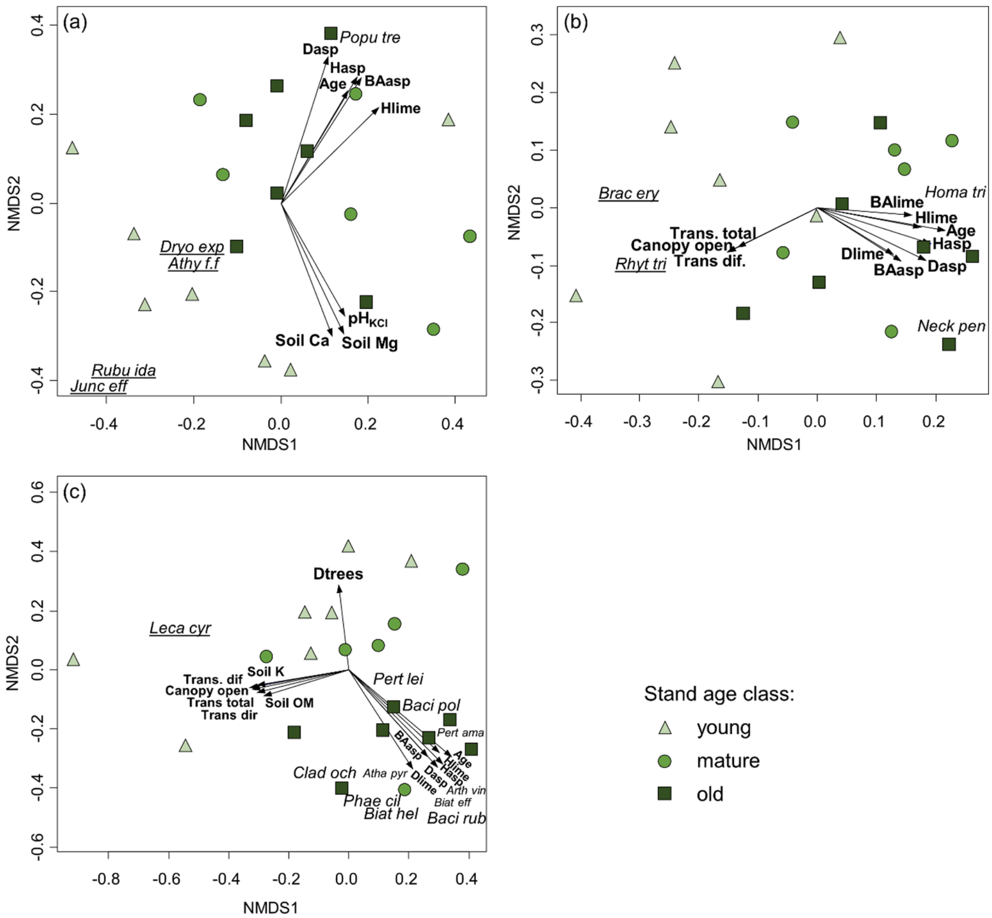

Fig. 4. NMDS ordination plot of a) vascular plant (2-dimensional solution, stress 0.19), b) bryophyte (stress 0.20) and c) lichen (stress 0.18) assemblages. Stand and site factors that were significantly ($p < 0.05$) related to ordination axes are presented: Age – age of aspen stands, Hasp – Height of aspens, Dasp – Diameter of aspens, BAasp – Basal area of aspens, Hlime – Height of limes, Dlime – Diameter of limes, BAlime – Basal area of limes, pH_{KCl} – soil pH_{KCl}, Soil K – soil K, Soil OM – soil organic matter content, Soil Mg – soil Mg, Soil Ca – soil Ca, Trans. dir – canopy-transmitted direct radiation, Trans. dif – canopy-transmitted diffuse radiation, Trans. total – canopy-transmitted total radiation, Canopy open – canopy openness, Dtrees – tree species diversity. Species that, according to Indicator Species Analysis, were characteristic of young and old stands are shown on the plot. Species abbreviations: Athy f.f – Athyrium filix-femina, Dryo exp – Dryopteris expansa, Junc eff – Juncus effusus, Popu tre – Populus tremula, Rubu ida – Rubus idaeus, Brac ery – Brachythecium erythrorrhizon, Homa tri – Homalia trichomanoides, Neck pen – Neckera pennata, Rhyt tri – Rhytidiadelphus triquetrus, Arth vin – Arthonia vinosa, Atha pyr – Athallia pyracea, Baci pol – Bacidia polychroa, Baci rub – Bacidia rubella, Biat eff – Biatora efflorescens, Biat hel – Biatora helvola, Clad och – Cladonia ochrochlora, Leca cyr – Lecania cyrtella, Pert ama – Pertusaria amara, Pert lei – Pertusaria leioplaca, Phae cil – Phaeophyscia ciliata. Under-lined species abbreviations refer to indicator species of young stands.

Table 4
Results of MRPP testing for compositional differences in the assemblages of vascular plants, bryophytes and lichens among young (n = 7), mature (n = 6) and old (n = 7) aspen stands. Bold p-values indicate significant effects after Bonferroni corrections.

Test pair	Vascular plants *p*-value	Bryophytes *p*-value	Lichens *p*-value
Young *vs.* mature stands	0.061	0.026	0.027
Young *vs.* old stands	**0.010**	**0.004**	**<0.001**
Mature *vs.* old stands	0.482	0.104	**0.004**

4.1. Management suggestions

The minimum rotation age in managed pure aspen stands in the study region varies between 30 and 50 years, although in mixed stands, it is usually higher. However, our results indicated that some studied species groups may not recover within this time period. A higher stand age increased the richness of epiphytic bryophytes and lichens and impacted positively the richness of bryophytes and lichen species with a high conservation value. Among the latter, there were several species (e.g., *Neckera pennata*, *Anomodon longifolius*) that were only found in stands at least 55 years old or older. Therefore, in these aspen forests where species conservation is the main aim, the application of longer rotation period can be recommended. As some valuable lichenised fungal species (*Alyxoria varia, Pertusaria albescens)* were found only in stands older than 90 years, the maintenance of these species should require even longer rotations or ceasing of clear-cutting. This would also give late-successional cyanolichens (not found in the current study) a chance for colonisation.

At the same time, some of studied species groups were either not negatively affected by clear-cutting or showed a higher richness in younger stands. Hence, to maintain the vascular plant, bryophyte and lichen diversity associated with aspen stands, the combination of different management regimes on the landscape scale (variation from short to long rotations in different stands, maintaining retention trees and ceasing of clear-cutting in some stands) can be recommended. In aspen forests where lime trees naturally grow as co-dominants, it is important to preserve the species instead of removing it during thinning.

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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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119833.

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