Cryptogams in Estonian alvar forests: species composition and their substrata in stands of different age and management intensity

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Species-rich alvar forests represent a rare vegetation type in northern Europe. They grow locally on shallow soils formed on calcareous parent material. The aim of this study was to compare cryptogam species richness and composition on various substrata in alvar forests of different age and management rate. Altogether 101 bryophyte and 54 lichen species were recorded. Substratum explained species variance more than did the stand age or management intensity. Younger and older forests had a different bryophyte and lichen species composition. Decaying wood was the richest as cryptogam species substratum. It had quite a unique bryophyte composition, including a high amount of hepatics. *Juniperus communis* appeared to be an important substratum for cryptogam species diversity in alvar forests. Bryophyte species composition appeared to be similar on the bases of *Pinus sylvestris*, *Betula pendula* and *Picea abies* and different on *J. communis*. Most of the recorded threatened bryophyte species grew in old subnatural forests on stones or decaying wood.

Key words: bryophyte, decaying wood, lichen, stone, subnatural forest, tree base, windthrow

Introduction

Alvar forests represent one of the rarest forest types in Europe; their distribution is limited to limestone areas in western and nothwestern Estonia (islands included) and southern Sweden (Laasimer 1965, Pettersson 1965, Engelmark & Hytteborn 1999). Therefore, from the viewpoint of protection of biological diversity, these forests are the responsibility communities for Estonia. Due to their peculiar content of flora and com-munity structure, the alvar forests represent one of the most exciting vegetation types around the Baltic Sea (Sterner 1938, Laasimer 1975). According to the Estonian Forest Law (1998), alvar forests belong to the category of protected forests where, compared with commercial for-ests, cuttings have severe restrictions.

Alvar forests cover only 3.3% of the total forests area in Estonia (2 284 600 ha) (Yearbook Forest 2005). Historically, the alvar forests' area was much larger but it has shrunk due to the

clearance for agriculture and forestry (Laasimer 1965, Kaar 2001). Earlier investigations of these forests in Estonia were dealing mainly with forest typology (Lõhmus 1984), general floristics (Lippmaa 1940, Laasimer 1946, 1965) or forest economical problems (Karu 1958, Kaar 1959, 1986). Very little attention has been paid to the cryptogams (bryophytes and lichens) in the alvar forests; only Sõmermaa (1972) discussed the lichen ecology. It is evident from the overview compiled in 1997 that about 13% of the endangered and protection-demanding forest species in Estonia are restricted to alvar forests (~50% of mammals and ~25% of vascular plants) (Viilma 2001). In Sweden, only general overviews of forests include alvar forests (Pettersson 1965, Bjørndalen 1985, Diekmann 1994), but more detailed analyses are lacking. In our previous study (Meier *et al.* 2005), we dealt with the species richness in the alvar and boreo-nemoral forests; main attention was paid to forest management and impact of its age on the species richness. The results showed clearly the negative influence of forest management on species diversity as well as the importance of old alvar forests for maintenance of a rich species pool. Here we focus on the cryptogam species composition and substrata in these forests.

Differences in the substratum features are the main factors behind the phorophyte-dependent floristic variation in forest communities, though canopy structure and habitat preferences of the trees have also some influence (Sõmermaa 1972, Kuusinen 1996, Mežaka *et al.* 2005). The effect of management on cryptogam species composition and abundance depends on the forests' habitat conditions, i.e. to what site type the stands belong (Liira *et al.* 2007); the dependency is more pronounced in unmanaged forests than in managed ones (Vellak & Ingerpuu 2005). Management and age effect on the cryptogam species composition has been studied in forests of different types (Söderström 1988b, Lesica *et al.* 1991, Boudreault *et al.* 2002, Økland *et al.* 2003), but not in alvar forests.

Cryptogams, occupying various microhabitats and substrata, are an important part of the forest biodiversity (Kuusinen & Siitonen 1998, Lõhmus 2003). Living trees are the more thoroughly investigated lichen substrata, particularly the trunks of common forest tree species (*Pinus sylvestris*, *Picea abies*, *Betula* spp., *Alnus glutinosa*, *Populus tremula*), but less attention has been paid to fine and coarse woody debris, as well as to ground and stones (Kuusinen 1996, Uliczka & Angelstam 1999, Lõhmus 2003, Jüri-ado *et al.* 2003). Bryophytes on the ground, on decaying wood and on stones (boulders) have been investigated quite well (Söderström 1981, 1993, Andersson & Hytteborn 1991, Weibull 2000, Vellak *et al.* 2003, Virtanen & Oksanen 2007). However, there are few studies dealing with the different kinds of substrata together, and thus with bryophytes and lichens too.

The aims of this study are (1) to describe the cryptogam species composition in alvar forests of different management regimes and age groups, and (2) to discuss the variation of species richness and composition on different substrata in these forests.

Material and methods

Study area

The study area was located in Vardi forestry (Raplamaa district, northwestern Estonia, Fig. 1), where alvar forests are well represented (Kaar 2001). Eutrophic *Calamagrostis* site-type alvar *Pinus sylvestris* forests (*sensu* Paal 1997) were studied.

Alvar forests grow on shallow soils (thickness less than 30 cm) formed on limestone, gravel, grit or shingle. These soils are rich in carbonates but in summer they can often be very dry, containing some moisture only in microhollows (Lõhmus 2004). Therefore, alvar forests are of low productivity and with a peculiar xeromesophilous ground vegetation reminding meadow-steppes. The tree layer is rather scarce, overshadows the ground vegetation only modestly and enables the growth of xerophytes (e.g. *Arctostaphylos uva-ursi*, *Antennaria dioica*, *Thymus serpyllum*) together with calcareous meadow and steppe species (*Sesleria caerulea*, *Filipendula vulgaris*, *Galium verum*, *Primula veris*) as well as species of sub-nemoral forests (*Hepatica nobilis*, *Melica nutans*, *Brachypodium pinnatum*, etc.) (Laasimer & Masing 1995).

The sampling pattern setup was $2 \times 2 \times 3$, i.e. forests were represented by (i) intensively managed stands, and (ii) modestly managed subnatural stands; forests of every management class were further divided into two groups: (a) younger forests about 60–80 years of age, (b) forests older than 140 years. Each forest category (experiment variant) was replicated three times. In that way, 12 forests stands were included in the study.

Management intensity was at first estimated according to the inscriptions in the forests management plans, where the available information covered the period of the last 20–30 years. This information can be considered sufficient, because the typical management of Estonian forests are thinnings at 20-year intervals (Kaar 1986), but we also examined the stands' suitability for analysis directly in nature and on this basis the final selection was decided upon. If the planned intermediate cuttings were not done, the stand was qualified as slightly managed (subnatural); if these cuttings were all done in time, i.e. there were stumps and openings of thinnings in the forests, the stand was interpreted as intensively managed. Stands without regular intermediate cuttings but with some cuttings because of windstorm impairment in 1967, were also included in subnatural stands.

Data collection

For data collection, a circular sample plot with a radius of 25 meters was analysed in each stand.

Bryophyte and lichen species were recorded on: (i) bases (up to the height 0.7 m) of randomly selected ten dominating *Pinus sylvestris* and ten *Picea abies* trees, (ii) bases of other tree species if present in the stand (*Betula pendula* up to five trees, *Juniperus communis*, *Sorbus aucuparia* and *Salix caprea* up to some trees), (iii) fine woody debris (fallen branches), (iv) decaying wood (stems and stumps, coarse woody debris, $\varnothing \geq 0.1$ m), (v) windthrows, (vi) stones (erratic boulders and limestone rocks, up to five), and (vii) ground.

Species abundance was evaluated by rank values from one to six according to the Braun-Blanquet scale (Kreeb 1983). Specimens that were not identified in the field were collected for
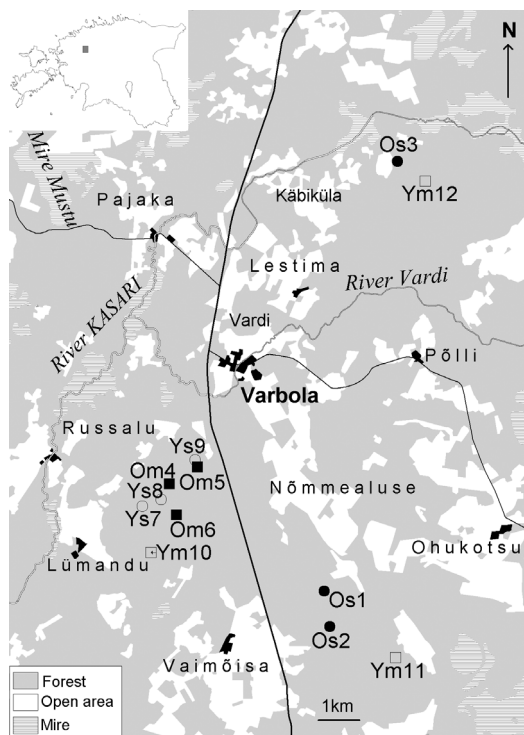
Fig. 1. Study area and location of sample plots. Notations for forest stands: Os = older subnatural, Om = older intensively managed, Ys = younger subnatural, Ym = younger intensively managed.

further laboratory investigation. It was not possible to identify all of the microlichens (sterile crustose species, e.g. *Lepraria* spp.) and we also did not identify epilithic species, due to the difficulties of collecting.

Nomenclature of bryophytes follows Ingerpuu and Vellak (1998) and that of lichens Randlane and Saag (1999). Hemerophobic species were qualified according to Trass *et al.* (1999). To those belong species sensitive to various human activities, i.e. species growing on the border of their distribution area and being rare for that reason, or growing on substrata and/or in specific ecological conditions lacking in managed forests. Red-listed species in the current study are indicated according to the Red Data Book of Estonia (Ingerpuu 1998).

Data processing

In the previous paper (Meier *et al.* 2005), we

tested the effects of forest management and age on plant species diversity by general linear models. In the current study, the variation in species composition in stands of different age and management intensity as well as on different substrata was explored using ordination techniques available in CANOCO program package (Ter Baak & Šmilauer 2002). In all analyses, lichens and bryophytes were treated separately. First, the length of the species variation gradient was estimated using the Detrended Correspondence Analysis (DCA). Second, as the gradient length appeared to be relatively short (< 2 SD), the Principal Components Analysis (PCA) — a method based on a linear relationship between species abundances and ordination axes — was used. The multi-response permutation procedures in the PC-ORD program package (MRPP-test; McCune & Mefford 1999) were used to test the cryptogam flora's compositional differences between the forests of different age and management groups: older — younger, subnatural — intensively managed stands, and four groups of forest stands: older subnatural (Os), older intensively managed (Om), younger subnatural (Ys), younger intensively managed (Ym). The indicator values of the species in forest groups were calculated according to the Dufrêne and Legrendre (1997) method included in the PC-ORD program package (McCune & Mefford 1999). Statistical significance of the obtained indicator values was evaluated with the Monte Carlo permutation test.

Next, the sample was defined according to all species growing on a certain substratum in one stand. Samples which included fewer than five species were removed from the analysis. Forest age, management intensity and substrata were treated as nominal variables and downweighting of rare species was applied. Because of the quite long (> 3 SD) gradient length revealed by the DCA, unimodal-analysis methods were exploited.

To establish forest age, management and age × management pure effects on the vegetation data, three separate partial CCA analyses were carried out, where one of the two variables and their interaction, or both considered variables in the case of testing their interaction effect, were treated respectively together with substrata variables as covariables. After that only variables having a significant effect on the analysed data were treated as covariables of substrata and analyses were repeated to estimate the pure effect of substrata. Then the CCA analysis was repeated without covariables and the variance decomposition of the considered effects was evaluated.

For ranking, all environmental variables in their importance for determining the species data the forward selection procedure available in the CCA was used.

To visualize the relationship between the vegetation data and environmental variables the Detrended Canonical Correspondence Analysis (DCCA) was chosen to avoid the distortions connected with arch effect. Detrending was done by second order polynomials. According to the results of the partial CCA, by ordination of bryophyte data, forest age and management were neglected as these variables did not have shared variance with substrata variables but by ordination of lichen data forest age was set as covariable so as in this case variance of that parameter was overlapping with substrata caused variance. At the same time, the substratum *Betula pendula* was removed from the analysis due to the high value (> 20) of the variance inflation factor, indicating multi-collinearity of this variable with some other environmental variables (Ter Baak & Šmilauer 2002).

Significance of all canonical axes (trace) and the correlation between species data and the first ordination axis was evaluated with the Monte Carlo permutation test (499 permutations).

For comparison of the species composition on different substrata, again the MRPP test and the species indicator value analysis (McCune & Mefford 1999) were performed. Cryptogams on scarce substrata such as *Sorbus aucuparia* and *Salix caprea* were excluded.

Results

Species content in forests of different management and age groups

Altogether 101 bryophyte (21 of them hepatics) and 54 lichen species were recorded (Appendices 1 and 2).

Fig. 2. Ordination (PCA) of forest stands by bryophyte data. Only hemerophobic (*) and red-listed (#) species are presented. Notations for forest stands: Os = older subnatural, Om = older intensively managed, Ys = younger subnatural, Ym = younger intensively managed. For full names of species *see* Appendix 1.
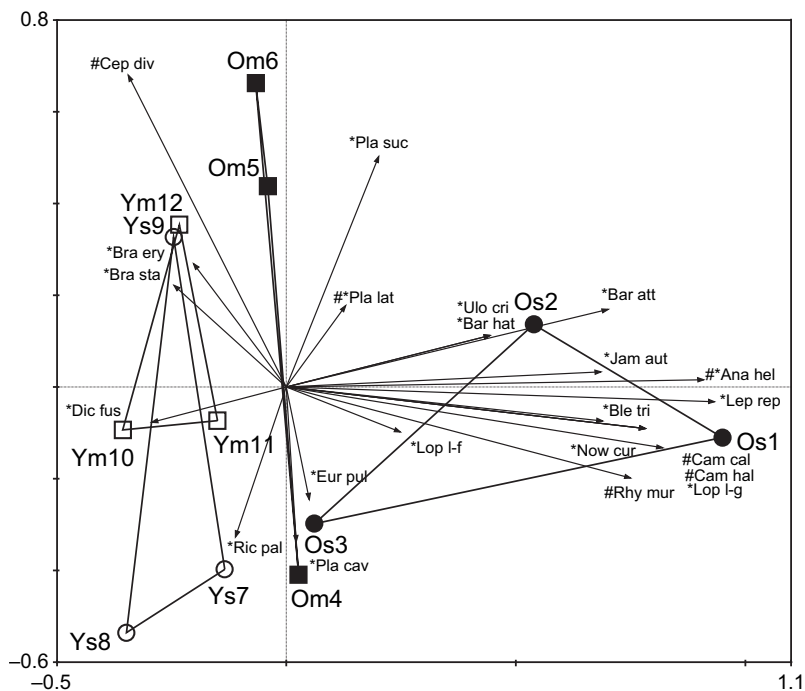
According to the bryophyte species PCA, older forests, especially subnatural ones, are rather clearly separated from younger stands in the ordination plot (Fig. 2). The first axis explained 22.7% of total variance and the second axis 14.9%. The first axis was positively correlated with the abundance of such species as *Dicranum majus* (r = 0.95), *Lepidozia reptans* (r = 0.93), *Anastrophyllum hellerianum* (r = 0.91), *Nowellia curvifolia* (r = 0.82), while a pronounced negative correlation with that axis was observed for *Brachythecium oedipodium* (r = –0.83) and *B. salebrosum* (r = –0.67). The difference in the bryophyte species composition between younger and older stands was significant as well (MRPP: p = 0.013), and the species composition differed significantly (MRPP: p = 0.007) also between all four groups of forests (Os, Om, Ys, Ym), while there was no difference in the species composition in subnatural and intensively managed forests. More hemerophobic, rare and threatened bryophyte species were bounded with older subnatural stands rather than with younger and well managed ones (Fig. 2). *Nowellia curvifolia* appeared to have a high indicator value for older forests and *Dicranum flagellare* for younger intensively managed ones.

Species indicative of older subnatural stands were *Dicranum majus*, *Ptilidium pulcherrimum* and *Blepharostoma trichophyllum* (Table 1).

Altogether 18 bryophyte species, among them 6 hemerophobes (incl. 4 hepatics), were recorded only in older subnatural forests. Six species were present only in younger intensively managed forest (incl. one hemerophobe) (Appendix 1).

On the ordination plot of lichen species, the forests of different age and management groups are, to some extent, overlapping but older and younger stands are still located separately (Fig. 3). Eigenvalues of the first and second axes were 0.217 and 0.180, respectively. The first axis was positively correlated with species such as *Imshaugia aleurites* (r = 0.84) and *Chaenotheca ferruginea* (r = 0.65) and negatively, *inter alia* with *Vulpicida pinastri* (r = –0.84), *Dimerella pineti* (r = –0.75), *Cladonia cenotea* (r = –0.65), *C. chlorophea* (r = –0.65) and *Loxospora elatina* (r = –0.65). Most of the *Cladonia* and *Cladina* species were associated with younger forests. *Imshaugia aleurites* appeared to be a good indicator for older forests and *Vulpicida pinastri* for younger forests (Table 2). Lichen species composition in older and younger forests was significantly different (MRPP: p = 0.016), while
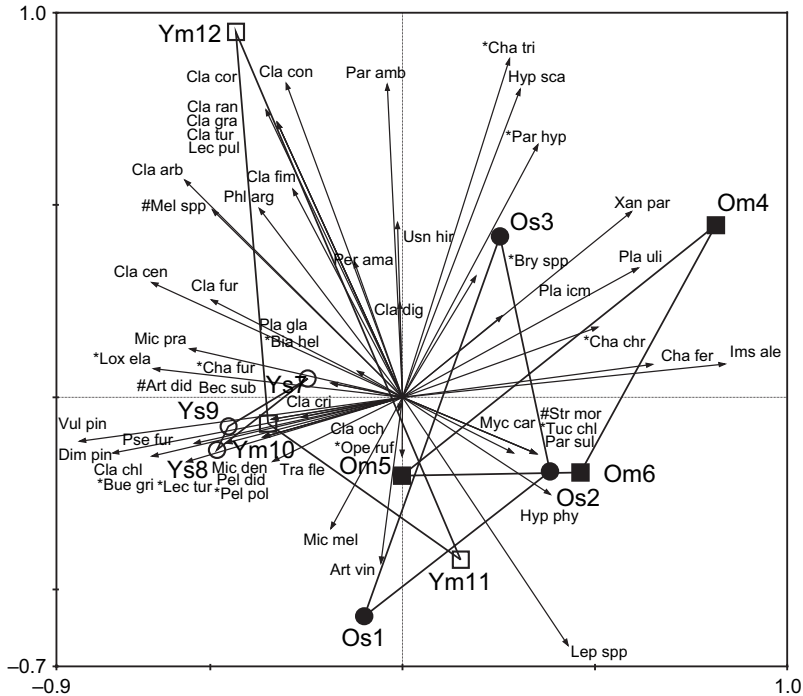
Fig. 3. Ordination (PCA) of forest stands by lichen data. Hemerophobic species are marked with an asterisk, very rare species found not more than five times in Estonia before with #. For full names of species *see* Appendix 2, other notations as in Fig. 2.

between subnatural and intensively managed forests and between all four forest groups (Os, Om, Ys, Ym) the differences were not significant. The number of hemerophobic species for subnatural stands was ten and for intensively managed stands eight (Appendix 2).

Species variance decomposition

According to the partial CCA test, forest age, management intensity and age × management interaction all had significant effects ($p = 0.002$) on bryophyte vegetation and were, therefore, further tested together with substrata data. Species variance explained by age and management (7%) was the same regardless if substrata variables were ignored or adjusted, indicating that there was no shared variance. Substratum variables explained 24% of the species total variance. 17% of total variance was connected with variables best explaining the species variance (ground, stone and windthrow).

For lichen data, forest management intensity as well as interaction of stands age and management did not have a significant effect, therefore only stand age was tested together with substratum factors. Species variance explained by age

Table 1. Bryophytes having high indicator value in forests of different age and management groups. Notations: Os = older subnatural stands, O = all older stands, Ym = younger intensively managed stands, IV$_{max}$ = maximum indicator value (%), IV$_{mean}$ = mean indicator value (%).

Species	Forest category	IV$_{max}$	IV$_{mean}$	SD	p
Dicranum majus	Os	85	34	16	0.040
Ptilidium pulcherrimum	Os	33	29	2	0.044
Blepharostoma trichophyllum	Os	80	33	15	0.045
Nowellia curvifolia	Os	50	36	9	0.076
Nowellia curvifolia	O	80	46	11	0.017
Dicranum flagellare	Ym	50	36	7	0.019
Tetraphis pellucida	Ym	54	35	11	0.076
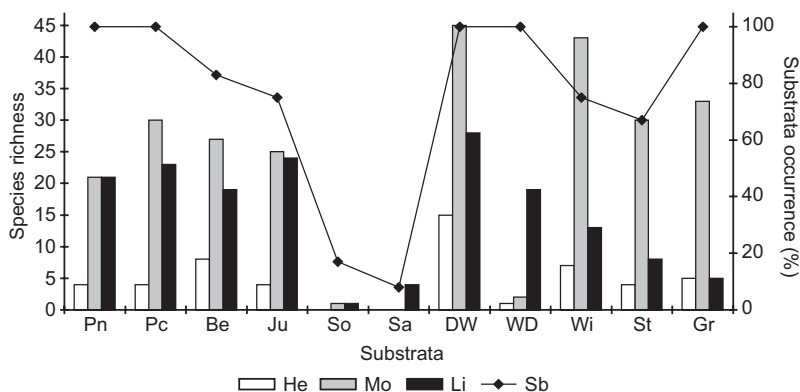
Fig. 4. Species richness on different substrata. Notations: He = hepatics, Mo = mosses, Li = lichens, Sb = substata occurrence (substrata availability in all studied stands). Pn = *Pinus sylvestris*, Pc = *Picea abies*, Be = *Betula pendula*, Ju = *Juniperus communis*, So = *Sorbus aucuparia*, Sa = *Salix caprea*, DW = decaying wood, WD = fine woody debris, Wi = windthrow, St = stone, Gr = ground.

was 5% when ignoring substratum variables and 4% when adjusting them. In that way, the amount of shared variance was only 1%. Considering the effect of age, substratum variables explained 37% of the total variance. The variables mainly determining lichen species variance were fine woody debris, stone and age, counting for 28% of the total variance.

Species richness and composition on different substrata

There was quite a striking variation in cryptogam species richness on different substrata (Fig. 4). Richness was the highest on decaying wood: 59% of the bryophyte species and 52% of the lichen species were recorded on this substratum. High bryophyte species richness was also remarkable on windthrows and that of lichen species on dif-ferent tree bases, especially on *Juniperus communis*, though the latter trees were growing only in 75% of the investigated stands. The bases of the dominant *Pinus sylvestris* were comparatively poor in bryophytes. Decaying wood was especially species-rich in hepatics (15 of the 21 registered hepatic species), likewise were the bases of *Betula pendula* and windthrows.

Comparison of species composition on different substrata (MRPP test) showed that remarkably different bryophytes grew on bases of *Juniperus communis* as compared with those on the other trees. Bryophyte assemblages on *Picea abies* were significantly different ($p < 0.05$) from those growing on *Pinus sylvestris*, while the bryophytes growing on *Betula pendula* did not significantly differ from those on both *P. abies* and *P. sylvestris* (Table 3). Lichen species composition on the various tree species was dissimilar, except for *B. pendula* and *J. communis*,

Table 2. Lichens having high indicator value in forests of different age and management groups: Notations: Y = all younger stands, O = all older stands, Ys = younger subnatural stands. IV$_{max}$ = maximum indicator value (%), IV$_{mean}$ = mean indicator value (%).

Species	Forest category	IV$_{max}$	IV$_{mean}$	SD	*p*
Imshaugia aleurites	O	83	36	12	0.023
Chaenotheca ferruginea	O	69	38	13	0.076
Vulpicida pinastri	Y	75	50	9	0.038
Cladonia cenotea	Y	73	46	11	0.045
Cladonia fimbriata	Ys	44	35	5	0.027

Table 3. Difference in bryophyte and lichen species composition on various substrata as revealed by the MRPP test (first *p* value for bryophytes, second for lichens).

	Pinus sylvestris	Picea abies	Betula pendula	Juniperus communis	Decaying wood	Fine woody debris	Windthrow	Stone
Picea abies	0.049/0.004	—	—	—	—	—	—	—
Betula pendula	0.993/< 0.001	0.336/0.003	—	—	—	—	—	—
Juniperus communis	0.001/< 0.001	0.001/0.001	0.003/0.392	—	—	—	—	—
Decaying wood	< 0.001/< 0.001	< 0.001/< 0.001	< 0.001/< 0.001	< 0.001/< 0.001	—	—	—	—
Fine woody debris	< 0.001/< 0.001	< 0.001/< 0.001	< 0.001/< 0.001	< 0.001/0.003	< 0.001/< 0.001	—	—	—
Windthrow	< 0.001/< 0.001	< 0.001/< 0.001	< 0.001/0.002	< 0.001/0.022	< 0.001/0.005	0.004/< 0.001	—	—
Stone	< 0.001/< 0.001	< 0.001/< 0.001	< 0.001/< 0.001	< 0.001/0.042	< 0.001/0.006	0.004/< 0.001	0.062/0.174	—
Ground	< 0.001/< 0.001	< 0.001/< 0.001	< 0.001/< 0.001	< 0.001/< 0.001	< 0.001/< 0.001	< 0.001/< 0.001	< 0.001/0.031	< 0.001/0.053

on which the species composition was rather similar. On decaying wood, fine woody debris, windthrows, stones and ground the composition of both bryophytes and lichens were different; overlapping appeared only for bryophytes growing on stones and windthrows, and for lichens recorded on stones and ground.

In the DCCA analysis of the bryophyte data (Fig. 5), the Monte Carlo permutation test confirmed that the relationship between the species data and the first ordination axis was highly significant ($p = 0.002$). The first two canonical axes explained together 14% of the species data variance and 58.4% of the species-environment relationship. Variation of the data along the first ordination axis was correlated mainly with the substratum ground (Fig. 5), along the second axis with substrata stone and windthrow.

In the DCCA ordination plot of lichen data (Fig. 6), the relationship between the species data and the first ordination axis was also highly significant ($p = 0.002$). The first two canonical axes explained together 20% of the species data variance and 51% of the species–environment relationship. Variation of the data along the first ordination axis was related mainly to variables stone and fine woody debris (Fig. 6), and the second axis to variables windthrow and stone.

The indicator value analysis of bryophyte and lichen species by different substrata confirms that numerous species are bounded with a particular substratum (Tables 4 and 5). Among bryophytes, the largest number of species with significant indicator value was characteristic for ground and decaying wood. Of the bryophytes on the latter substratum, a large fraction were hepatics. The number of lichen species having a reliable indicator value was highest for *Pinus sylvestris*, fine woody debris and stones.

From the six recorded bryophytes listed in Estonian Red Data Book, *Campylium calcareum*, *C. halleri* and *Rhynchostegium murale* were growing only on stones and *Anastrophyllum hellerianum* on decaying wood in old subnatural forests. We registered three lichen taxa found in Estonia no more than five times before (Randlane & Saag 2004): *Melaspilea* spp., associated with *Juniperus communis*, *Arthonia didyma*, related with decaying wood, and *Strangospora moriformis*, growing on *Picea abies*.

Fig. 5. Detrended canonical correspondence analysis (DCCA) of bryophyte species and their substrata. Notations for substrata as in Fig. 4. For full names of species *see* Appendix 1.

Discussion

Cryptogams in forests of different management and age groups

As we showed in our previous study (Meier *et al*. 2005), management effect on the bryophyte species richness was clear, but forest age did not influence cryptogam species richness significantly when both alvar and boreo-nemoral forests were analysed together. In the current, study the differences by species composition between forest age groups appeared to be more striking than differences between their management groups, and the older stands became clearly discriminated from younger ones, as it has been established earlier for different forests (e.g. Lesica *et al*. 1991, Hyvärinen *et al*. 1992, Crites & Dale 1998, Boudreault *et al*. 2002). Low management effect on the species composition in alvar forests can be explained by the removal of dead wood from subnatural stands at some

period under the Soviet rule for the purpose of "protecting" these valuable communities. We got that information from the forestry officers after vegetation analyses. The studied subnatural stands have been under local protection since 1978 (Ehrpais & Ehrpais 1986). Anyway, the high number of hemerophobic bryophyte species in the unmanaged forests indicates their quite good state of naturalness (Trass *et al*. 1999, Vellak & Paal 1999) in spite of inadequate protection measures. At the same time, a considerably large number of hemerophobic lichen species in intensively managed alvar forests show that these forests form quite a natural habitat in spite of thinnings. Thinning effect is often associated with lower humidity and enhanced illumination of bottom layers (Söderström 1988b, Larsson 2001), but alvar forests are already naturally quite dry and open (Laasimer 1965), and this can be another explanation for the similar species composition in subnatural and intensively managed stands.
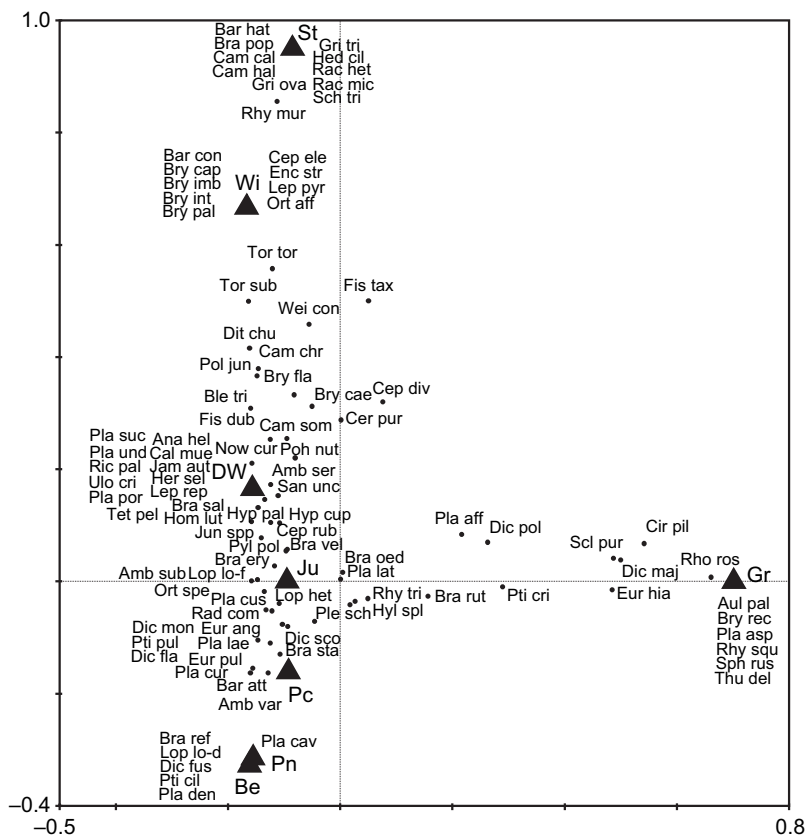
Fig. 6. Detrended canonical correspondence analysis (DCCA) of lichen species and their substrata. Notations for substrata as in Fig. 4, for full names of species *see* Appendix 2.

ies (Andersson & Hytteborn 1991, Söderström 1988b) only in subnatural forests, and according to Söderström (1988a) it prefers very large logs and can grow, therefore, in old forests as recorded also in our study.

Species of the lichen genera *Cladonia* and *Cladina*, associated with younger forests, have been found to be more numerous and abundant in second-growth stands (Söderström 1988b, Lesica *et al*. 1991). In younger stands, the bottom layer gets more light while humidity is comparatively low, i.e. the prevailing conditions are those to which the respective species are adapted (Söderström 1988b). The foliose lichen *Imshaugia aleurites*, recorded by us only in old forests, is considered a characteristic species of ecological continuity of native pinewoods in the British Isles as well (Coppins & Coppins 2002).

Cryptogam species richness on different substrata

A large proportion of organisms (incl. cryptogams) living in the forests are dependent on the presence of dead wood (Esseen *et al*. 1997, Jonsson & Jonsell 1999, Larsson 2001). High species diversity is evidently connected with large microsite heterogeneity constituted by decaying wood. That is caused by several factors, e.g. by size of wood fragments, bark and wood texture, nutrient composition, water-holding capacity and microclimatic conditions (Esseen *et al*. 1997). Therefore, as expected by comparison of different substrata, the cryptogam species richness was highest on decaying wood. Several studies confirm decaying wood being a very important substratum for lichens in quite dry pinewoods in contrast to humid spruce forests (cf. Humphrey *et al*. 2002). In particular, a high hepatic species richness on decaying wood has been shown earlier by Lesica *et al*. (1991), Samuelson *et al*. (1994), Humphrey *et al*. (2002) and Vellak and Ingerpuu (2005). Hepatics strongly prefer shady and moist habitats, therefore, decaying wood with much higher water-holding capacity than that of bark (Barkmann 1958) facilitates their growth.

A considerably high bryophyte species richness was recorded on windthrows. Jonsson and

Among the bryophyte species having a significant indicator value in old subnatural stands, *Nowellia curvifolia* and *Blepharostoma trichophyllum* are also characteristic of old-growth natural forests (Trass *et al*. 1999), and *Ptilidium pulcherrimum* to old stands (Lesica *et al*. 1991). More bryophyte species (also red-listed, hemerophobic and/or hepatic species) were found in older, subnatural stands than in younger, intensively managed ones. Several bryophyte species are sensitive to human impact and prefer older forests (Söderström 1988b, Andersson & Hytteborn 1991, Kuusinen 1996, Trass *et al*. 1999) and usually these species have a low abundance (Cooper-Ellis 1998). Hepatics are characteristic of old subnatural stands, mainly because there is more humidity on the level of undergrowth and presence of dead wood in different decay stages (Söderström 1988b, Samuelson *et al*. 1994). The red-listed epixylic bryophyte *Anastrophyllum hellerianum* has also been found in earlier stud-

Table 4. Bryophytes on different substrata having a significant ($p < 0.05$) indicator value. Sb = substratum, IV_{max} = maximum indicator value (%), IV_{mean} = mean indicator value (%). Abbreviations as in Fig. 4.

Species	Sb	IV_{max}	IV_{mean}	SD	p
Brachythecium oedipodium	Pc	20	13	4	0.032
Hylocomium splendens	Pc	16	14	1	0.001
Plagiothecium laetum	Pc	21	12	4	0.022
Pleurozium schreberi	Pc	16	14	1	0.002
Dicranum scoparium	Be	20	14	3	0.013
Orthotrichum speciosum	Ju	22	8	5	0.037
Blepharostoma trichophyllum	DW	22	9	6	0.041
Cephaloziella rubella	DW	28	10	5	0.013
Hypnum cupressiforme	DW	21	13	3	0.046
Jamesoniella autumnalis	DW	25	9	6	0.022
Lophocolea heterophylla	DW	32	13	3	0.001
Nowellia curvifolia	DW	59	9	5	0.001
Sanionia uncinata	DW	30	12	5	0.007
Tetraphis pellucida	DW	29	9	5	0.006
Barbula convoluta	Wi	22	9	5	0.042
Bryum capillare	Wi	22	8	5	0.032
Bryum pallens	Wi	33	9	5	0.003
Fissidens taxifolius	Wi	27	9	5	0.020
Weissia controversa	Wi	32	9	5	0.008
Grimmia ovalis	St	50	9	6	0.001
Racomitrium heterostichum	St	38	8	6	0.006
Racomitrium microcarpon	St	25	9	5	0.013
Cirriphyllum piliferum	Gr	53	9	5	0.001
Dicranum majus	Gr	26	9	5	0.020
Dicranum polysetum	Gr	34	11	4	0.003
Eurhynchium hians	Gr	40	10	5	0.001
Plagiochila asplenioides	Gr	25	9	6	0.017
Plagiomnium affine	Gr	28	12	4	0.010
Ptilium crista-castrensis	Gr	36	11	5	0.003
Rhodobryum roseum	Gr	64	9	5	0.001
Rhytidiadelphus triquetrus	Gr	18	14	2	0.031

Table 5. Lichens on different substrata having a significant ($p < 0.05$) indicator value. Notations: Sb = substratum, IV_{max} = maximum indicator value (%), IV_{mean} = mean indicator value (%). Abbreviations as in Fig. 4.

Species	Sb	IV_{max}	IV_{mean}	SD	p
Chaenotheca ferruginea	Pn	27	9	5	0.013
Cladonia digitata	Pn	31	13	4	0.001
Hypocenomyce scalaris	Pn	21	9	5	0.045
Parmeliopsis ambigua	Pn	35	13	4	0.001
Lepraria spp	Pc	26	14	2	0.001
Dimerella pineti	Ju	35	12	5	0.009
Melaspilea spp.	Ju	22	9	6	0.026
Micarea prasina	Ju	21	13	4	0.048
Cladonia coniocraea	DW	20	14	3	0.047
Cladonia cornuta	DW	25	9	5	0.021
Hypogymnia physodes	WD	27	14	3	0.001
Platismatia glauca	WD	73	11	5	0.001
Pseudevernia furfuracea	WD	81	10	5	0.001
Usnea hirta (coll.)	WD	25	9	5	0.026
Cladina rangiferina	St	25	11	4	0.043
Cladonia furcata	St	32	9	6	0.014
Cladonia gracilis	St	25	11	4	0.043
Cladonia turgida	St	25	11	4	0.043

Esseen (1990) emphasized the importance of windthrows as a substratum for bryophytes. Uprooting creates space for bryophyte colonization that is free from potential competitors. A number of various substrata (humus, mineral soil, stones and roots) are exposed on both the tip-up mounds and the pits, resulting together in high micro-habitat heterogeneity (Jonsson & Esseen 1990, Ulanova 2000). Windthrows are not scarce in alvar forests, where the soil is thin and tree roots can not entrench deep (Laasimer 1965).

It appeared that on *Juniperus communis* the lichen species richness was the highest among the studied trees though the number of these bushes or small trees was very low in comparison with that of the dominating trees. Up to now, little attention has been paid to *J. communis* as a cryptogam substratum, and the former studies carried out in Germany, Sweden and Finland (cf. Barkmann 1958) do not report a very high epiphytic species richness on it. Differences in bark characteristics, particularly in bark acidity, are the most prominent factors influencing the floristic differences of epiphytic species growing on various tree species. High pH of bark is usually considered to support the establishment of most epiphytic lichens and bryophytes (Kuusinen 1996). The bark of *J. communis* is less acid (pH > 5) than that of *Picea abies*, *Pinus sylvestris* or *Betula pendula*, being similar to that of deciduous trees (Barkmann 1958). This seems to be the reason why a larger number of species can grow on *J. communis* as compared with other coniferous trees.

After comparing epiphytic lichen species richness on *Pinus sylvestris*, *Picea abies* and *Betula pendula* Jüriado *et al*. (2003) found that there are more species on *P. abies* than on *P. sylvestris*, but *B. pendula* is the most species-rich among these tree species. According to our results, fewer lichen species grow on *B. pendula* than on *P. sylvestris* and *P. abies*. This can be due to the small number of *B. pendula* trees in alvar forests. Kuusinen (1996) recorded less lichens and bryophytes on *P. abies* than on *P. sylvestris* and *B. pendula*. The studies of Jüriado *et al*. (2003) and Kuusinen (1996) are quite general, dealing with forests of very different site types. Cryptogam species richness and composition on

same tree species vary in different ecological conditions (site types) (Sõmermaa 1972). However, we did not register species above 0.7 m on tree stems, so there can be no significant difference between lichen species numbers on tree base and on stem at breast height in the case of conifers (Sõmermaa 1972).

Cryptogam species composition on different substrata

Substrata explained more of the cryptogam species variance than did stand age or management intensity. Usually cryptogams are divided according to their substratum preference as species of ground (epigeic species), living trees (epiphytes), decaying wood (epixylic species) and stones (epilithic species) (Samuelson *et al*. 1994, Frahm 2001). There are also species which grow on very different substrata (habitat generalists; Kuusinen 1996) and thereby the partition of species into those categories is not so simple.

Among the bryophyte species of decaying wood, epixylic specialists had considerable indicator value (e.g. *Lophocolea heterophylla*, *Nowellia curvifolia*, *Tetraphis pellucida*, *Blepharostoma trichophyllum*), as did also opportunistic generalists (*Cephaloziella rubella* and *Hypnum cupressiforme*) (Andersson & Hytteborn 1991). In the midst of indicative species of *Picea abies* such typical ground species as *Hylocomium splendens* and *Pleurozium schreberi* were also represented. *Picea abies* has roots near the soil surface and usually there is no clear distinction between bryophyte assemblages on ground and tree bases with roots.

The bryophyte species composition was similar on *Pinus sylvestris*, *Betula pendula* and *Picea abies*. These trees are quite poor in specialist species that are confined to one tree species (Kuusinen 1996). *Betula pendula* is an exception among the deciduous trees, having about the same epiphytic flora as conifers (Barkmann 1958, Kuusinen 1996). Bryophyte species composition on *Juniperus communis* differed from the other tree species, confirming once again the importance of this substratum in alvar forests.

We registered more red-listed bryophyte

species on stones than on other substrata: *Campylium calcareum*, *C. halleri* and *Rhynchostegium murale*. These species prefer to grow on limestone rocks (Ingerpuu *et al*. 1994) which, compared with other stones, have more porous structure which enables preserving moisture and warmth, both very important for bryophyte growth (Ingerpuu & Vellak 2000). Among the Estonian obligatory and facultative stone species 45% are red-listed (Ingerpuu & Vellak 2000) and many of them prefer the shade of forest canopy (Ingerpuu 1998).

Lichen species such as *Cladonia digitata*, *Parmeliopsis ambigua*, *Chaenotheca ferruginea* and *Hypocenomyce scalaris*, growing on *Pinus sylvestris* and having a high indicator value, have been found to be the most frequent on *P. sylvestris* also by other authors (Sõmermaa 1972, Jüriado *et al*. 2003). A high frequency of *Lepraria* species on *Picea abies* has been reported earlier by Jüriado *et al*. (2003). The composition of lichen species on *Juniperus communis* was most similar to that on *Betula pendula*, probably because the *B. pendula* bark is more alkaline than that of *P. sylvestris* and *P. abies* (Barkmann 1958). Of species growing on decaying wood, those of the genera *Cladonia*, such as *C. coniocrea* and *C. cornuta*, had a high indicator value. Several *Cladonia* species have been found frequently on logs, particularly in open habitats in Scandinavia as well (Kuusinen & Siitonen 1998).

All the lichen species related by indicator value to stones were previously qualified as lichens confined to ground (Randlane & Saag 1999). Forest stones are covered with a shallow layer of humus, which makes this substratum similar to ground. On the other hand, the bedrock surface is frequently opened on alvar forest ground, making the latter similar to the stone substratum.

Summing up, we can recognise that while the results of our previous study (Meier *et al*. 2005) confirmed the importance of forest management intensity on the bryophyte species richness, the current study reveals also the importance of forest age on both bryophyte and lichen species composition. Availability of different substrata appeared even more essential for cryptogam diversity and species composition.

Acknowledgements

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Appendix 1. Total list of recorded bryophyte species, their occurrence in forests of different age and management groups and on different substrata. The figures in table show in how many stands the species was recorded. With asterisk are marked the hemerophobic species, with # the red-listed species. Notations for forest stands: Os = older subnatural, Om = older subnatural, Ys = younger subnatural, Ym = younger intensively managed; Other notations: Pn = *Pinus sylvestris*, Pc = *Picea abies*, Be = *Betula* spp., Ju = *Juniperus communis*, So = *Sorbus aucuparia*, DW = decaying wood, WD = fine woody debris, Wi = windthrow, St = stone, Gr = ground; n = number of stands; Abbr. = abbreviations.

Abbr.	Species	Age/Management				Substrata									
		Os (n=3)	Om (n=3)	Ys (n=3)	Ym (n=3)	Pn (n=12)	Pc (n=12)	Be (n=10)	Ju (n=9)	So (n=2)	DW (n=12)	WD (n=12)	Wi (n=9)	St (n=8)	Gr (n=12)
Hepatics															
Ana hel	#*Anastrophyllum hellarianum	2	–	–	–	–	–	–	–	–	2	–	–	–	–
Bar att	*Barbilophozia attenuata	1	1	–	–	–	–	–	–	–	1	–	–	–	–
Bar hat	*Barbilophozia hatcheri	1	–	–	–	–	–	1	–	–	–	–	–	1	–
Ble tri	*Blepharostoma trichophyllum	3	–	–	1	–	–	–	–	–	4	–	1	–	–
Cal mue	Calypogeia muelleriana	–	–	1	1	–	–	–	–	–	1	–	–	–	–
Cep div	#Cephaloziella divaricata	–	1	1	2	–	–	–	–	–	2	–	–	–	2
Cep ele	Cephaloziella elegans	1	–	–	–	–	–	–	–	–	–	–	1	–	–
Cep rub	Cephaloziella rubella	3	2	3	2	2	–	3	1	–	7	–	1	–	2
Jam aut	*Jamesoniella autumnalis	2	–	–	1	–	–	–	–	–	3	–	–	–	–
Jun spp	Jungermannia spp.	2	–	1	–	1	1	–	–	–	1	–	1	–	–
Lep rep	*Lepidozia reptans	2	–	–	–	–	–	–	–	–	2	–	–	–	–
Lop het	Lophocolea heterophylla	3	3	3	3	7	4	6	4	–	12	–	3	–	3
Lop l-d	*Lophozia longidens	1	–	–	–	–	–	1	–	–	1	–	–	–	–
Lop l-f	*Lophozia longiflora	1	–	–	1	–	–	1	–	–	1	–	–	–	–
Now cur	*Nowellia curvifolia	3	3	2	–	–	–	–	–	–	8	–	1	–	–
Pla asp	Plagiochila asplenioides	2	–	–	1	–	–	–	–	–	–	–	–	–	3
Pla por	Plagiochila porelloides	1	–	–	1	–	–	–	–	–	2	–	–	–	–
Pti cil	Ptilidium ciliare	1	–	–	–	–	–	1	–	–	–	–	–	–	–
Pti pul	Ptilidium pulcherrimum	3	3	3	3	12	11	8	7	–	11	4	3	1	1
Rad com	Radula complanata	1	1	–	1	–	2	1	3	–	–	–	–	1	–
Ric pal	*Riccardia palmata	–	–	1	–	–	–	–	–	–	1	–	–	–	–
Mosses															
Amb ser	Amblystegium serpens	–	3	2	1	–	2	2	1	–	1	–	1	1	–
Amb sub	Amblystegium subtile	2	1	–	1	–	1	1	–	–	1	–	1	–	–
Amb var	Amblystegium varium	–	–	–	1	–	–	1	1	–	–	–	–	–	–
Aul pal	Aulacomnium palustre	1	–	–	–	–	–	–	–	–	–	–	–	–	1
Bar con	Barbula convoluta	1	–	1	–	–	–	–	–	–	–	–	2	–	–
Bra ery	*Brachythecium erythrorrhizon	–	–	1	–	–	–	–	1	–	–	–	–	–	–
Bra oed	Brachythecium oedipodium	1	3	3	3	2	9	3	3	–	7	–	4	1	6

Abbr.	Species	1	2	3	4	5	6	7	8	9	10	11	12	13
Bra pop	*Brachythecium populeum*	1	–	–	–	–	–	–	–	–	–	–	1	–
Bra ref	*Brachythecium reflexum*	–	–	–	–	–	–	1	–	–	–	–	–	–
Bra rut	*Brachythecium rutabulum*	1	1	–	1	–	3	–	–	1	1	–	–	2
Bra sal	*Brachythecium salebrosum*	–	2	3	2	–	1	–	2	1	4	1	–	–
Bra sta	*Brachythecium starkei*	–	–	1	1	–	1	1	1	–	–	–	–	–
Bra vel	*Brachythecium velutinum*	3	3	3	2	1	5	3	3	–	5	4	–	1
Bry rec	*Bryoerythrophyllum recurvirostrum*	–	–	1	–	–	1	1	–	–	–	–	1	1
Bry cae	*Bryum caespiticium*	1	2	2	3	–	1	1	–	–	1	4	–	1
Bry cap	*Bryum capillare*	–	–	1	1	–	–	–	–	–	–	2	2	–
Bry fla	*Bryum flaccidum*	2	–	2	2	–	–	–	–	–	4	3	–	1
Bry imb	*Bryum imbricatum*	1	–	–	–	–	–	–	–	–	–	1	–	–
Bry int	*Bryum intermedium*	–	–	1	–	–	–	–	–	–	–	1	–	–
Bry pal	*Bryum pallens*	–	1	2	–	–	–	–	–	–	–	3	–	–
Cam cal	#*Campylium calcareum*	1	–	–	1	–	–	–	–	–	–	–	1	–
Cam chr	*Campylium chrysophyllum*	–	1	2	1	–	–	–	–	–	2	2	1	1
Cam hal	#*Campylium halleri*	1	–	–	–	–	–	–	–	–	–	–	1	1
Cam som	*Campylium sommerfeltii*	3	2	3	2	–	1	–	3	–	3	4	–	1
Cer pur	*Ceratodon purpureus*	1	–	3	1	–	1	–	–	–	2	2	–	1
Cir pil	*Cirriphyllum piliferum*	2	1	2	3	–	–	–	–	–	1	1	–	8
Dic fla	*Dicranum flagellare*	2	1	3	3	–	5	5	1	–	7	2	–	–
Dic fus	*Dicranum fuscescens*	2	–	–	1	6	5	1	–	1	–	–	–	–
Dic maj	*Dicranum majus*	3	1	–	3	–	–	–	–	–	2	–	–	4
Dic mon	*Dicranum montanum*	3	3	3	3	9	10	5	3	–	10	5	1	1
Dic pol	*Dicranum polysetum*	2	2	3	3	2	2	1	–	–	4	3	–	9
Dic sco	*Dicranum scoparium*	3	3	3	3	11	9	9	6	–	9	2	2	7
Dit spp	*Ditrichum* spp.	1	–	–	–	–	–	–	–	–	1	1	–	–
Enc str	*Encalypta streptocarpa*	1	–	–	–	–	–	–	–	–	–	1	–	–
Eur ang	*Eurhynchium angustirete*	–	1	1	1	–	1	1	1	–	–	–	–	7
Eur hia	*Eurhynchium hians*	3	1	2	2	–	2	3	3	–	–	–	–	–
Eur pul	*Eurhynchium pulchellum*	1	–	–	–	1	1	1	1	–	1	–	–	–
Fis dub	*Fissidens dubius*	3	2	3	3	–	1	3	3	1	2	2	1	–
Fis tax	*Fissidens taxifolius*	1	–	2	1	–	–	–	–	–	–	3	–	1
Gri ova	*Grimmia ovalis*	1	1	1	1	–	–	–	–	–	–	–	4	–
Gri tri	*Grimmia trichophylla*	–	–	–	1	–	–	–	–	–	–	–	1	–
Hed cil	*Hedwigia ciliata*	–	–	1	–	–	–	–	–	–	–	–	1	–
Her sel	*Herzogiella seligeri*	1	1	–	1	–	–	–	–	–	–	–	–	–
Hom lut	*Homalothecium lutescens*	3	1	1	1	–	1	1	–	–	2	–	1	–
Hyl spl	*Hylocomium splendens*	3	3	3	3	12	12	9	7	–	12	5	5	11
Hyp cup	*Hypnum cupressiforme*	3	3	2	2	7	8	3	4	–	10	5	3	2
Hyp pal	*Hypnum pallescens*	–	2	1	1	–	1	1	–	–	1	–	1	–

Appendix 1. Continued.

Abbr.	Species	Age/Management								Substrata					
		Os (n = 3)	Om (n = 3)	Ys (n = 3)	Ym (n = 3)	Pn (n = 12)	Pc (n = 12)	Be (n = 10)	Ju (n = 9)	So (n = 2)	DW (n = 12)	WD (n = 12)	Wi (n = 9)	St (n = 8)	Gr (n = 12)
Lep pyr	*Leptobryum pyriforme*	–	–	1	–	–	–	–	–	–	–	–	1	–	–
Ort aff	*Orthotrichum affine*	–	–	1	–	–	–	–	–	–	–	–	1	–	–
Ort spe	*Orthotrichum speciosum*	–	1	1	–	–	–	–	2	–	–	–	–	–	–
Pla aff	*Plagiomnium affine*	2	2	3	3	2	5	1	1	–	5	–	4	4	9
Pla cus	*Plagiomnium cuspidatum*	1	1	1	1	–	2	1	–	–	2	–	1	–	–
Pla und	*Plagiomnium undulatum*	1	–	–	–	–	–	–	–	–	1	–	–	–	–
Pla cav	**Plagiothecium cavifolium*	–	1	–	–	1	–	–	–	–	–	–	–	–	–
Pla cur	*Plagiothecium curvifolium*	1	–	–	1	1	–	–	–	–	1	–	–	–	–
Pla den	*Plagiothecium denticulatum*	–	1	–	1	–	–	1	–	–	–	–	1	–	1
Pla lae	*Plagiothecium laetum*	3	2	3	3	8	9	7	–	–	5	–	3	2	2
Pla lat	*#*Plagiothecium latebricola*	2	1	2	1	1	1	–	2	–	–	–	1	–	1
Pla suc	**Plagiothecium succulentum*	1	1	–	–	–	–	–	–	–	2	–	–	–	–
Ple sch	*Pleurozium schreberi*	3	3	3	3	12	12	9	7	–	12	–	4	4	11
Poh nut	*Pohlia nutans*	1	2	–	1	2	–	–	–	–	3	–	1	2	2
Pol jun	*Polytrichum juniperinum*	2	–	1	–	1	–	–	–	–	3	–	2	1	–
Pti cri	*Ptilium crista-castrensis*	3	3	3	1	2	3	2	2	–	4	–	1	–	9
Pyl pol	*Pylaisia polyantha*	1	–	1	–	–	1	1	2	–	1	–	–	1	–
Rac het	*Racomitrium heterostichum*	–	1	–	2	–	–	–	–	–	–	–	–	3	–
Rac mic	*Racomitrium microcarpon*	–	–	1	1	–	–	–	–	–	–	–	–	2	–
Rho ros	*Rhodobryum roseum*	1	2	3	3	–	–	–	–	–	1	–	–	–	8
Rhy mur	*#Rhynchostegium murale*	2	–	–	–	–	–	–	–	–	–	–	1	1	–
Rhy squ	*Rhytidiadelphus squarrosus*	–	–	1	1	–	–	–	–	–	–	–	–	–	2
Rhy tri	*Rhytidiadelphus triquetrus*	3	3	3	3	9	10	8	5	–	11	–	3	3	11
San unc	*Sanionia uncinata*	3	3	3	2	–	4	1	4	–	10	–	2	3	1
Sch tri	*Schistidium trichodon*	–	–	1	–	–	–	–	–	–	–	–	–	1	–
Scl pur	*Scleropodium purum*	–	–	1	2	–	–	–	–	–	1	–	–	–	2
Sph rus	*Sphagnum russowii*	1	–	–	–	–	–	–	–	–	–	–	–	–	1
Tet pel	*Tetraphis pellucida*	2	2	–	3	2	–	1	–	–	6	–	1	–	–
Thu del	*Thuidium delicatulum*	–	–	–	1	–	–	–	–	–	–	–	–	–	1
Tor tor	*Tortella tortuosa*	1	1	–	–	–	–	–	–	–	1	–	–	1	–
Tor sub	*Tortula subulata*	1	1	–	–	–	–	–	–	–	1	–	2	–	–
Ulo cri	**Ulota crispa*	1	–	2	1	–	–	–	–	–	1	–	–	–	–
Wei con	*Weissia controversa*	1	–	–	–	–	–	–	–	–	1	1	4	–	1
	Total number of species	70	50	57	61	25	34	35	29	1	60	3	50	34	38

Appendix 2. Total list of recorded lichen species, their occurrence in forests of different age and management groups and on different substrata. The figures in table show in how many stands the species was recorded. With asterisk are marked the hemerophobic species, with # very rare species found not more than five times in Estonia before. Notations: Sa = *Salix caprea*, other notations as in Appendix 1.

Abbr.	Species	Age/Management								Substrata						
		Os (n=3)	Om (n=3)	Ys (n=3)	Ym (n=3)	Pn (n=12)	Pc (n=12)	Be (n=10)	Ju (n=9)	So (n=2)	Sa (n=1)	DW (n=12)	WD (n=12)	Wi (n=9)	St (n=8)	Gr (n=12)
Art did	#*Arthonia didyma*	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
Art vin	*Arthonia vinosa*	1	1	–	–	–	1	2	–	–	–	–	–	–	–	–
Bac sub	*Bacidia subincompta*	–	–	1	–	–	–	–	1	–	–	–	–	–	–	–
Bia hel	*Biatora helvola*	–	–	1	–	–	1	–	1	–	–	–	–	–	–	–
Bry spp	*Bryoria* spp.	1	–	–	–	–	–	–	–	–	–	–	1	–	–	–
Bue gri	*Buellia griseovirens*	1	2	2	2	3	–	2	1	–	–	1	1	–	–	–
Cha chr	*Chaenotheca chrysocephala*	3	3	1	2	5	5	1	2	–	–	–	1	1	–	–
Cha fer	*Chaenotheca ferruginea*	2	3	–	1	5	3	–	–	–	–	–	–	–	–	–
Cha fur	*Chaenotheca furfuracea*	–	–	1	–	–	–	–	–	–	–	–	–	1	–	–
Cha tri	*Chaenotheca trichialis*	1	1	–	1	–	2	1	–	–	–	–	–	–	–	–
Cla arb	*Cladina arbuscula*	–	–	1	2	–	–	–	–	–	–	2	–	–	1	2
Cla ran	*Cladina rangiferina*	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–
Cla cen	*Cladonia cenotea*	1	1	3	3	2	2	2	2	–	–	3	–	–	2	–
Cla chl	*Cladonia chlorophaea*	2	2	3	2	4	3	1	2	–	1	4	–	1	–	3
Cla con	*Cladonia coniocraea*	3	3	3	3	9	11	5	5	–	–	11	2	2	3	4
Cla cor	*Cladonia cornuta*	1	–	1	1	–	–	–	–	–	–	3	–	–	–	–
Cla cri	*Cladonia crispata*	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–
Cla dig	*Cladonia digitata*	3	3	3	3	11	8	3	3	–	–	8	1	1	–	1
Cla fim	*Cladonia fimbriata*	2	3	3	2	4	5	5	3	–	–	9	–	1	–	2
Cla fur	*Cladonia furcata*	2	–	2	1	–	–	–	–	–	–	2	–	1	2	–
Cla gra	*Cladonia gracilis*	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–
Cla och	*Cladonia ochroclora*	–	1	1	–	1	–	1	–	–	–	1	–	–	–	–
Cla tur	*Cladonia turgida*	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–
Dim pin	*Dimerella pineti*	3	1	3	3	4	4	4	7	–	–	2	–	–	–	–
Hyp sca	*Hypocenomyce scalaris*	2	1	–	1	4	–	–	–	–	–	1	1	–	–	–
Hyp phy	*Hypogymnia physodes*	3	3	3	3	12	11	8	6	–	–	3	12	1	–	–
Ims ale	*Imshaugia aleurites*	3	2	–	–	2	1	–	2	–	–	1	1	–	–	–
Lec pul	*Lecanora pulicaris*	–	–	1	1	–	–	1	–	–	–	–	–	–	–	–
Lec tur	*Lecidea turgidula*	1	–	1	1	2	–	–	–	–	–	–	–	1	1	–
Lep spp	*Lepraria* spp.	3	3	3	3	12	12	10	9	–	1	9	8	1	–	–
Lox ela	*Loxospora elatina*	1	–	2	1	–	2	–	2	–	–	–	–	–	–	–

Appendix 2. Continued

Abbr.	Species	Age/Management								Substrata						
		Os (n=3)	Om (n=3)	Ys (n=3)	Ym (n=3)	Pn (n=12)	Pc (n=12)	Be (n=10)	Ju (n=9)	So (n=2)	Sa (n=1)	DW (n=12)	WD (n=12)	Wi (n=9)	St (n=8)	Gr (n=12)
Mel spp	#Melaspilea spp.	–	–	–	1	–	–	–	2	–	–	–	–	–	–	–
Mic den	Micarea denigrata	–	–	1	1	–	–	–	–	–	–	1	–	–	–	–
Mic mel	Micarea melaena	1	1	1	2	1	–	1	1	–	–	5	–	–	–	–
Mic pra	Micarea prasina	3	3	3	3	8	6	6	7	–	1	6	2	–	–	–
Myc car	Mycobilimbia carneoalbida	1	–	–	–	–	–	–	1	–	–	–	–	–	–	–
Ope ruf	*Opegrapha rufescens	–	1	–	–	–	–	–	1	–	–	–	–	–	–	–
Par sul	Parmelia sulcata	–	1	–	–	–	–	–	–	–	–	1	–	–	–	–
Par amb	Parmeliopsis ambigua	3	3	3	3	12	8	4	3	–	–	2	8	–	–	–
Par hyp	*Parmeliopsis hyperopta	1	2	1	2	4	–	–	2	–	–	2	1	1	–	–
Pel did	Peltigera didactyla	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
Pel pol	*Peltigera polydactyla	–	–	1	–	–	–	–	–	–	–	–	–	1	–	–
Per ama	Pertusaria amara	2	2	1	2	–	2	2	3	1	1	1	1	–	–	–
Phl arg	Phlyctis argena	–	1	1	1	–	–	–	1	–	1	1	–	–	–	–
Pla icm	Placynthiella icmalea	–	1	–	1	–	–	–	–	–	1	1	–	1	–	–
Pla uli	Placynthiella uliginosa	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
Pla gla	Platismatia glauca	3	3	3	3	1	3	–	–	–	–	1	11	–	–	–
Pse fur	Pseudevernia furfuracea	3	2	3	3	–	2	–	–	–	–	1	11	–	–	–
Str mor	#Strangospora moriformis	–	1	–	–	–	1	–	–	–	–	–	–	–	–	–
Tra fle	Trapeliopsis flexuosa	–	1	1	–	–	–	1	–	–	–	1	1	–	–	–
Tuc chl	*Tuckermannopsis chlorophylla	–	1	–	–	–	–	–	–	–	–	–	1	–	–	–
Usn hir	Usnea hirta (coll.)	1	–	–	2	–	–	–	–	–	–	–	3	–	–	–
Vul pin	Vulpicida pinastri	2	1	3	3	6	4	5	3	–	–	4	4	–	–	–
Xan par	Xanthoria parietina	1	1	–	–	–	2	–	–	–	–	–	1	–	–	–
	Total number of species	30	33	34	35	21	23	19	24	1	4	28	19	13	8	5