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Epiphytic and epixylic lichen species diversity in Estonian natural forests

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Abstract. The epiphytic and epixylic lichen flora of natural forests was recorded in different parts of Estonia. Altogether 232 taxa of lichens, lichenicolous fungi, or non-lichenized fungi were recorded, 10 of them listed in the Estonian Red Data Book. We found regional differences in lichen species composition and diversity caused by differences in the forest types. The tree-species-rich boreo-nemoral forests had the most diverse lichen flora, while the boreal forest dominated by coniferous trees or birch had the lowest diversity. The stand age proved to be significant in regard to the number of lichen species in a forest. The most remarkable effect on the diversity of forest lichen species was caused by the presence of *Populus tremula*. Aspen had the highest number of lichen species on the basal trunk and twigs, and also the highest number of host-specific lichen species.

Nomenclature
The nomenclature follows Randlane and Saag (1999) and Jüriado et al. (2000).

Introduction

The destruction and fragmentation of old forest stands, due to increasing forest management intensity, has drawn attention to the maintenance of the biodiversitity of species confined to old-growth forests (Esseen et al. 1997). The stand age, stand continuity, and the presence of different substrate types for lichen species are considered the most important factors distinguishing old-growth forests from young or managed stands (Lesica et al. 1991; Hyvärinen et al. 1992; Goward 1994; Selva 1994; Crites and Dale 1998; Kuusinen and Siitonen 1998). Besides management, at stand scale, the soil type and/or hydrological regime influences the lichen flora in forests (Oksanen 1988; Cieśliński et al. 1996b; Holien 1996; Kuusinen 1996c).

Earlier studies of lichens in Estonian forests focus on four dominating indigenous tree species (*Alnus glutinosa*, *Betula pubescens*, *Picea abies*, *Pinus sylvestris*). Sõmermaa (1972) showed that the distribution of lichens on trees depends on tree age, forest type, location height, and trunk exposition. Lõhmus and Lõhmus (2001) described the essential differences of lichen flora on living trees and snags. They emphasized the importance of snags for the diversity of the forest lichen community. Martin and Martin (1998, 2000) studied the epiphytic macrolichen frequencies in Estonian forests and Trass et al. (1999) defined the hemerophobic species. However, these papers do not give a sufficient overview of the lichen flora in Estonian forests. The aim of this study was to describe the epiphytic and epixylic lichen flora at forest community level, considering all tree species and different substrate types. We analysed the influence of some general forest-stand and environmental parameters on lichen diversity. During the study, we also revised the locations and frequencies of Red Data Book lichens.

Methods

Study areas and environmental variables

Field work was carried out in 1998 and 1999 as part of the project ‘Estonian Forest Conservation Area Network’ (Viilma et al. 2001). Particular attention was paid to forests, (i) belonging to rare or threatened forest types (e.g. eutrophic boreo-nemoral, eutrophic paludifying forests, *sensu* Paal 1998, 2001), (ii) having a tree layer composed of greater than four species, (iii) with unevenly aged trees, (iv) containing numerous dead trees (>50 m^3 ha^{-1}), (v) with the age of the dominant deciduous trees >50 years, or coniferous trees >80 years (Viilma et al. 2001). For the preliminary selection, the Forest Survey Database of Estonian State Forests was used, and natural forests with low anthropogenic influence were preferred. Altogether, 130 forest stands were analysed, 35 located in northeastern, 48 in southeastern, 35 in southwestern, and 12 in western Estonia (Figure 1).

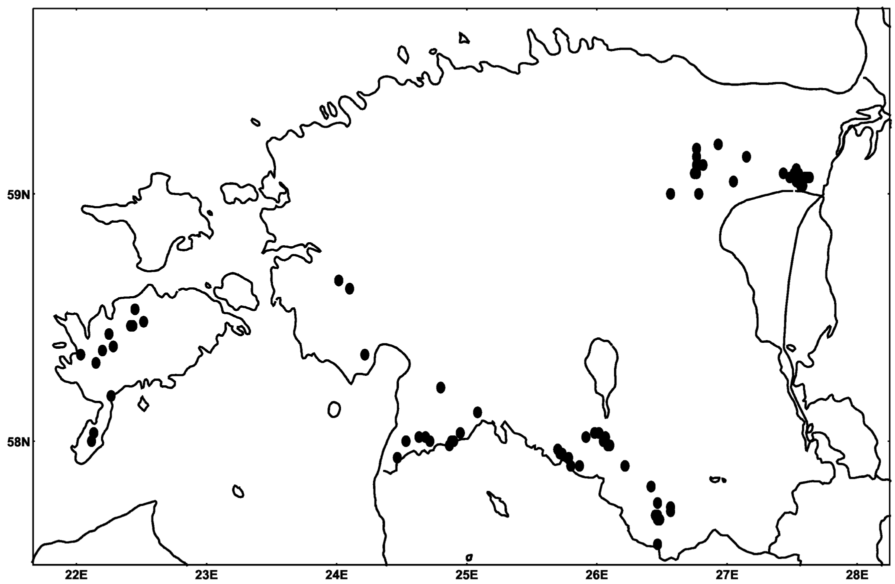

Figure 1. Locations of studied forests in Estonia.

Forests were divided into sub-compartments based on stand characteristics (e.g. dominating tree species and tree age) and environmental conditions (e.g. moisture regime and nutritional status of soil) according to Lõhmus (1984). The average size of the studied sub-compartments was 2.8 ha (range 0.2–18.4 ha). Lichen flora was recorded within forest sub-compartments (= forest stands). The analysed samples represent 22 forest site types of the total of 26 Estonian forest site types established by Lõhmus (1984). Stands of oligo-mesotrophic boreal, mesotrophic boreal, eutrophic boreo-nemoral, eutrophic paludifying, and minerotrophic swamp forest site-type groups (Paal 1997, 2001) were most frequent.

Estonia is located in the hemiboreal sub-zone of the boreal forest zone, i.e. in the transitional area where the southern taiga forest sub-zone changes into the spruce-hardwood sub-zone (Laasimer and Masing 1995). *Betula* spp., *Picea abies* and *Pinus sylvestris* were the most common tree species in the studied stands (the frequencies in the studied stands were respectively 90, 85 and 68%), *Populus tremula* occurred in a little more than half of the stands (55%), and *Alnus glutinosa* in almost half of them (48%). The broad-leaved trees were represented less frequently (occurrence in studied stands: *Acer platanoides* 10%, *Fraxinus excelsior* 18%, *Tilia cordata* 13% and *Ulmus glabra* 3%). Eleven percent of stands had one to two species per sub-compartment, 80% of stands had three to five species, and 9% had more than six tree species. On average, there were four tree species per stand. The average age of studied forests was 108 years (21% of stands were 40–75 years old, 46% 80–120 years old and 33% 130–230 years old), whereas only two forests were older than 200 years.

Altogether 16 environmental variables were recorded (Table 1). Forest stand was characterised by age, relative density, number of tree species, soil moisture regime, soil nutritional conditions, and the proportion of different tree species in the forest. Due to the rare occurrence of *Acer platanoides*, *Fraxinus excelsior*, *Tilia cordata* and *Ulmus glabra*, their relative abundance was summarized and treated as variable 'Broad-leaved trees'. *Quercus robur* was observed separately since the bark pH of oak is known to be more acidic than that of other broad-leaved trees (Barkman 1958; Watson et al. 1988; Wirth 1995). Considering the low occurrence of *Salix caprea*, *Sorbus aucuparia* and *S. intermedia* in the studied forests, the relative abundances of these species were summarized and considered as the variable 'Willow and rowan'.

Sampling

The trunks of different tree species were selected at random within the sub-compartment. The lichen species, lichenicolous fungi and some non-lichenized fungi were recorded on tree trunks, up to a height of 2 m. Additionally, lichens were also registered on lower branches of living trees, on trunks and branches of fallen dead trees, on snags, logs, stumps, and on the roots of uprooted trees, where respective substrates were present. The relative abundance of every lichen species was evaluated for the whole forest sub-compartment on a four-point scale (1: one specimen per sub-compartment, 2: up to 10 specimens, 3: sporadically, found only

Table 1. Environmental variables exploited in data analysis.

Variables	Comments
Latitude and Longitude	The geographical co-ordinates were recorded by means of GPS
Moisture regime	The parameter of moisture regime of the considered forest site type according to Lõhmus (1984)
Number of tree species[a]	The number of tree species in the stand
Nutritional conditions	The parameter of nutritional conditions of the considered forest site type according to Lõhmus (1984)
Relative density[b]	Density of tree layer estimated relatively to the density of standard stand
Stand age[b]	The age of oldest trees in the stand
Aspen[b]	Percent of *Populus tremula* in the stand
Birch[b]	Percent of *Betula pubescens* and *B. pendula* in the stand
Black alder[b]	Percent of *Alnus glutinosa* in the stand
Broad-leaved trees[a]	Total percent of *Acer platanoides*, *Fraxinus excelsior*, *Tilia cordata* and *Ulmus glabra* in the stand
Grey alder[b]	Percent of *Alnus incana* in the stand
Oak[b]	Percent of *Quercus robur* in the stand
Pine[b]	Percent of *Pinus sylvestris* in the stand
Spruce[b]	Percent of *Picea abies* in the stand
Willow and rowan[a]	Total percent of *Salix caprea*, *Sorbus aucuparia* and *S. intermedia* in the stand

[a]Value of the parameter was calculated, based on the data of Forest Survey Database and field observations. [b]Value of the parameter was taken from Forest Survey Database.

in some places or on particular substrates, 4: numerous). The investigation time was limited to 45–90 min in every sub-compartment. The specimens that were not identified in the field, were collected for further laboratory investigation. All together, about 1000 specimens were collected and deposited in the herbarium of the University of Tartu (TU). Species of genus *Arthopyrenia* were treated at the generic level.

Data analysis

Detrended canonical correspondence analysis (DCCA) was used to evaluate the relationship between the species composition and environmental parameters (Ter Braak and Šmilauer 1998). Detrending by segments was applied, the species data was not transformed, and the species appearing only once or twice in the data set were removed from the analysis. The environmental variable 'Birch' was removed from DCCA analysis due to the high value of the variance inflation factor (VIF > 20), indicating multi-collinearity among the environmental variables (Ter Braak and Šmilauer 1998). The Monte Carlo permutation test was used to evaluate the significance of the correlation between species data and the first ordination axis.

In addition to descriptive ordination analysis, a general linear model (GLM) analysis (SAS Institute Inc. 1989) was applied to study the dependence of lichen species diversity (the number of lichen species) on the considered environmental variables. The environmental variables used were: 'Latitude', 'Longitude', 'Stand

Table 2. Estonian Red Data Book lichen species recorded in the current study, their present threat category (Randlane 1998) and proposed threat category.

Species	Present category	Proposed category
Bryoria nadvornikiana	2	2
Cetrelia cetrarioides	0	1
Collema subnigrescens	0	2
Evernia divaricata	2	2
Evernia mesomorpha	4	4
Hypocenomyce anthracophila	3	4
Hypocenomyce sorophora	3	–
Lobaria pulmonaria	4	4
Menegazzia terebrata	4	4
Nephroma laevigatum	2	2

0 – extinct or probably extinct, 1 – endangered, 2 – vulnerable, 3 – rare, 4 – care demanding.

age', 'Relative density', 'Nutritional conditions', 'Moisture regime'; the presence/absence records of tree species (parameters 'Aspen', 'Birch', 'Black alder', 'Grey alder', 'Spruce', 'Pine' 'Oak', 'Broad-leaved trees', 'Willow and rowan') and the forest community type ('Forest type'). In 'Forest type', the forests were divided into two groups: (1) boreal forests – stands dominated by coniferous trees (*Picea abies*, *Pinus sylvestris*) or by birch (*Betula* spp.), containing up to 10% of other deciduous tree species, and (2) boreo-nemoral forests – stands dominated by deciduous trees other than birch, or mixed forests (coniferous trees or birch <50%).

Results

Floristical results

Altogether, 232 taxa of lichens (including lichenicolous and allied fungi) were found (Appendix 1), 10 of which were listed in the Red Data Book of Estonia (Randlane 1998) (Table 2). Two hundred and nine lichen species were recorded from the basal trunks of trees, 74 species were registered on twigs and 77 on dead wood. Six species (*Cetraria sepincola*, *Evernia divaricata*, *Lecania fuscella*, *Ramalina fastigiata*, *Rinodina pyrina* and *R. sophodes*) were found only on twigs, and 19 species (e.g. *Calicium* spp., *Placynthiella icmalea* and *Trapeliopsis flexuosa*) were found growing exclusively on dead wood (Appendix 1).

The basal trunks of *Populus tremula* had more lichen species (110 lichenized taxa) than other tree species (Figure 2). The trunks and bases of *Betula* spp., *Alnus glutinosa*, *Picea abies* and *Pinus sylvestris* had, respectively, 75, 74, 65 and 62 lichen species. Other tree species had fewer lichen species (e.g. *Fraxinus excelsior* 53, *Quercus robur* 52, *Acer platanoides* 38 and *Tilia cordata* 36). On twigs the highest number of lichen species was registered for *Populus tremula* and *Picea abies* (39 and 23, respectively). The dead wood snags of *Pinus sylvestris* and *Picea abies* accounted for most of the epixylic species (42 and 31, respectively).

We found 76 host-tree-specific lichen species (32% of the total species list). The

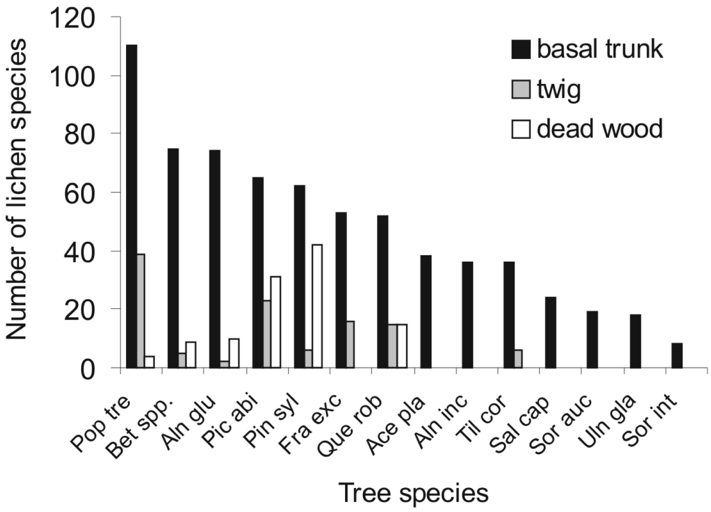

Figure 2. Number of lichen species recorded on different tree species. Ace pla – *Acer platanoides*, Aln inc – *Alnus incana*, Aln glu – *Alnus glutinosa*, Bet spp. – *Betula pubescens* and *Betula pendula*, Fra exc – *Fraxinus excelsior*, Que rob – *Quercus robur*, Pic abi – *Picea abies*, Pin syl – *Pinus sylvestris*, Pop tre – *Populus tremula*, Sal cap – *Salix caprea*, Sor auc – *Sorbus aucuparia*, Sor int – *Sorbus intermedia*, Til cor – *Tilia cordata*, Ulm gla – *Ulmus glabra*.

highest number (28) of specialists was confined to *Populus tremula*, eight species were associated with *Pinus sylvestris*, while other trees had four or less host-specific lichen species (Appendix 1).

Ordination

The first two axes obtained by DCCA analysis have eigenvalues of 0.29 and 0.11. The Monte Carlo permutation test confirms that the relationship between species data and first ordination axis is highly significant ($P = 0.005$). The first two canonical axes together explain 8.6% of the variance of the species data, and the percentage of the variance of the species–environment relationship explained by the first two canonical axes is 38.9%.

The studied forests constitute one rather continuous cluster on the DCCA ordination plot (Figure 3). Nevertheless, the sub-clusters formed according to the geographical origin of sites can be distinguished. On this basis, the gradient from northeast to southwest, as well as from southeast to southwest, can be traced.

The importance of the geographical factors ‘Latitude’ and ‘Longitude’ also appears clearly from ordination of the environmental variables (Figure 4), confirmed by the canonical coefficients and their *t*-values (Table 3). Moreover, the ordination plot (Figure 4) explicitly shows the gradient directed along the first ordination axis and related to the number of tree species in forests. The negative side of the axis coincides with the environmental parameter ‘Pine’, i.e. with species-poor tree stands, while the covariation directed towards the positive side of the axis is

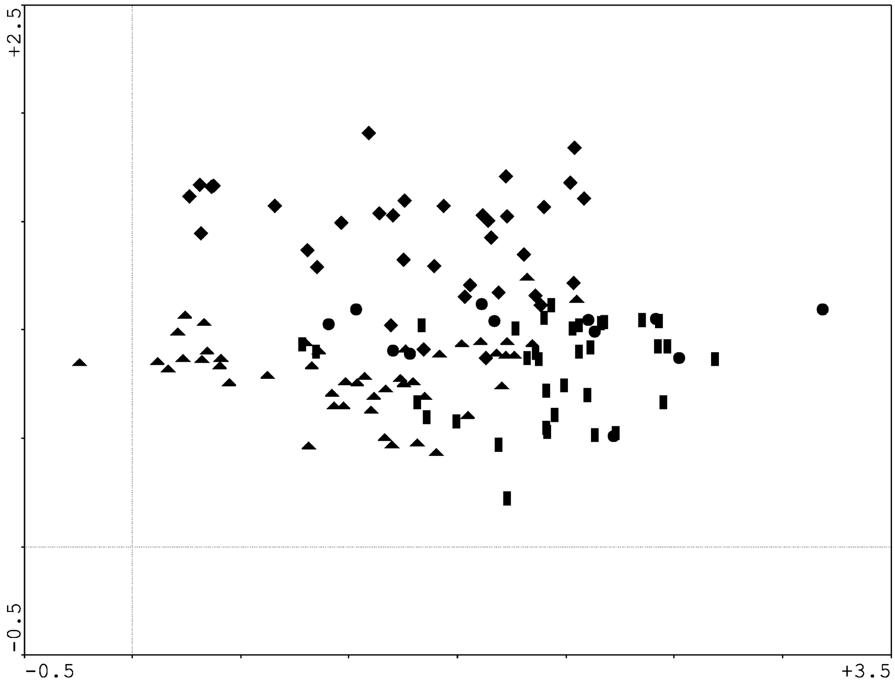

Figure 3. DCCA ordination of study sites. Sites are marked as follows: (♦) Northeast, (▲) Southeast, (●) Southwest, and (■) West Estonia.

determined by the variable 'Number of tree species'. This phenomenon is more specifically demonstrated in Figure 5, where the tree species-richness values are plotted on the ordination plane of sites. Parameters such as 'Nutritional conditions', 'Broad-leaved trees' and 'Aspen' are also rather strongly positively correlated with the first axis but, according to the corresponding canonical coefficients and *t*-values of DCCA (Table 3), these variables do not contribute essentially to the regression of sample scores.

Variation of the data along the second ordination axis is mainly related to the parameter 'Latitude' and the parameter 'Spruce'. Other environmental variables do not provide reliable information for data interpretation, since the *t*-values of their canonical coefficients, or the coefficients of the respective inter-set correlation, are too low (Table 3).

Ordination of lichen species (Figure 6) is in good concordance with the ordination of sites and environmental parameters. Lichen species usually growing on trunks and twigs of *Populus tremula* in northeastern Estonia (e.g. *Anaptychia ciliaris*, *Lecanora allophana*, *Physconia distorta* and *Rinodina pyrina*) are located on the upper right side of the scatter diagram. The species more characteristic to the forests of southwestern or western Estonia are in the middle and lower right side part of the ordination plot (e.g. *Acrocordia gemmata*, *Arthopyrenia* spp., *Arthonia radiata*,

Table 3. The canonical coefficients, *t*-values of canonical coefficients and inter-set correlations of the first and second ordination axes.

Variable	Canonical coefficient		*t*-value of the canonical coefficient		Inter-set correlation	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Latitude	0.15	0.25	4.91	8.92	0.10	0.65
Longitude	−0.21	0.08	−5.62	2.45	−0.40	0.40
Moisture regime	−0.10	−0.08	−2.77	−2.46	0.11	−0.04
Number of tree species	0.19	0.02	5.58	0.54	0.71	−0.11
Nutritional conditions	0.03	−0.05	0.85	−1.31	0.61	−0.02
Relative density	0.01	0.00	0.36	0.00	0.01	0.27
Stand age	−0.02	−0.08	−0.59	−2.51	−0.30	−0.20
Aspen	0.04	−0.01	1.12	−0.23	0.42	0.20
Black alder	0.03	−0.06	0.93	−1.84	0.23	−0.17
Broad-leaved trees	0.08	0.01	3.04	0.13	0.36	−0.06
Grey alder	0.01	0.04	0.41	1.53	0.14	0.16
Oak	0.05	−0.03	−1.55	−1.12	0.20	0.00
Pine	−0.36	−0.06	−5.92	−1.09	−0.77	0.05
Spruce	−0.02	−0.19	−0.63	−5.40	0.13	−0.35
Willow and rowan	0.04	−0.02	1.35	−0.87	0.23	−0.21

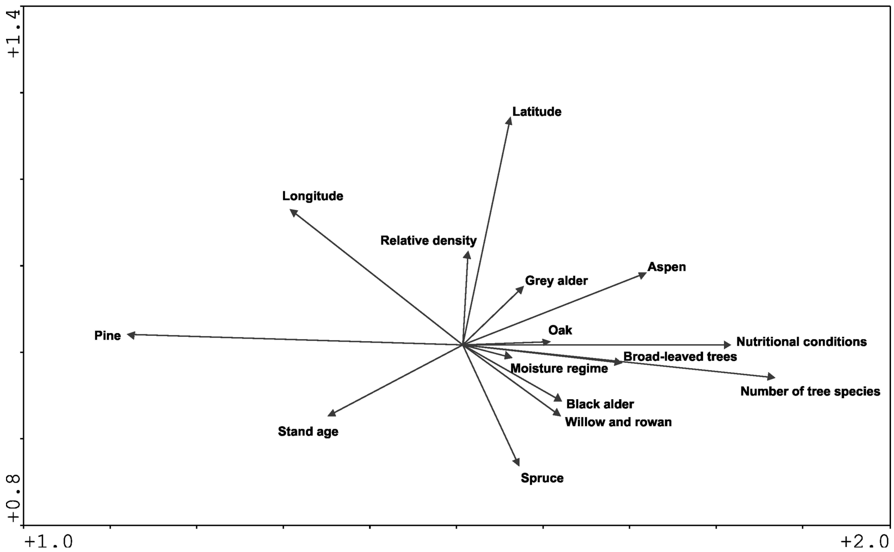

Figure 4. DCCA ordination of environmental variables.

Lecanactis abietina, *Opegrapha vulgata*, *Pertusaria leioplaca* and *Thelotrema lepadinum*).

In the upper left part of the ordination plot are located some species collected only or mainly from northeastern Estonia (e.g. *Hypocenomyce caradocensis*, *H. scalaris*

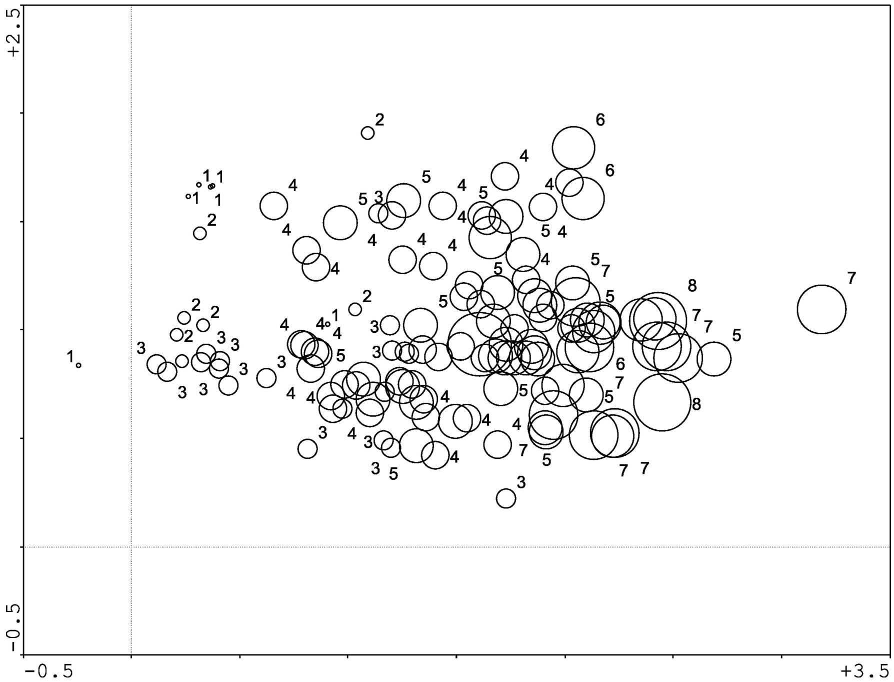

Figure 5. Distribution of values of the variable ‘Number of tree species’ on the DCCA site ordination plot.

and *Micarea melaena*). In the lower left part, there are scattered species that grow more frequently or only in the forests of southeastern Estonia (*Biatoropsis usnearum*, *Bryoria* spp., *Placynthiella icmalea* and *Usnea* spp.). The species that are negatively correlated with the first axis (e.g. *Imshaugia aleurites*, *Lecidea turgidula*, *Mycocalicium subtile* and *Trapeliopsis flexuosa*) are more often recorded on *Pinus sylvestris*, *Betula* spp., on decorticated snags, or on other kinds of dead wood.

GLM analysis

According to the results of GLM analysis, the environmental variables ‘Latitude’, ‘Stand age’, ‘Forest type’ and ‘Aspen’ have a statistically significant impact on the diversity of lichen species (Table 4). As the slope of the factor ‘Latitude’ is positive, the forests in northern Estonia appeared to be more species-rich in lichens than the forests in southern Estonia. Also, older forests have more lichen species than younger forests (the estimated slope of stand age is 0.055); on average, the addition of one lichen species occurs for every 18 year of forest age (Table 4). The tree species composition of a forest has a significant influence on the lichen diversity – there are on average six more lichen species in boreo-nemoral than in boreal forests (Figure 7). *Populus tremula* is the tree species that has the most significant effect on

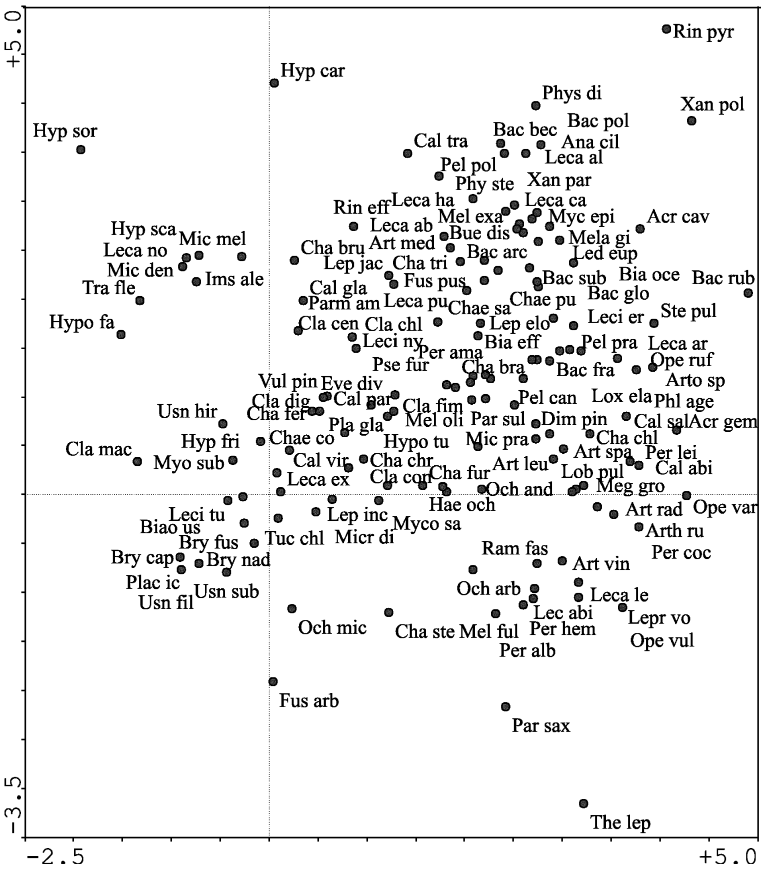

Figure 6. DCCA ordination of lichen species. For abbreviations of lichen species see Appendix 1.

the number of lichen species in Estonian natural forests. On average, there are five more lichen species in forests with *Populus* than in those without it (Figure 8).

Discussion

The 232 taxa recorded in the investigated natural forests constitute approximately 1/4 of the entire currently known Estonian lichen flora (Randlane and Saag 1999). The field work of the present study considerably extended the knowledge about the distribution and occurrence of numerous rare species (Jüriado et al. 2000).

The Estonian Red Data Book (Randlane 1998) includes only macrolichens (*sensu* Trass and Randlane 1994), although the respective analysis of endangered microlichens in Estonia has yet to be carried out. *Cetrelia cetrarioides* and *Collema subnigrescens*, belonging to the category ‘extinct or probably extinct species’, were

Table 4. Evaluation of the influence of the environmental factors on the diversity of lichen species, by means of GLM analysis.

Continuous factors	DF	*F*	*P*	Slope (±SE)	
Latitude	1; 113	5.93	0.016	3.941 (±1.618)	
Longitude	1; 113	0.13	0.722	−0.230 (±0.646)	
Moisture regime	1; 113	0.04	0.844	−0.085 (±0.427)	
Nutritional conditions	1; 113	0.08	0.782	0.132 (±0.475)	
Relative density	1; 113	1.48	0.226	−0.061 (±0.051)	
Stand age	1; 113	5.27	0.024	0.055 (±0.024)	
Categorical factors	**DF**	***F***	***P***	**Mean by factor level (±SE)**	
				Boreal	Boreo-nemoral
Forest type	1; 113	7.43	0.007	19.72 (±2.99)	25.78 (±2.26)
				Absent	Present
Aspen	1; 113	9.00	0.003	20.31 (±2.39)	25.20 (±2.69)
Birch	1; 113	0.66	0.419	21.69 (±3.13)	23.81 (±2.30)
Black alder	1; 113	0.99	0.321	21.76 (±2.36)	23.75 (±2.84)
Broad-leaved trees	1; 113	0.32	0.575	23.24 (±2.32)	22.27 (±2.78)
Grey alder	1; 113	2.19	0.142	21.25 (±2.11)	24.25 (±3.04)
Oak	1; 113	0.04	0.843	23.10 (±1.73)	22.41 (±3.83)
Pine	1; 113	1.25	0.265	21.79 (±2.57)	23.72 (±2.55)
Spruce	1; 113	0.21	0.646	22.23 (±2.83)	23.28 (±2.49)
Willow and rowan	1; 113	0.16	0.688	23.15 (±2.31)	22.36 (±2.87)

DF – degrees of freedom, *F* – value of *F*-criterion, *P* – significance level, Slope – slope of the regression line, SE – standard error.

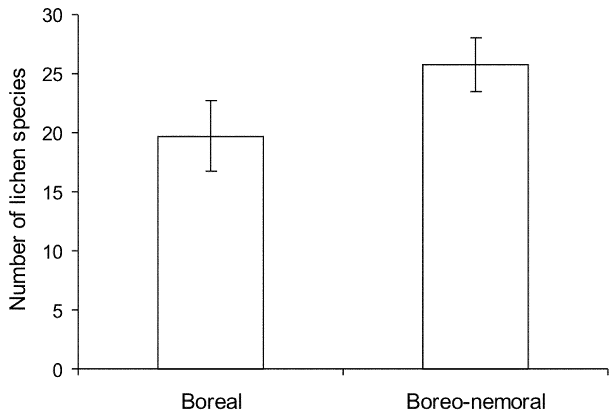

Figure 7. Number of lichen species in boreal and boreo-nemoral forests. Bars indicate the standard error, means are different at $P = 0.007$ (see Table 4).

re-found. *Hypocenomyce sorophora*, which currently belongs to the category 'rare species', should be re-qualified as frequent for Estonia and should therefore be excluded from the Red Data Book. The other recorded red-listed species (Table 2) – *Bryoria nadvornikiana*, *Evernia divaricata*, *E. mesomorpha*, *Menegazzia terebrata*,

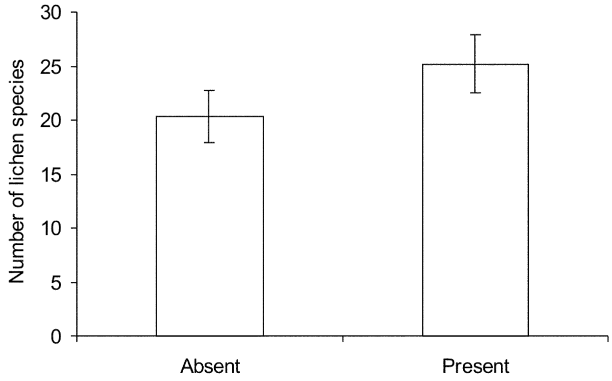

Figure 8. Number of lichen species in forests with and without *Populus tremula*. Bars indicate the standard error, means are different at $P = 0.003$ (see Table 4).

and *Nephroma laevigatum* – are rather frequent in Estonia, having 11–20 localities (Randlane and Saag 1999; Jüriado et al. 2000), but are confined to old-growth forests (Trass et al. 1999). These species are endangered by the ongoing extensive logging in Estonia. The only exception is *Evernia mesomorpha*, which tends to prefer well-lit bog forests, which are not yet under economic pressure in our country.

During the field work numerous new localities of *Lobaria pulmonaria* were discovered. With data from other studies, *Lobaria* has ca. 300 localities in Estonia, most densely distributed in the northeastern and southwestern forests (Jüriado, personal notes). This species is endangered or extinct in large areas of Europe (Rose 1988), but seems to be remarkably vital in our area.

Time-limited sampling may have caused some bias in the estimation of lichen flora on different substrates, with the possible underestimation of flora for less accessible substrate types, particularly for twigs. Most species were recorded from the basal trunk of trees, probably because trunks are the most common substrate type and are most accessible for researchers in time-limited sampling. *Populus tremula* and *Picea abies* were the most usual fallen tree species in forests, and this simplified the estimation of the lichen flora for twigs (Figure 2). The number of lichen species found on the decorticated snags of *Pinus sylvestris* is higher than on snags of other tree species. This is probably because the decorticated snags of *Pinus sylvestris* have a slow decomposition rate and are more common than snags of other tree species (Harmon et al. 1986; Lõhmus and Lõhmus 2001). However, we still believe that the over- and under-sampling of some substrate types only amplify the patterns existing in nature.

Broad-leaved trees (*Acer platanoides*, *Fraxinus excelsior*, *Quercus robur*, *Tilia cordata*, *Ulmus glabra*) have a limited distribution in Estonia (Kaar 1974). Fewer lichen species were recorded on broad-leaved trees than on the common forest tree species of our region such as *Alnus glutinosa, Betula* spp., *Picea abies*, *Pinus* *sylvestris* or *Populus tremula* (Figure 2). In other studies from the central or western part of Europe (Barkman 1958; Watson et al. 1988; Cieśliński et al. 1995) a considerably higher number of lichen species has been found on broad-leaved trees. This confirms the opinion of Barkman (1958), who has noted that there are usually less epiphyte species on tree species growing near the limits of their natural distribution area than on the same tree species in the more central part of their distribution area.

The largest number of host-tree-specific lichen species (28) was found on *Populus tremula*. Several of these species, *Anaptyhia ciliaris*, *Candelariella* spp., *Lecania* spp., *Physcia* spp. and *Physconia* spp., were found both on trunks and twigs. They belong to the alliance *Xanthorion parietinae* Ochsn., a widespread nitrophytic or nitrophilous alliance, usually represented in well-lit places and on subneutrophytic bark (Barkman 1958; James et al. 1977). Another distinct group of species recorded only on the basal trunk of *Populus tremula* includes cyanobacterial lichens (*Collema* spp., *Leptogium saturninum*, *Nephroma laevigatum*, *Peltigera* spp.) characteristic to the *Lobarion pulmonariae* Ochsn. alliance (Barkman 1958; James et al. 1977). Many species of *Lobarion* are threatened in various regions of Europe (Rose 1985, 1988; Gauslaa 1995). The importance of *Populus tremula* in supporting cyanobacterial lichens in boreal forests has been pointed out in several studies from northern Europe (Kuusinen 1994, 1996a, 1996b; Uliczka and Angelstam 1999; Hedenås and Ericson 2000).

The composition of tree species in forests creates a gradient for epiphytic lichen vegetation, from oligotrophic pine forests to eutrophic herb-rich forests in many countries of Europe (Oksanen 1988; Cieśliński et al. 1996b; Holien 1996). Our results show that boreo-nemoral forests on fertile soils, which are rich in tree species, have the most diverse lichen flora, while boreal forests on nutrient-poor soils, dominated by coniferous trees or birch, have lower diversity of lichens. Consequently, the tree species diversity is also important for creating the conditions necessary for the establishment of many different lichen species.

According to the DCCA (Table 3) 'Stand age' does not contribute essentially to the variation of composition of lichen flora. However, GLM analysis proves that 'Stand age' is significant for enhancing lichen diversity in a forest stand (Table 4). The tree bark characteristics (pH, roughness) and forest environmental conditions (moisture and light regime) change with stand age, and this has been noted to be important for lichens (Hyvärinen et al. 1992; McCune 1993; Cieśliński et al. 1996a). The durability of a forest community and the presence or development of different substrate types in natural forests are critical for specific lichen groups, such as cyanobacterial and calicioid lichens (Tibell 1992; Goward 1994; Selva 1994; Kuusinen 1996a).

The observed regional differences (Figure 3) in lichen species composition are obviously connected with the representation of forest types, but also with atmospheric pollution. Oligotrophic boreal pine forests and swamp forests are common in southeastern Estonia, while eutrophic boreo-nemoral forests are more frequent in southwestern Estonia. Since the number of lichen species is, on average, higher in boreo-nemoral forests than in boreal forests (Figure 7), the forests of southwestern Estonia are therefore more species rich in lichens than those of southeastern Estonia.

The northeastern–southwestern air pollution gradient in Estonia (Martin and Martin 2000) might be the reason for the distinction of northeastern forests from the forests of other regions. The northeastern part of Estonia has been seriously polluted with both sulphur dioxide and alkaline emissions (ash, cement dust) originating from electricity power plants and a cement plant (Haapala et al. 1996; Liblik et al. 2000). It has been shown that in the vicinity of these pollution sources the natural lichen communities on trees have changed (Martin and Nilson 1992; Nilson 1995; Martin and Martin 2000). The stands investigated in this study in northeastern Estonia were located approximately 30–40 km from the power plants. The peculiarity of northeastern forests is the higher abundance of nutrient-enriched-bark-favoured lichen species of the *Xanthorion* on *Populus tremula*, which is probably caused by alkaline emissions. The change of substrate characteristics might be a reason why forests in northern Estonia appeared to be generally more species-rich in lichens than forests in southern Estonia.

An important phytogeographic borderline crosses Estonia, separating western and eastern Estonia (Lippmaa 1935; Laasimer 1965; Ahti et al. 1968). This border is also recognised in the distribution of lichenized fungi (Randlane and Saag 2000). We found that several species (e.g. *Acrocordia gemmata*, *Lecanactis abietina*, *Parmelia saxatilis*, *Thelotrema lepadinum*) were more characteristic of the forests of southwestern and western areas. These species may prefer the milder climate in West Estonia compared to the more continental eastern part of Estonia. In the winter period, for example, the difference between isotherms in western and eastern Estonia is up to 4–5 °C (Jõgi and Tarand 1995).

In conclusion, we found the highest diversity of the lichen flora in tree-species-rich boreo-nemoral forests and old-growth forests. At forest community composition level, the presence of *Populus tremula* has the strongest impact on the number of lichen species. Additionally to the specific cyanobacterial lichens, *Populus tremula* supports a multitude of common species and remarkably increases the lichen diversity of a stand. In addition to forest age and stand diversity, the importance of *Populus tremula* for the conservation of lichen species diversity should be considered.

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Appendix 1

List of recorded lichen, lichenicolous fungus (#) and non-lichenized fungus (+) species, their frequency of occurrence on different substrate types and on different tree species.

Species	B	T	W	Ai	Ag	Bs	Qr	Pa	Ps	Pt	B-l	SS	Od	Oc	%
Acrocordia cavata (Acr cav)	5									1	3		1		4
Acrocordia gemmata (Acr gem)	12						2			3	7				8
Anaptychia ciliaris (Ana cil)	10	7								17					12
Arthonia apatetica			2				1	1							1
Arthonia byssacea	1						1								1
Arthonia didyma	2			1						1					1
Arthonia leucopellaea (Art leu)	63		1		8	18		33	2		3				30
Arthonia mediella (Art med)	4						1			3					3
Arthonia radiata (Art rad)	8	2		1			1				5	1	2		8
Arthonia spadicea (Art spa)	15	1		2	4		3	1		1	2		3		10
Arthonia vinosa (Art vin)	3				2						1				2
Arthopyrenia spp. (Arto sp)	4	1									4	1			4
Arthothelium ruanum (Arth ru)	13	2		1						1	7	4	2		9
Bacidia arceutina (Bac arc)	19			1	1	1				13	2		1		14
Bacidia bagliettoana	1									1					1
'*Bacidia*' *beckhausii* (Bac bec)	4									2	2				3
Bacidia biatorina	1									1					1
Bacidia fraxinea (Bac fra)	24									17	7				15
'*Bacidia*' *globulosa* (Bac glo)	3	1				1	1				2				3
Bacidia incompta	2									1	1				1
Bacidia laurocerasi	2										2				1
Bacidia polychroa (Bac pol)	3									3					2
Bacidia rubella (Bac rub)	6						1			1	4				5
Bacidia subincompta (Bac sub)	9				1					6	2				7
Bacidina arnoldiana			1										1		1
Bacidina phacodes	2									1			1		1
Biatora chrysantha	2			1	1										1
Biatora efflorescens (Bia eff)	16	1		3	4	2				3			4	1	13
Biatora helvola	13	1			3	1	1	1		3	3		2		11
Biatora ocelliformis (Bia oce)	4									2	1		1		3
Biatoridium monasteriense			1												1
#*Biatoropsis usnearum* (Biao us)	3					1		2							2
Bryoria capillaris (Bry cap)	18	4	1			4		17	1						15
Bryoria fuscescens (Bry fus)	7	1				2		4	2						5
Bryoria nadvornikiana (Bry nad)	5					2		2	1						4
Buellia disciformis (Bue dis)	10			2	1	2	2			1	2				8
Buellia erubescens	1						1								1
Buellia griseovirens	44	4	3	9	6	3	4	1	1	5	12	2	6	1	32
Buellia pharcidia	1									1					1
Calicium abietinum (Cal abi)			3				2	1							2
Calicium adspersum	1							1							1
Calicium glaucellum (Cal gla)	1		19		1	1	1	4	11				1		14
Calicium parvum (Cal par)	3								3						2
Calicium salicinum (Cal sal)	2	1	5		1	1	5	1							6
Calicium trabinellum (Cal tra)			3						2						2
Calicium viride (Cal vir)	9				1			7	1						7

Appendix 1. (*continued*)

Species	B	T	W	Ai	Ag	Bs	Qr	Pa	Ps	Pt	B-l	SS	Od	Oc	%
Caloplaca cerina	3	1								4					3
Caloplaca flavorubescens	17	11								27			1		19
Caloplaca holocarpa	2	4								5				1	5
Candelariella aurella	1	1								2					1
Candelariella vitellina	4	1								5					4
Candelariella xanthostigma	1													1	1
'*Cetraria*' *sepincola*		1											1		1
Cetrelia cetrarioides	1											1			1
Chaenotheca brachypoda (Cha bra)	3		14		2	5	1	1	1	4	1		2		12
Chaenotheca brunneola (Cha bru)	1		10		1		1	4	4				1		8
Chaenotheca chlorella (Cha chl)	2		7		3		2						4		7
Chaenotheca chrysocephala (Cha chr)	77	1	9		5	7		49	22						55
Chaenotheca ferruginea (Cha fer)	83	1	11		2	11	1	35	44						48
Chaenotheca furfuracea (Cha fur)	4		24		5			9	1						20
Chaenotheca stemonea (Cha ste)	3		3					4	2						5
Chaenotheca trichialis (Cha tri)	12	1	12		5	2	1	7	8	1					16
Chaenotheca xyloxena	1		13		1	2		1	8				2		11
#*Chaenothecopsis consociata* (Chae co)	5					1		4							4
+*Chaenothecopsis haematopus*			1										1		1
+*Chaenothecopsis pusilla* (Chae pu)	1		4				1		3				1		4
+*Chaenothecopsis pusiola*			2						2						1
+*Chaenothecopsis rubescens*			1			1									1
+*Chaenothecopsis savonica* (Chae sa)			6					1	3				1		4
#*Chaenothecopsis vainioana*	1						1								1
Chrysotrix candelaris	2				1		1								1
Cladina rangiferina			1												1
Cladonia cenotea (Cla cen)	23		8	1	1	12		3	6	1			1		23
Cladonia chlorophaea (Cla chl)	7		2					2	3	2	1				7
Cladonia coniocraea (Cla con)	81		11		11	31	4	17	14	3	1	1	1	1	56
Cladonia cornuta			1												1
Cladonia digitata (Cla dig)	117		26		11	39		22	43	2	1		1		70
Cladonia fimbriata (Cla fim)	59	1	9		6	15	6	8	7	9	3	1	2	1	47
Cladonia macilenta (Cla mac)	2		2			1	1						1		3
Cladonia ochrochlora	2					2									1
Cladonia pyxidata	1													1	1
Cladonia sulphurina			1												1
Cliostomum griffithii	2						1						1		1
Collema subnigrescens	1									1					1
Dimerella lutea	1									1					1
Dimerella pineti (Dim pin)	8		2		2	5	1		1				1		8
Evernia divaricata (Eve div)		3						3							2
Evernia mesomorpha	1	1						1	1						1
Evernia prunastri	74	6	6		11	7	5	31	6	7	4	2	7	1	52
Fuscidea arboricola (Fus arb)	3							1	2						2
Fuscidea pusilla (Fus pus)	8			3	2		2	1							5
Graphis scripta	83	6		9	12	12	3			1	29	7	16		42
Gyalecta truncigena	2									2					1
Haematomma ochroleucum var. *porphyrium* (Hae och)	3					1			1		1				2
Hypocenomyce anthracophila	1		2						3						2

Appendix 1. (*continued*)

Species	B	T	W	Ai	Ag	Bs	Qr	Pa	Ps	Pt	B-l	SS	Od	Oc	%
Hypocenomyce caradocensis (Hyp car)			3						3						2
Hypocenomyce friesii (Hyp fri)	5		3					5	3						6
Hypocenomyce scalaris (Hyp sca)	21		13			1			23						18
Hypocenomyce sorophora (Hyp sor)	11	1	3						15						10
Hypogymnia farinacea (Hypo fa)	5					1		1	3						4
Hypogymnia physodes	290	6	7	6	25	73	4	91	54	15	13	1	9	8	94
Hypogymnia tubulosa (Hypo tu)	33	9	1		1	7		22	5	1	2	1	4		30
Imshaugia aleurites (Ims ale)	44		8	1		8	1	5	30					1	28
Lecanactis abietina (Lec abi)	63		2		8	16		35	3	1	1				27
Lecania cyrtella	3			1	1					1					2
Lecania fuscella		1								1					1
Lecania naegelii	1									1					1
Lecanora albella (Leca ab)	7				2	1	2				1		1		5
Lecanora allophana (Leca al)	21	9			1					28				1	18
Lecanora argentata (Leca ar)	29	4		1			7			6	8	4	5		18
Lecanora cadubriae	1								1						1
Lecanora carpinea (Leca ca)	18	7		3	2	2	2			9	2		5		18
Lecanora chlarotera	30	15		2	1	2	4			18	9		6	1	29
Lecanora conizaeoides	2					1		1							1
Lecanora expallens (Leca ex)	1		3				1	1							3
Lecanora hagenii (Leca ha)	3	2								5					4
Lecanora leptyrodes (Leca le)	2	1								1	2				2
Lecanora norvegica (Leca no)	3		1	1					3						3
Lecanora phaeostigma	2								2						1
Lecanora populicola	1									1					1
Lecanora pulicaris (Leca pu)	31	10	4	3	3	8	1	1	12		5	2	8	1	27
Lecanora rugosella	4									3	1				3
Lecanora saligna	2									1			1		1
Lecanora sambuci	1												1		1
Lecanora strobilina	1													1	1
Lecanora symmicta	9	3	4		3			2	2	2	4			1	12
Lecanora varia	1		1			1									1
'*Lecidea*' *erythrophaea* (Leci er)	5				1					2	2				4
'*Lecidea*' *nylanderi* (Leci ny)	31					14		2	13	1			1		22
'*Lecidea*' *turgidula* (Leci tu)	8		4			2		3	6						8
Lecidella elaeochroma	30	5		1			2			11	9	3	7		20
Lecidella euphorea (Led eup)	19	7		1						13	5	2	3		18
Lecidella subviridis	1				1										1
Lepraria eburnea	2									2					1
Lepraria elobata (Lep elo)	5		1		1	3				1					4
Lepraria frigida	1									1					1
Lepraria incana (Lep inc)	52	1			8	14	3	17	8	1	1	1			35
Lepraria jackii (Lep jac)	15		1	1	1	7		1	4					1	10
Lepraria lobificans	11				3	1			1	2	2	2			8
Lepraria umbricola	1												1		1
Lepraria spp.	93		2		9	15	3	40	14	5	5	1		1	50
Leproloma vouauxii (Lepr vo)	4				1	2	1								3
Leptogium saturninum	2									2					1
Lobaria pulmonaria (Lob pul)	22			1			1			10	6	4			15
Loxospora elatina (Lox ela)	22				1	11		6		1	1	2			15
Megalaria grossa (Meg gro)	6									4	2				5
Melanelia exasperatula (Mel exa)	14	8			1	1		9		5	2	1	3		15

Appendix 1. (*continued*)

Species	B	T	W	Ai	Ag	Bs	Qr	Pa	Ps	Pt	B-l	SS	Od	Oc	%
Melanelia fuliginosa (Mel ful)	32	2		2	5		2	1	2	4	9	4	4	1	22
Melanelia olivacea (Mel oli)	9	1			1	2		2		1	1		3		8
Melanelia subaurifera	14	5		2	1	1	3	2		1	4		3	2	15
+*Melaspilea gibberulosa* (Mela gi)	2	1								2			1		2
Menegazzia terebrata	1				1										1
Micarea denigrata (Mic den)	4		2						5						5
Micarea elachista	3								3						1
Micarea hedlundii	1					1									1
Micarea melaena (Mic mel)	23		11			9			18						20
Micarea melanobola	1							1							1
Micarea misella			2						1						1
Micarea peliocarpa	1										1				1
Micarea prasina (Mic pra)	26		1		4	5	1	2	6	2	4		1	1	18
#*Microcalicium disseminatum* (Micr di)	1		3					2	2						3
Mycobilimbia carneoalbida	15				1	1				13					9
Mycobilimbia epixanthoides (Myc epi)	7			1			1			3			1	1	5
Mycoblastus fucatus	7	1	1			3		1	3			1	1		7
Mycoblastus sanguinarius (Myco sa)	5					5									4
+*Mycocalicium subtile* (Myo sub)	2		25		1	2	2	4	14	2			1		21
Nephroma laevigatum	1									1					1
Normandina acroglypta	1									1					1
Ochrolechia androgyna (Och and)	25	1	2		6	8	1	5	1	3			2		18
Ochrolechia arborea (Och arb)	3	1			2					1	1				2
Ochrolechia microstictoides (Och mic)	8	1			2	2			4	1					6
Ochrolechia szatalaënsis	2	1					1			2					2
Omphalina umbellifera			2												1
Opegrapha rufescens (Ope ruf)	10				1		1			4	4				8
Opegrapha varia (Ope var)	6						1				5				4
Opegrapha vulgata (Ope vul)	5							1		1	2		1		3
Pachyphiale fagicola	2									2					1
Parmelia saxatilis (Par sax)	22	5	1		4	4		9		4	1	1	4		15
Parmelia sulcata (Par sul)	148	23		4	23	34	6	34	1	23	12	4	18	4	78
Parmeliopsis ambigua (Parm am)	107		7		3	33	1	9	60	3					64
Parmeliopsis hyperopta	2					1			1						1
Peltigera canina (Pel can)	10		1		1					7	1		1		8
Peltigera leucophlebia	1									1					1
Peltigera neopolydactyla	1									1					1
Peltigera polydactyla (Pel pol)	4									2	1		1		2
Peltigera praetextata (Pel pra)	37						3	2		18	8		6		25
Pertusaria albescens (Per alb)	7	3			2					4	4				7
Pertusaria amara (Per ama)	117	4	1	10	23	20	8	8	2	20	17	6	7		61
Pertusaria coccodes (Per coc)	10		1	1			4			1	2	1	1	1	8
Pertusaria hemisphaerica (Per hem)	4				2		1			1					3
Pertusaria leioplaca (Per lei)	14	4		2			4				3	3	6		11
Pertusaria pertusa	1												1		1
Pertusaria pupillaris	1				1										1
Phlyctis agelaea (Phl age)	7				1						4		2		5
Phlyctis argena	180	7		11	32	7	7	19	4	40	36	6	15	10	75
Physcia adscendens	2									1		1			1

Appendix 1. (*continued*)

Species	B	T	W	Ai	Ag	Bs	Qr	Pa	Ps	Pt	B-l	SS	Od	Oc	%
Physcia aipolia	6	13								19					14
Physcia stellaris (Phy ste)	5	4								8			1		6
Physcia tenella	7	4						1		8		1	1		7
Physconia distorta (Phys di)	9	4								13					9
Physconia enteroxantha	2									1			1		1
Physconia perisidiosa	1									1					1
Placynthiella icmalea (Plac ic)			4					1							3
Platismatia glauca (Pla gla)	157	13	1	1	10	41		68	31	9	3	1	4	2	80
Pseudevernia furfuracea (Pse fur)	114	18	3		7	20	1	65	22	4	2	1	9	2	75
Psilolechia clavulifera			1										1		1
Psilolechia lucida	2							2							1
Pyrenula laevigata	2										1		1		1
Pyrenula nitidella	1										1				1
Pyrrhospora quernea	1	1					1		1						1
Ramalina farinacea	63	3	2	5	13	3	3	7	3	15	9	5	5		40
Ramalina fastigiata (Ram fas)		3							1	2					2
Ramalina fraxinea	1	1								2					1
Rinodina efflorescens (Rin eff)	3					2							1		2
Rinodina pyrina (Rin pyr)		3								2	1				2
Rinodina sophodes		1									1				1
Ropalospora viridis	8			1	2	3		1		1					6
Schismatomma percileum	3					1	1	1							2
Sclerophora coniophaea	1						1								1
+*Stenocybe pullatula* (Ste pul)	4			4											3
#*Stigmidium microspilum*	1												1		1
Tephromela atra	1									1					1
Thelotrema lepadinum (The lep)	21				4			1		1	11	3	1		5
Trapeliopsis flexuosa (Tra fle)			11					2	2						8
Trapeliopsis granulosa			1												1
Tuckermannopsis chlorophylla (Tuc chl)	23	4				2		18	3	1			3		19
Usnea filipendula (Usn fil)	24		1		1	9		12	2			1			15
Usnea hirta (Usn hir)	41	3	3			4		27	12				3		32
Usnea subfloridana (Usn sub)	22				2	4		13	1			2			14
Vulpicida pinastri (Vul pin)	60	1	8		3	24		21	16	1		1			42
Xanthoria parietina (Xan par)	13	16						2		27					21
Xanthoria polycarpa (Xan pol)	1	2									2		1		2

B – basal trunk, T – twig, W – dead wood, Ai – *Alnus incana*, Ag – *Alnus glutinosa*, Bs – *Betula* spp. (*Betula pubescens* and *Betula pendula*), Qr – *Quercus robur*, Pa – *Picea abies*, Ps – *Pinus sylvestris*, Pt – *Populus tremula*, B-l – broad-leaved trees (*Acer platanoides*, *Fraxinus excelsior*, *Tilia cordata*, *Ulmus glabra*), SS – *Salix caprea*, *Sorbus aucuparia* and *S. intermedia*, Od – other deciduous trees and bushes (e.g. *Corylus avellana*, *Frangula alnus*, *Padus avium*), Oc – other coniferous trees (*Juniperus communis*), % – frequency percent of lichen species in 130 studied forests.

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