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EPIPHYTE FLORA AND DIVERSITY ON BASAL TRUNKS OF SIX OLD-GROWTH FOREST TREE SPECIES IN SOUTHERN AND MIDDLE BOREAL FINLAND

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Abstract: Epiphytic lichen and bryophyte species composition, richness and diversity were surveyed on basal trunks of six common old-growth forest tree species, *Picea abies*, *Pinus sylvestris*, *Betula pendula*, *Alnus incana*, *Salix caprea* and *Populus tremula*, in two old-growth forest areas, one in southern and one in middle boreal Finland. The average species numbers per tree ranged from 18 (*Picea*) to 27 (*Salix*) in the southern and from 20 (*Populus*) to 31 (*Salix*) in the middle boreal area. A few widespread habitat-generalist species, such as the foliose lichens *Hypogymnia physodes* and *Platismatia glauca*, were most abundant on all the tree species, except *Populus*. Most other epiphyte species showed at least a slight preference for one or two tree species. *Populus* proved to have the most distinct flora characterized by the abundance of certain, rather specialized crustose lichens and bryophytes. The number of species that occurred on only one tree species was highest on *Populus* (9) in the southern and on *Alnus* (18) in the middle boreal area. Differences in bark acidity and structure were the most likely explanations for the differences between tree species in the epiphytic flora and diversity. *Salix* and *Populus* were the most important of the tree species studied for the conservation of epiphyte diversity in the boreal forests of Finland.

Introduction

Modern forestry has severely impoverished the epiphyte diversity in boreal forests in Fennoscandia (Esseen *et al.* 1992). Several structural elements that are rare in managed forests, such as old deciduous trees or large dead trees, support a particularly rich and/or unique epiphytic flora (Ahti 1977; Esseen *et al.* 1992; Kuusinen 1994*a*, *b*). Only a few species that have efficient dispersal capacity and thrive well on the now dominant, commercially most important tree species, *Picea abies*, *Pinus sylvestris* and *Betula* spp., may not have suffered from forest management.

Significant differences between the tree species in their epiphytic lichen and bryophyte flora and diversity have been demonstrated in a large number of studies in various temperature and boreal areas (Culberson 1955; Hale 1955; Barkman 1958; Brodo 1961; Kalgutkar & Bird 1969; Adams & Risser 1971; Jesberger & Sheard 1973; Sõmermaa 1972; Gough 1975; Rasmussen 1975; Slack 1976; Bates & Brown 1981; Esseen 1981; Studlar 1982; Trynoski & Glime 1982; Palmer 1986; Eversman *et al.* 1987; Bates 1992). In Finland, Kujala (1926), Räsänen (1927) and Koskinen (1955) compared the flora on all the major forest trees in different parts of the country in their extensive

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lichen surveys. More recently some quantitative data has been published by Halonen *et al.* (1991) and Hyvärinen *et al.* (1992) for *Picea* and *Pinus* in middle boreal Finland.

During the preparation of two earlier papers concerning epiphytic lichen diversity and flora on basal trunks of old deciduous trees in boreal forests of Finland (Kuusinen 1994*a b*), it became evident that a comprehensive quantitative survey covering all the major forest tree species was urgently needed. Only after producing this primary data would it be possible to explicitly quantify the importance of other more specific habitats for the maintenance of epiphyte diversity and flora. The earlier floristic data published from Finland by Kujala (1926), Räsänen (1927) and Koskinen (1955) is not particularly suitable for this purpose for at least three major reasons: (1) their descriptive data is not collected with quantitative sampling and comparable methodology, (2) several common sterile crustose lichen species are missing from their data, and (3) the separation of the phorophyte-dependent variation from the effects of various other factors is difficult.

The main aim of this study was to evaluate the contribution of basal trunks of the six most common forest tree species, *Picea abies*, *Pinus sylvestris*, *Betula pendula*, *Alnus incana*, *Salix caprea* and *Populus tremula*, to the total epiphytic lichen and bryophyte flora, species richness and diversity in the boreal forests of Finland. The effect of phorophyte-independent environmental factors, such as the forest site type or successional stage, was reduced by sampling old trees in as similar habitats as possible. For comparison, data was collected from two old-growth forest areas, one situated in southern and one in middle boreal Finland. This study is part of a long-term project seeking the most important habitats for epiphyte diversity in old-growth, i.e. old and ± primaeval, boreal forests of Finland.

Material and Methods

Study areas

Two *c.* 200-ha old-growth forest areas were selected for the study, one (Evo; 61°12′N, 25°12′E) in the southern and one (Kuhmo; 63°53′N, 20°42′E) in the middle boreal subzone (Ahti *et al.* 1968) of Finland. Only one area per vegetation zone was selected as earlier, geographically more extensive, data of *Salix* and *Populus* (Kuusinen 1994*a*, *b*) showed that the major characteristics of the epiphyte flora and diversity can be evaluated in one carefully selected area. The forest stands were mostly dominated by *Picea abies* with mixed *Pinus sylvestris* and *Betula* spp., as well as more scattered individuals of *Populus tremula*, *Alnus incana* and *Salix caprea*. In the southern boreal area some human impact, such as signs of old selective logging and mire drainage, was visible, but the middle boreal area was of primaeval nature. Managed forests, clear-cuts and mires surrounded both the old-growth forest patches.

The dominant forest site types were the herb-rich *Oxalis-Myrtillus* type (OMT) and the mesic *Myrtillus* type (MT) in the southern boreal area and the corresponding *Geranium-Oxalis-Myrtillus* (GOMT) and *Vaccinium-Myrtillus* type (VMT) in the middle boreal area (for the Finnish forest site type classification, see Kalela 1961).

The altitude of the southern boreal area was 150–170 m a.s.l., and in the middle boreal area 230–270 m a.s.l. General information about the climate in the areas is given in Kuusinen (1996). The most significant climatic difference between the southern and middle boreal areas is the higher humidity, measured as the difference between precipitation and evaporation, in the latter area. This value, counted from the disappearance of snow in spring to the end of July, is *c.* − 60 mm in the southern and *c.* +40 mm in the middle boreal area (Alalammi 1987). There are no major differences in precipitation values between the areas, but the evaporation values are considerably lower in the middle boreal areas due to a cooler climate. The background sulphur deposition values in 1987 were *c.* 800 mg S m^{-2} $year^{-1}$ in the southern and <600 mg S m^{-2} $year^{-1}$ in the middle boreal area (Tuovinen *et al.* 1990). The areas were not affected by local pollution sources.

Sampling

As the six tree species studied showed differences in abundance, habitat preference and/or spatial pattern, three different procedures were used in sampling. The most common species, *Picea abies*, *Pinus sylvestris* and *Betula pendula* were sampled using two 50 × 200 m sample plots in each study area. The sample plots were located on homogeneous stands of spruce-dominated forest on mineral soil. Ten trees of each species were sampled in each of the four plots using random co-ordinates. As the *Populus tremula* trees typically occurred as clumped clone groups in the study forests these were used as sample units. Two clone groups with 22–32 *Populus* trunks were located using random co-ordinates inside both study areas and ten trees were randomly sampled of each of four clone groups. Only straight, living *Picea*, *Pinus*, *Betula* and *Populus* trees with a diameter at breast height (DBH) of at least 18 cm were included in the sample. Spruces with many twigs below 2 m on the trunk were avoided. As *Alnus* and *Salix* were much sparser than the other tree species, all individuals of these tree species were sampled in the study areas. When possible, a total of 20 living trunks of both species were selected in each area. Trees of DBH less than 8 cm and strongly leaning trunks were excluded. The sample size was thus 20 for all tree species in both areas, except for *Salix* in the southern boreal area, where only 13 trees could be found.

The occurrence of all lichen and bryophyte species on the basal trunk below 2 m in height was recorded on the sample trees. The basal trunks of trees were selected for the study for four major reasons: (1) they were easily accessible, (2) comparable data could be collected from all tree species, (3) the basal parts of boreal forest trees have generally the highest epiphyte species richness (Koskinen 1955) and (4) species concentrated on the humid basal trunks were supposed to be most vulnerable to forest management (cf. Barkman 1958; McCune 1993).

To obtain cover estimates, 20 × 50 cm sample plots on *Picea, Pinus, Betula* and *Populus* and 10 × 50 cm on *Alnus* and *Salix* were marked out with transparent plastic sheet at 80 cm height above ground, on the south and north sides of the trunk. The 20 × 50 cm rectangle was divided into 100 and the 10 × 50 cm rectangle into fifty 2 × 5 cm subunits, and a single point was randomly placed in each of these. The number of points hit by each species were counted and these point frequency values were used as an estimate of the species' cover percentage on the sample plot. The point frequency values for *Alnus* and *Salix* were doubled to obtain comparable cover estimates. The values on the south and north sides of the trunk were combined for the analyses.

Specimens of difficult crustose species were collected for identification with a microscope and standard thin-layer chromatography (White & James 1985). Voucher specimens were deposited at the Botanical Museum of the University of Helsinki (H).

The DBH and height of each sample tree were measured. Canopy cover above each sample tree was estimated in 10% classes. Distance from the sample tree to the three closest living trees (DBH>4 cm) was measured to obtain an estimate of stem density. Ages of some (3–13) *Picea*, *Pinus* and *Betula* trees were measured with an increment borer. Accurate age estimates could not be obtained from *Alnus*, *Salix* or *Populus*, because the growth-rings were poorly visible and the heartwood often decayed on these trees.

Bark samples were collected from the trunks at 0·5–1·5 m above ground outside the sample plots. Two or three grams of surface bark in small pieces was incubated in 25 or 37 ml of distilled water for 24 h and the pH value of the extract was measured with a standard pH meter.

Data analysis

Species diversity on each tree species was determined with the Shannon-Wiener diversity index (H′) using the species cover estimates. The index was calculated using the formula

$$H' = -\sum_{i=1}^{s} p_i \ln p_i,$$

where p_i is the proportion of the total cover contributed by the *i*:th species. The jackknife procedure proposed by Zahl (1977) and Routledge (1980) was used to estimate the diversity indices. This method is based on resampling the data by omitting the sample trees one at a time, and it provides an estimate of the accuracy of the diversity index.

Statistical comparisons in species number and diversity between the tree species were performed with one-way analyses of variance (ANOVA) using tree species as the treatment variable. Pairwise multiple comparisons were performed with Tukey's HSD test using the 5% significance level. Separate analyses were performed for the two study areas.

The overall pattern of the species cover data was explored with non-metric multidimensional scaling (NMDS) using the programme package DECODA (Minchin 1989). Only species occurring on at least two trees were included in the analyses. The original cover values were square root transformed to downweight the influence of very abundant species. The species dissimilarity between each pair of trees was computed using the Bray-Curtis coefficient (Bray & Curtis 1957), shown by Faith *et al.* (1987) to be a robust quantitative dissimilarity measure. The NMDS was computed using 20 random starts and 1–3 dimensions. The ordination co-ordinates for the species were calculated as weighted averages of the scores of the trees on which each species occurred. The monotone relationship between the ordination patterns and three significant environmental variables (DBH, bark pH and canopy cover) was sought using a vector-fitting procedure. This option calculates a vector for each environmental variable through the ordination configuration, along which the scores of the trees have maximum correlation with that variable (Minchin 1989). A Monte-Carlo approach with 99 random permutations was used to test the significance of these vectors. Separate ordination analyses were performed for the southern and middle boreal trees.

The nomenclature follows Santesson (1993) for lichens, and Koponen *et al.* (1977) for bryophytes.

Results

Sample tree characteristics

The *Picea*, *Pinus*, *Betula* and *Populus* trees were generally thicker and taller than the *Alnus* and *Salix* trees (Table 1). The former trees usually reach the upper canopy whereas the latter two are often overshadowed. All tree species were on average 5–10 m taller in the southern than in the middle boreal areas. The tree species could be divided into three distinct groups according to the acidity of the surface bark. *Picea* and *Pinus* had a bark pH well below 4, *Betula* between 4 and 5 and *Alnus*, *Salix* and *Populus* about or slightly above 5 (Table 1).

The canopy cover values ranged between 70 and 90% for most of the trees studied in both areas (Table 1). The only distinct exceptions were the middle boreal *Alnus* trees, which had much lower canopy cover values than other trees. In the middle boreal areas most *Alnus* trees tended to occur in fairly open patches at mire and spring margins, often on thin peat. This is also reflected in the slightly larger values in mean distance to the three closest trees on *Alnus* than on the other trees (Table 1). The mean distance values show the stands to be somewhat denser in the middle than in the southern boreal area.

The sample trees were mostly well over 100 years old, the oldest individuals even over 200 years (Table 1). Some fairly inaccurate age estimates indicated that the *Salix* and *Populus* trees were approximately as old as the conifers and *Betula*, but the *Alnus* trees seemed to be much younger, perhaps only *c.* 60–80 years old. However, as *Alnus* has the capability of continuously producing new trunks from root suckers, it may remain at a site for a much longer time than the average age on an individual trunk. The trees were generally older in the middle boreal than in the southern boreal area.

TABLE 1. *Characteristics of the sampled trees in the solution (Evo) and middle boreal (Kuhmo) study area*

Parameters	Study area	*Picea**	*Pinus*	*Betula*	*Alnus*	*Salix*	*Populus*
DBH (cm)‡	Evo	33 ± 7	39 ± 6	33 ± 6	18 ± 3	20 ± 6	34 ± 7
mean ± S.D.	Kuhmo	26 ± 6	40 ± 7	26 ± 4	13 ± 3	22 ± 8	32 ± 8
Tree height (m)	Evo	28 ± 2	28 ± 1	28 ± 2	19 ± 3	17 ± 4	27 ± 2
mean ± S.D.	Kuhmo	20 ± 3	23 ± 2	21 ± 2	9 ± 3	12 ± 2	21 ± 3
Acidity of bark (pH)	Evo	3·5 ± 0·2	3·8 ± 0·3	4·5 ± 0·5	5·1 ± 0·1	4·9 ± 0·5	5·3 ± 0·4
mean ± S.D.	Kuhmo	3·3 ± 0·2	3·6 ± 0·2	4·4 ± 0·4	5·0 ± 0·2	5·0 ± 0·4	5·4 ± 0·7
Mean distance to the three closest trees (m)	Evo	2·8 ± 0·8	2·4 ± 0·6	2·8 ± 1·0	3·0 ± 0·8	2·6 ± 0·6	2·3 ± 0·7
mean ± S.D.	Kuhmo	2·2 ± 0·6	2·2 ± 0·5	2·1 ± 0·5	2·5 ± 0·9	2·3 ± 1·0	2·1 ± 0·6
Canopy cover (%)	Evo	90	80	80	80	80	80
median	Kuhmo	80	80	80	40	70	80
Tree age (year)	Evo	90–154 (13)	120–160 (6)	125–150 (5)	—	—	—
min.–max. (*n*)	Kuhmo	145–285 (7)	160–175 (4)	160–170 (3)	—	—	—

**n*=20, except for *Salix* in Evo (12) and tree age.
‡Diameter at breast height.

Species number and diversity

Significant differences were observed between the tree species in bryophyte, lichen and total species numbers as well as in species diversity in both study areas (Table 2). *Salix* and *Alnus* had the highest total species numbers per tree in both study areas; the highest individual value, 42, was found on *Salix* in the middle boreal area. *Alnus* had a particularly high number of lichen species and *Salix* of bryophyte species. The lowest total species numbers were observed on *Picea* in the southern boreal area and on *Populus* in the middle boreal area (Table 2). *Populus* had the lowest number of lichens in both areas. The deciduous trees, especially *Salix* and *Populus*, tended to support more bryophytes than the conifers in both areas.

There were generally more bryophyte and fewer lichen species on the southern boreal than on the middle boreal trees (Table 2). The number of bryophytes was significantly higher on *Pinus*, *Alnus*, *Salix* and *Populus* in the southern than in the middle boreal area, and correspondingly the number of lichens was significantly lower on all other tree species except on *Populus* (t-test for independent samples, $P<0{\cdot}05$ for all comparisons). The total species number was significantly lower on *Picea*, *Pinus*, *Betula* and *Salix* in the southern than in the middle boreal area, and this difference was particularly large on *Pinus* (*c.* nine species, Table 2).

The jackknife estimates of the Shannon-Wiener diversity index were highest on *Salix* in both areas, and lowest on *Picea* in the southern boreal and *Pinus* in the middle boreal area (Table 2). The high diversity on *Salix* was both due to large total species number and the lack of strong dominance by one or two species.

The total numbers of species found on each tree species reflected the mean species numbers per tree: *Salix* and *Alnus* had the highest numbers and *Pinus* the lowest in both areas (Table 3). The number and proportion of specific species, i.e. species that were found only on one tree species, was calculated for each tree species. Of all the species found 31·4% in the southern and 40·7% in the middle boreal area were such specific species (Table 3). The proportion of specific species was highest on *Populus* in both areas, although the number of these species was higher on *Alnus* in the middle boreal area. *Pinus* and *Betula* had the fewest specific species in both areas.

Ordinations

The minimum stress values obtained in the NMDS ordinations were 0·204 in one dimension, 0·134 in two dimensions and 0·101 in three dimensions for the southern boreal data and correspondingly 0·154, 0·116 and 0·092 for the middle boreal data. After preliminary examination of the ordination patterns the two-dimensional solution was selected as the simplest acceptable for further analysis.

The compositional patterns of the two-dimensional ordinations were quite similar in both data sets (Fig. 1). The main gradient of the data represented by the first dimension is strongly related to tree species: the conifers represent one end of this gradient and *Populus* the other. *Picea*, *Pinus* and *Betula* trees formed a group in both data sets, indicating only slight differences in their epiphytic

TABLE 2. *The mean ± S.D. of the number of lichen and bryophyte species per tree as well as the jackknife estimates of the Shannon-Wiener diversity index (H′) for the six tree species in the two study areas (Evo: southern boreal; Kuhmo: middle boreal)**

Parameters	Study area	*Picea*	*Pinus*	*Betula*	*Alnus*	*Salix*	*Populus*	*F*	*P*
Bryophytes	Evo	4·8 ± 1·3 A	5·4 ± 1·1 A	5·8 ± 1·4 AB	6·8 ± 1·7 B	9·3 ± 1·1 C	10·1 ± 2·0 C	39·1	0·000
(species/tree)	Kuhmo	5·0 ± 1·1 B	3·3 ± 1·3 A	5·7 ± 1·7 BC	4·8 ± 1·8 B	7·2 ± 1·7 D	7·1 ± 1·7 CD	17·7	0·000
Lichens	Evo	13·6 ± 2·1 AB	14·8 ± 3·0 BC	17·2 ± 2·3 CD	19·2 ± 3·1 D	17·8 ± 4·0 CD	12·1 ± 2·7 A	17·4	0·000
(species/tree)	Kuhmo	22·0 ± 2·6 B	22·2 ± 2·2 B	20·8 ± 2·9 B	23·8 ± 5·0 B	23·7 ± 4·8 B	12·9 ± 6·3 A	18·4	0·000
Total	Evo	18·4 ± 2·5 A	20·2 ± 3·6 AB	23·0 ± 3·2 BC	26·0 ± 3·5 CD	27·1 ± 4·1 D	22·2 ± 3·9 B	15·9	0·000
(species/tree)	Kuhmo	26·9 ± 3·2 BC	25·5 ± 2·4 B	26·4 ± 3·6 B	28·6 ± 5·7 BC	30·9 ± 5·3 C	20·0 ± 6·7 A	12·0	0·000
H′	Evo	1·02 ± 0·37 A	1·59 ± 0·39 CB	1·53 ± 0·56 AB	2·06 ± 0·45 CD	2·93 ± 0·57 E	2·10 ± 0·86 D	21·1	0·000
	Kuhmo	1·95 ± 0·93 B	1·22 ± 0·69 A	1·89 ± 0·52 AB	2·30 ± 0·52 BC	2·82 ± 0·51 C	1·77 ± 1·09 AB	10·4	0·000

*Differences between the tree species were tested with one-way ANOVA and pairwise multiple comparisons with Tukey's HSD test. The two last columns show the *F*-value and probability for no difference between the tree species. The letters after the values indicate the grouping of the tree species at 5% significance level. $n=20$, except 12 for *Salix* in Evo.

TABLE 3. *The frequency (number of observations, southern boreal/middle boreal area) of all lichens and bryophytes found on the six tree species in the two study areas‡ [Evo, southern boreal (left)/Kuhmo, middle boreal (right)]*

Species	*Picea*	*Pinus*	*Betula*	*Alnus*	*Salix*	*Populus*	Total	Grand total
*Ptilidium pulcherrimum**	18/19	19/14	20/20	19/18	12/20	20/17	108/108	216
Cladonia coniocraea, etc.	20/20	17/20	20/20	19/7	12/20	19/10	107/97	204
Hypogymnia physodes	20/20	20/20	20/20	20/19	11/20	3/9	94/108	202
Parmeliopsis ambigua	20/20	20/19	20/19	16/20	5/19	9/9	90/106	196
Lepraria spp.	20/20	19/20	20/16	19/4	12/16	19/6	109/92	191
Parmeliopsis hyperopta	20/19	20/18	20/20	16/20	6/18	4/8	86/103	189
*Pleurozium schreberi**	16/20	12/13	14/16	10/9	9/18	13/15	74/91	165
*Dicranum scoparium**	20/11	16/2	19/12	18/9	12/20	17/8	102/62	164
*Plagiothecium laetum**	19/18	19/6	18/13	17/12	11/10	13/8	97/67	164
Platismatia glauca	8/17	15/17	17/18	13/14	2/17	./6	55/89	144
*Dicranum fuscescens**	9/16	20/18	19/19	13/5	6/7	8/3	75/68	143
Vulpicida pinastri	15/4	5/4	16/9	17/19	11/20	5/9	69/65	134
Ochrolechia androgyna	2/17	5/19	17/19	16/11	5/9	2/4	47/79	126
Cladonia cenotea	19/19	20/20	20/18	3/1	3/2	./.	65/60	125
Ochrolechia microstictoides	18/19	19/20	15/18	9/6	./.	./1	61/61	122
Brachythecium spp.*	5/7	./.	6/2	16/11	12/12	19/20	58/52	110
*Hylocomium splendens**	./1	1/.	1/5	11/11	12/19	19/17	44/53	97
*Sanionia uncinata**	1/1	./.	4/1	17/6	12/16	20/20	54/43	97
Fuscidea pusilla	./.	2/4	4/18	17/14	3/.	17/15	43/51	94
Lecidea nylanderi	17/7	18/11	16/.	16/9	./.	./.	67/27	94
Biatora efflorescens	./1	./.	./.	20/16	12/19	18/6	50/42	92
Usnea spp.	3/11	3/7	14/14	2/15	2/12	./9	24/68	92
Cladonia digitata	16/17	17/18	11/12	./.	./.	./.	44/47	91
Loxospora elatina	11/13	5/11	19/16	5/4	3/2	./.	43/46	89
Parmelia sulcata	./1	./.	5/11	19/18	10/20	1/3	35/53	88
Bryoria capillaris	4/20	12/20	3/15	./4	./6	./.	19/65	84
Mycoblastus sanguinarius	./16	3/17	3/20	./15	./9	./1	6/78	84
Pertusaria borealis/pupillaris	./7	./13	4/13	9/18	4/8	2/6	19/65	84
Phlyctis argena	./.	./.	./.	13/3	10/15	20/17	43/35	78
Micarea prasina	8/6	4/1	5/6	13/.	7/7	16/3	53/23	76
Pertusaria amara	./2	./.	4/8	15/12	11/19	1/4	31/45	76
Micarea melaena	9/.	20/18	20/2	1/.	1/.	./.	51/20	71
Mycoblastus alpinus	1/11	5/18	6/19	1/4	1/1	./.	14/53	67
Bryoria fuscescens	./18	./20	./17	./4	./7	./.	./66	66
Alectoria sarmentosa	./12	./19	./15	./3	1/7	./.	1/56	57
Mycoblastus affinis	./16	./16	./9	./7	./8	./.	./56	56
Lophozia spp.*	3/5	1/.	3/10	./3	11/9	6/2	24/29	53
Biatora chrysantha	2/3	./.	./2	5/6	11/14	4/3	22/28	50
Biatora helvola	4/.	./.	./.	11/4	9/3	18/.	42/7	49
Japewia subaurifera	4/1	2/9	7/12	2/3	./7	./.	15/32	47
Biatora epixanthoides	./.	./.	3/.	./.	./5	18/20	21/25	46
Chaenotheca chrysocephala	19/20	2/3	1/1	./.	./.	./.	22/24	46
Hypogymnia tubulosa	1/.	./.	10/1	9/15	3/4	./2	23/22	45
Lecidea albofuscescens	./1	./.	./1	13/8	9/10	1/.	23/20	43
Biatora carneoalbida	./.	./.	1/.	./.	./1	15/19	16/20	36
Nephroma bellum	./.	./.	./.	./.	2/14	3/14	5/28	33
Lobaria pulmonaria	./.	./.	./.	./1	6/17	3/4	9/22	31
*Lophocolea heterophylla**	2/.	6/.	2/.	2/.	5/.	14/.	31/.	31

TABLE 3. *Continued*

Species	*Picea*	*Pinus*	*Betula*	*Alnus*	*Salix*	*Populus*	Total	Grand total
Bacidia subincompta	./.	./.	./.	./.	./3	10/17	10/20	30
Ochrolechia alboflavescens	./5	7/13	2/2	./.	./.	./.	9/20	29
Buellia disciformis	./.	./.	./.	9/19	./.	./.	9/19	28
Cetraria chlorophylla	1/10	1/1	./2	./4	./7	./2	2/26	28
Biatora ocelliformis	./.	./.	./.	3/4	7/2	12/.	22/6	28
Hypocenomyce scalaris	./1	13/10	2/1	./.	./.	./.	15/12	27
Nephroma parile	./.	./.	./.	./1	5/8	9/4	14/13	27
Pertusaria ophthalmiza	./.	./.	./.	5/15	1/5	./1	6/21	27
Buellia griseovirens	./.	./.	./.	12/12	1/1	./.	13/13	26
Dimerella pineti	./.	4/1	5/3	5/.	4/2	./.	18/6	24
*Rhytidiadelphus triquetrus**	./.	./.	./.	./4	2/2	11/4	13/10	23
Lopadium disciforme	./.	./.	./2	1/1	2/13	./2	3/18	21
Rinodina cinereovirens	./.	./.	./.	./3	1/17	./.	1/20	21
Ropalospora viridis	./.	./.	6/.	13/2	./.	./.	19/2	21
Varicellaria rhodocarpa	./3	./.	./7	./7	./3	./.	./20	20
*Blepharostoma trichophylla**	./.	1/.	1/2	11/.	2/.	2/.	17/2	19
Lecanora allophana	./.	./.	./.	./.	3/.	./15	3/15	18
*Barbilophozia attenuata**	./.	./3	2/11	./1	./.	./.	2/15	17
Lecidea erythrophaea	./.	./.	./.	./1	./5	5/6	5/12	17
*Radula complanata**	./.	./.	./.	./.	./.	14/3	14/3	17
Lecanora cateilea	./.	./.	./.	./15	./.	./.	./15	15
*Tetraphis pellucida**	./1	7/2	2/.	1/1	./1	./.	10/5	15
Japewia tornoënsis	./.	./.	./.	./9	./5	./.	./14	14
Lecanora circumborealis	./1	./.	./.	./13	./.	./.	./14	14
Pertusaria coccodes	./1	./.	./.	1/3	6/3	./.	7/7	14
*Barbilophozia barbata**	./.	./.	./.	./1	1/3	5/3	6/7	13
Chaenotheca subroscida	./13	./.	./.	./.	./.	./.	./13	13
Arthothelium scandinavicum+	1/11	./.	./.	./.	./.	./.	1/11	12
*Pylaisia polyantha**	./.	./.	./.	./.	./.	7/5	7/5	12
Lecanora pulicaris	./3	./.	./.	6/.	./2	./.	6/5	11
Chaenotheca ferruginea	1/.	7/2	./.	./.	./.	./.	8/2	10
Lecanora hypopta	./5	./5	./.	./.	./.	./.	./10	10
Nephroma resupinatum	./.	./.	./.	./.	1/6	./3	1/9	10
*Orthodicranum montanum**	2/.	4/.	3/.	1/.	./.	./.	10/.	10
Pertusaria carneopallida	./.	./.	./.	./10	./.	./.	./10	10
*Plagiomnium cuspidatum**	./.	./.	./.	./1	4/.	1/4	5/5	10
Calicium glaucellum	./5	./1	./.	./.	./3	./.	./9	9
Imshaugia aleurites	./.	./9	./.	./.	./.	./.	./9	9
Orthotrichum spp.*	./.	./.	./.	./.	./.	9/.	9/.	9
Caloplaca borealis	./.	./.	./.	./8	./.	./.	./8	8
Cladonia cornuta	1/.	./3	2/2	./.	./.	./.	3/5	8
Lecidea leprarioides	./8	./.	./.	./.	./.	./.	./8	8
Fuscidea arboricola	./.	./.	./.	./7	./.	./.	./7	7
Pertusaria leioplaca	./.	./.	./.	1/6	./.	./.	1/6	7
Placynthiella dasaea	./.	4/.	./.	./3	./.	./.	4/3	7
Pseudevernia furfuracea	./.	./.	1/.	./5	./.	./1	1/6	7
Calicium parvum	./.	./6	./.	./.	./.	./.	./6	6
*Calypogeia integristipula**	./.	./3	./1	./1	./1	./.	./6	6

TABLE 3. *Continued*

Species	*Picea*	*Pinus*	*Betula*	*Alnus*	*Salix*	*Populus*	Total	Grand total
Hypogymnia farinacea	./.	5/.	1/.	./.	./.	./.	6/.	6
Lecidea pullata	./.	./.	./2	./4	./.	./.	./6	6
Pannaria pezizoides	./.	./.	./.	./.	./2	./4	./6	6
*Pohlia nutans**	./1	./1	./.	./.	./1	./3	./6	6
Bacidia globulosa	./.	./.	./.	./.	./4	./1	./5	5
*Barbilophozia lycopodioides**	./.	./.	./.	./1	./4	./.	./5	5
Bryoria furcellata	./.	./4	./.	./1	./.	./.	./5	5
Calicium viride	./5	./.	./.	./.	./.	./.	./5	5
*Campylium sommerfeltii**	./.	./.	./.	./.	./.	1/4	1/4	5
Lecanora symmicta coll.	./.	./.	./.	./5	./.	./.	./5	5
*Lepidozia reptans**	./.	./3	1/1	./.	./.	./.	1/4	5
Peltigera praetextata	./.	./.	1/.	./.	1/.	3/.	5/.	5
Rinodina degeliana	./.	./.	./.	./.	2/3	./.	2/3	5
Bryoria fremontii	./.	./2	./.	./.	./2	./.	./4	4
Chaenotheca trichialis	./4	./.	./.	./.	./.	./.	./4	4
Lecanora expallens	./.	./.	./.	./1	./3	./.	./4	4
Leptogium saturninum	./.	./.	./.	./.	./.	1/3	1/3	4
Peltigera canina	./.	./.	./.	./.	./.	./4	./4	4
Peltigera degenii	./.	./.	1/.	1/.	./.	2/.	4/.	4
Arthonia incarnata	./1	./.	./.	./.	./2	./.	./3	3
Bacidia circumspecta	./.	./.	./.	./.	1/2	./.	1/2	3
Calicium trabinellum	1/.	./.	./.	./.	./2	./.	1/2	3
*Cephalozia lunulifolia**	./.	1/1	1/.	./.	./.	./.	2/1	3
Chaenotheca furfuracea	1/.	./.	./2	./.	./.	./.	1/2	3
Chaenothecopsis viridialba+	./3	./.	./.	./.	./.	./.	./3	3
Cladonia sulphurina	./.	./2	./.	./1	./.	./.	./3	3
*Dicranum polysetum**	./.	./.	./.	./1	./.	./2	./3	3
Evernia prunastri	1/.	./.	./.	1/.	1/.	./.	3/.	3
*Fissidens adianthoides**	./.	./.	./.	./.	./.	2/1	2/1	3
Graphis scripta	./.	./.	./.	3/.	./.	./.	3/.	3
*Hypnum cupressiforme**	1/.	./.	./.	./.	1/.	1/.	3/.	3
Ramalina farinacea	./.	./.	./.	1/.	2/.	./.	3/.	3
Ramalina thrausta	./.	./.	./.	./.	./3	./.	./3	3
Anisomeridium nyssaegenum	./.	./.	./.	2/.	./.	./.	2/.	2
Arthonia vinosa	./.	./.	./.	./.	./2	./.	./2	2
Chaenotheca brachypoda	./.	./.	1/.	./.	./1	./.	1/1	2
Chaenotheca brunneola	./.	./.	./.	./.	./2	./.	./2	2
Chaenotheca laevigata	./.	./.	./.	./.	1/1	./.	1/1	2
Cladonia crispata	./.	./.	./2	./.	./.	./.	./2	2
Cliostomun leprosum	1/1	./.	./.	./.	./.	./.	1/1	2
Cyphelium inquinans	./2	./.	./.	./.	./.	./.	./2	2
Hypocenomyce sorophora	./1	./1	./.	./.	./.	./.	./2	2
Lecidea turgidula	1/.	1/.	./.	./.	./.	./.	2/.	2
Lecidella euphorea	./.	./.	./.	./.	./.	./2	./2	2
Leptogium subtile	./.	./.	./.	./.	./.	./2	./2	2
Micarea denigrata	./.	./.	./.	./2	./.	./.	./2	2
Melanelia olivacea	./.	./.	./.	./2	./.	./.	./2	2
Peltigera neopolydactyla	./.	./.	./.	./.	2/.	./.	2/.	2

TABLE 3. *Continued*

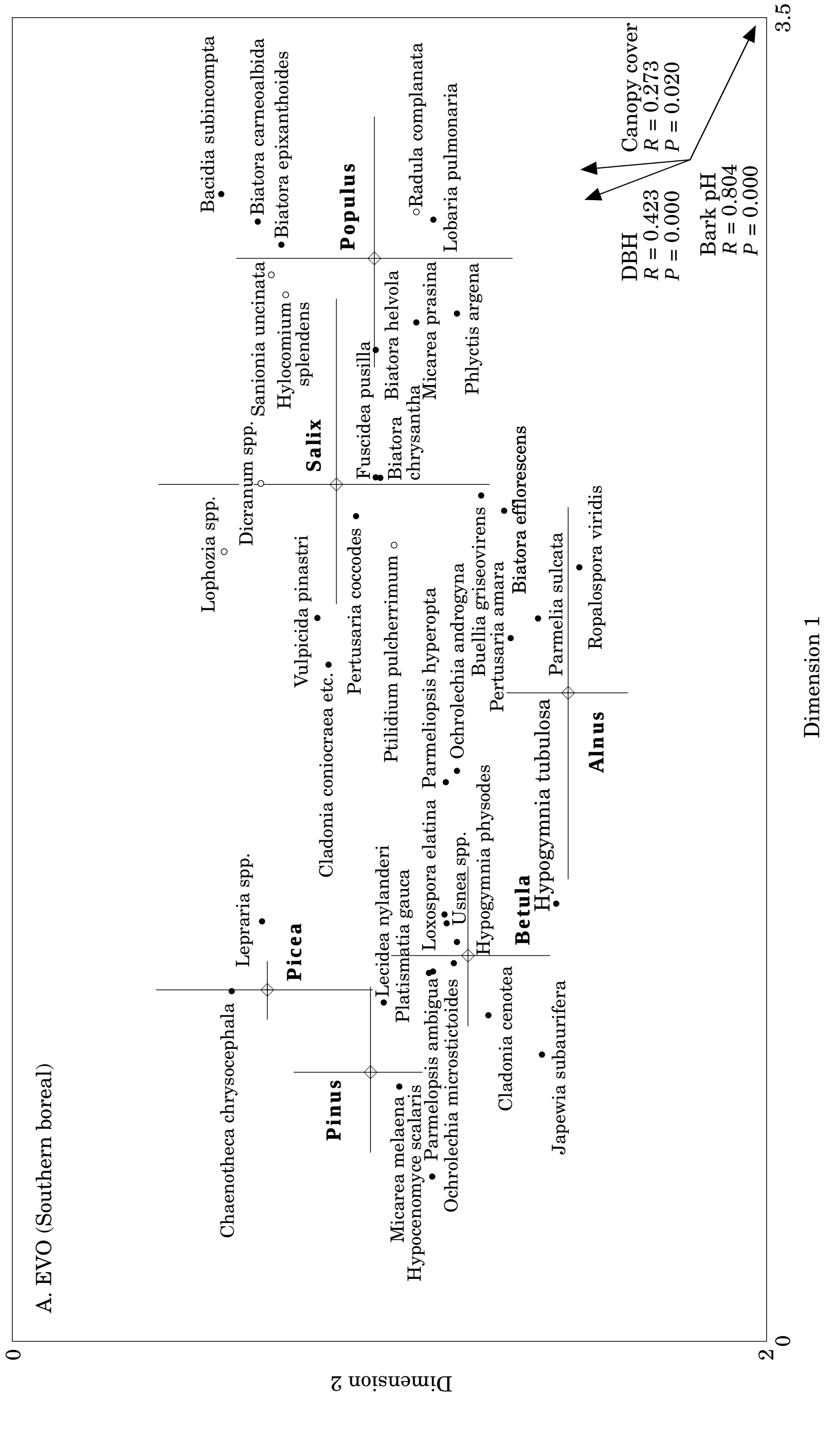
Species	*Picea*	*Pinus*	*Betula*	*Alnus*	*Salix*	*Populus*	Total	Grand total
Ramalina dilacerata	./.	./.	./.	./1	./1	./.	./2	2
Arthonia didyma	./.	./.	./.	./.	./.	./1	./1	1
Arthonia radiata	./.	./.	./.	./1	./.	./.	./1	1
*Aulacomnium palustre**	./.	./.	./.	./1	./.	./.	./1	1
Bacidia igniarii	./.	./.	./.	./1	./.	./.	./1	1
Bacidia pallens	./.	./.	./.	./1	./.	./.	./1	1
Bryoria nadvornikiana	./.	./.	./.	./1	./.	./.	./1	1
Chaenotheca gracillima	./.	./.	./.	./.	./1	./.	./1	1
Cladonia carneola	./1	./.	./.	./.	./.	./.	./1	1
Cladonia deformis	./.	1/.	./.	./.	./.	./.	1/.	1
Cladonia phyllophora	./.	./.	./.	./1	./.	./.	./1	1
Cladonia pleurota	./.	./1	./.	./.	./.	./.	./1	1
Hypogymnia vittata	./.	./.	./1	./.	./.	./.	./1	1
Lecanactis abietina	1/.	./.	./.	./.	./.	./.	1/.	1
Leptogium teretiusculum	./.	./.	./.	./.	./.	1/.	1/.	1
*Orthotrichum obtusifolium**	./.	./.	./.	./.	./.	./1	./1	1
Pachyphiale fagicola	./.	./.	./.	./.	./1	./.	./1	1
Parmeliella triptophylla	./.	./.	./.	./.	./.	./1	./1	1
Peltigera aphthosa	./.	./.	./.	./.	./1	./.	./1	1
Peltigera leucophlebia	./.	./.	./.	./.	./.	./1	./1	1
Physcia aipolia	./.	./.	./.	./1	./.	./.	./1	1
*Ptilium crista-castrensis**	./.	./.	./.	./.	./.	./1	./1	1
Lichen species number	33/49	31/41	38/41	42/66	44/65	29/42	80/122	134
Bryophyte species number	11/10	12/11	16/13	12/18	15/15	20/20	25/28	32
Total number of species	44/59	43/52	54/54	54/84	59/80	49/62	105/150	166
Number of specific species	5/9	2/5	4/4	5/18	8/11	9/14	33/61	
Proportion of specific species (%)	11·4/15·3	4·7/9·6	7·4/7·4	9·3/21·4	13·6/13·8	18·4/22·6	31·4/40·7	

‡The taxa are arranged according to the total abundance on all trees. The maximum is 20 for all tree species, except 12 for *Salix* in the southern boreal area. *Bryophytes, +two non-lichenized fungi. The specific species are species that were found on only one tree species in either study area.

floras. The *Alnus* and *Salix* trees were more scattered in the ordination space but fairly well separated from each other and from the other tree species. *Populus* differed most from the other tree species, especially in the middle boreal area.

Most of the epiphytes showed at least a slight preference to one or two tree species (Fig. 1). Only the most abundant species, such as *Hypogymnia physodes* and *Platismatia glauca*, were positioned close to the centroid of the ordination space due to their wide occurrence on most tree species.

Three environmental variables showed significant monotone trends in both ordinations (Fig. 1). DBH and canopy cover were positively correlated with each other and the second dimension. Bark acidity was negatively correlated with the other two variables. It should, however, be remembered that all the three environmental variables were correlated also with the species of tree (cf. Table 1).


A. EVO (Southern boreal)
Dimension 1
Dimension 2
0
2
0
3.5
Pinus
Picea
Betula
Alnus
Salix
Populus
Chaenotheca chrysocephala
Lepraria spp.
Micarea melaena
Hypocenomyce scalaris
Parmelopsis ambigua
Ochrolechia microstictoides
Cladonia cenotea
Japewia subaurifera
Lecidea nylanderi
Platismatia gauca
Loxospora elatina
Usnea spp.
Hypogymnia physodes
Hypogymnia tubulosa
Cladonia coniocraea etc.
Vulpicida pinastri
Pertusaria coccodes
Ptilidium pulcherrimum
Parmeliopsis hyperopta
Ochrolechia androgyna
Buellia griseovirens
Pertusaria amara
Biatora efflorescens
Parmelia sulcata
Ropalospora viridis
Lophozia spp.
Dicranum spp.
Sanionia uncinata
Hylocomium splendens
Fuscidea pusilla
Biatora chrysantha
Biatora helvola
Micarea prasina
Phlyctis argena
Bacidia subincompta
Biatora carneoalbida
Biatora epixanthoides
Radula complanata
Lobaria pulmonaria
Canopy cover
R = 0.273
P = 0.020
DBH
R = 0.423
P = 0.000
Bark pH
R = 0.804
P = 0.000

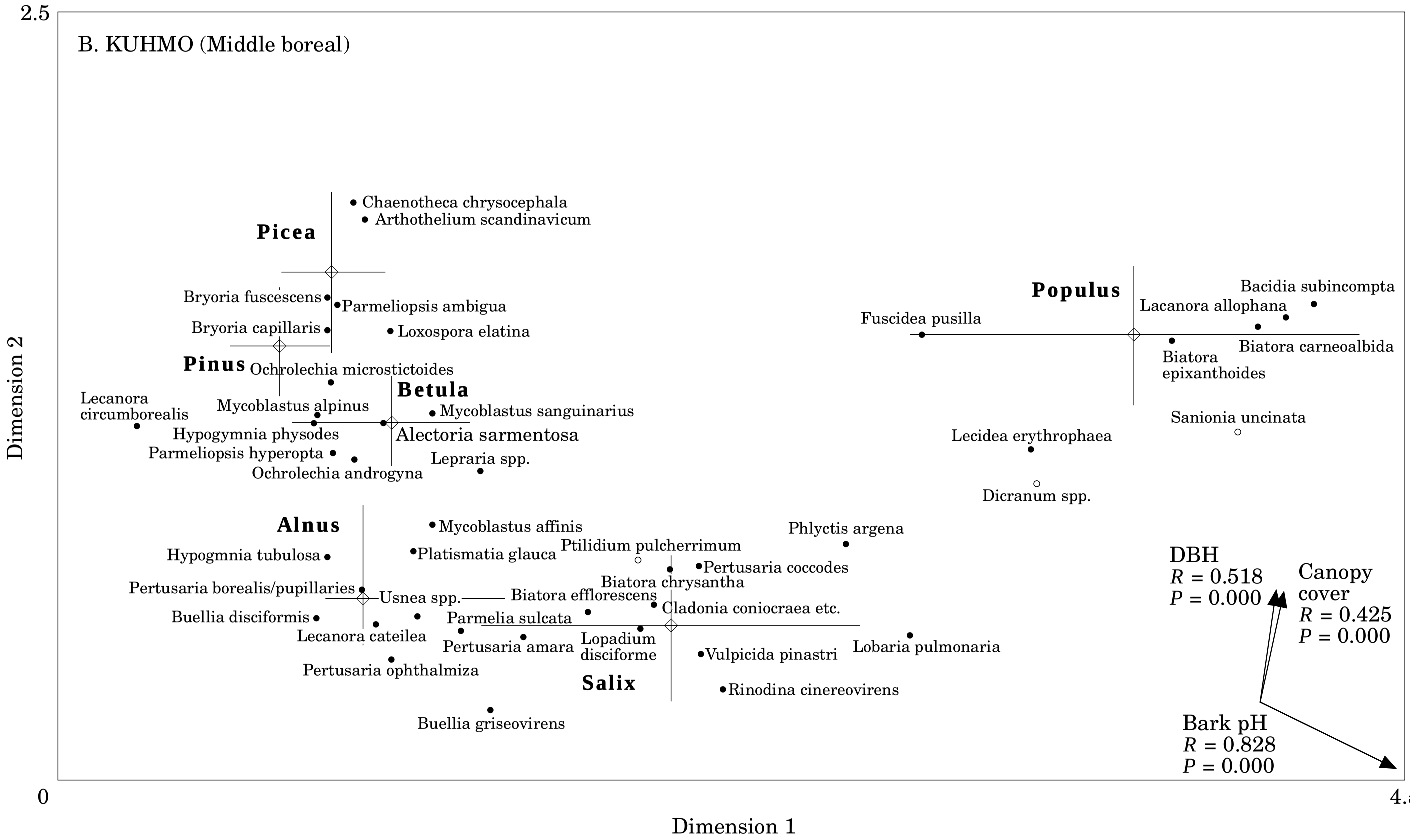


FIG. 1. Two dimensional solutions of the NMDS ordinations. Mean ± S.D. of the ordination co-ordinates for each of the six tree species are shown. The species co-ordinates are derived as weighted averages of the tree scores. Bryophytes are marked with open circles. The vectors indicate directions of maximum correlation of three environmental variables: DBH, bark acidity and canopy cover. Maximum correlation (R) and Monte-Carlo significance values are shown adjacent to each vector. A, Southern boreal sample trees (Evo); B, Middle boreal sample trees (Kuhmo): $n=20$ for each tree species, except 12 for *Salix* in the southern boreal area. Note that the vertical axis is shown reversed in Fig. A.

Species composition and cover

A total of 166 epiphytic lichen and bryophyte species (including two non-lichenized fungi) were found on the trees studied (Table 3). The most common species, *Ptilidium pulcherrimum*, *Hypogymnia physodes* and *Parmeliopsis* spp., occurred on most trees in both areas, but none of them on every tree. Among the most common species were some essentially forest floor bryophytes, such as *Pleurozium schreberi*, *Dicranum* spp., *Brachythecium* spp. and *Hylocomium splendens*, which usually thrive only on the very base of trees (<0·5 m height), except on leaning trunks. Of the lichens, all *Cladonias* are similar predominantly tree-base species.

Some species were combined or treated collectively in the data due to taxonomic problems or difficulties in identification in the field. *Cladonia coniocraea* includes: *C. bacilliformis*, *C. coniocraea*, *C. fimbriata* and *C. norvegica*. *Usnea* species contains mostly poorly developed specimens of *U. filipendula*, and *Lophozia* species is mostly *L. longidens*. *Pertusaria borealis* and *P. pupillaris* were combined in the data. *Biatora epixanthoides* includes also *B. tetramera*, and *Biatora chrysantha* (*B. gyrophorica*) includes *Biatora fallax*. *Buellia disciformis* includes *B. erubescens*. All *Lepraria* and *Brachythecium* species were treated collectively. In addition to lichens and bryophytes, two conspicuous non-lichenized fungi, *Arthothelium scandinavicum* and *Chaenothecopsis viridialba*, were included in the data. They were considered as lichens in the species number and diversity calculations.

Considerable variation was observed in the epiphyte cover values between individual trees as indicated by large standard deviations in Fig. 2. The highest total covers values were observed on deciduous trees, especially on *Alnus* and *Salix*, and lowest on the conifers (Fig. 2). The total cover values below 50% on most trees indicated that there was usually plenty of uncolonized space on the trunks. The most conspicuous qualitative difference between the conifers and the deciduous trees was the absence of bryophytes on the former trees. The bryophytes tended also to be more abundant on the southern boreal trees. The scarcity of foliose lichens and the dominance of crustose lichens especially in the middle boreal area were the most distinct features of *Populus* trees. Cyanobacterial lichens were found only on *Salix* and *Populus* and they were most abundant in the middle boreal area. Fruticose lichens, mostly *Alectoria sarmentosa*, *Bryoria* species and *Usnea* species, had generally quite low cover on the middle boreal trees and were absent from most of the southern boreal trees (Fig. 2).

The crustose lichens *Chaenotheca chrysocephala*, *Lecidea nylanderi*, *Lepraria jackii* and *Loxospora elatina* as well as the non-lichenized fungus *Arthothelium scandinavicum* were the most characteristic species on *Picea* (Table 3, Fig. 1). Several rare crustose lichens, such as *Chaenotheca subroscida*, *Cyphelium inquinans*, *Cliostomum leprosum* and *Lecanactis abietina*, were mostly confined to the basal trunks of old *Picea* trees. The epiphyte flora on *Pinus* and *Betula* resembled that on *Picea* (Table 3, Fig. 1). The most characteristic species on *Pinus* were the crustose lichens *Calicium parvum*, *Chaenotheca ferruginea*, *Hypocenomyce scalaris*, *Micarea melaena* and *Ochrolechia alboflavescens*. On *Betula* the crustose lichens *Japewia subaurifera*, *Loxospora elatina*, *Mycoblastus*

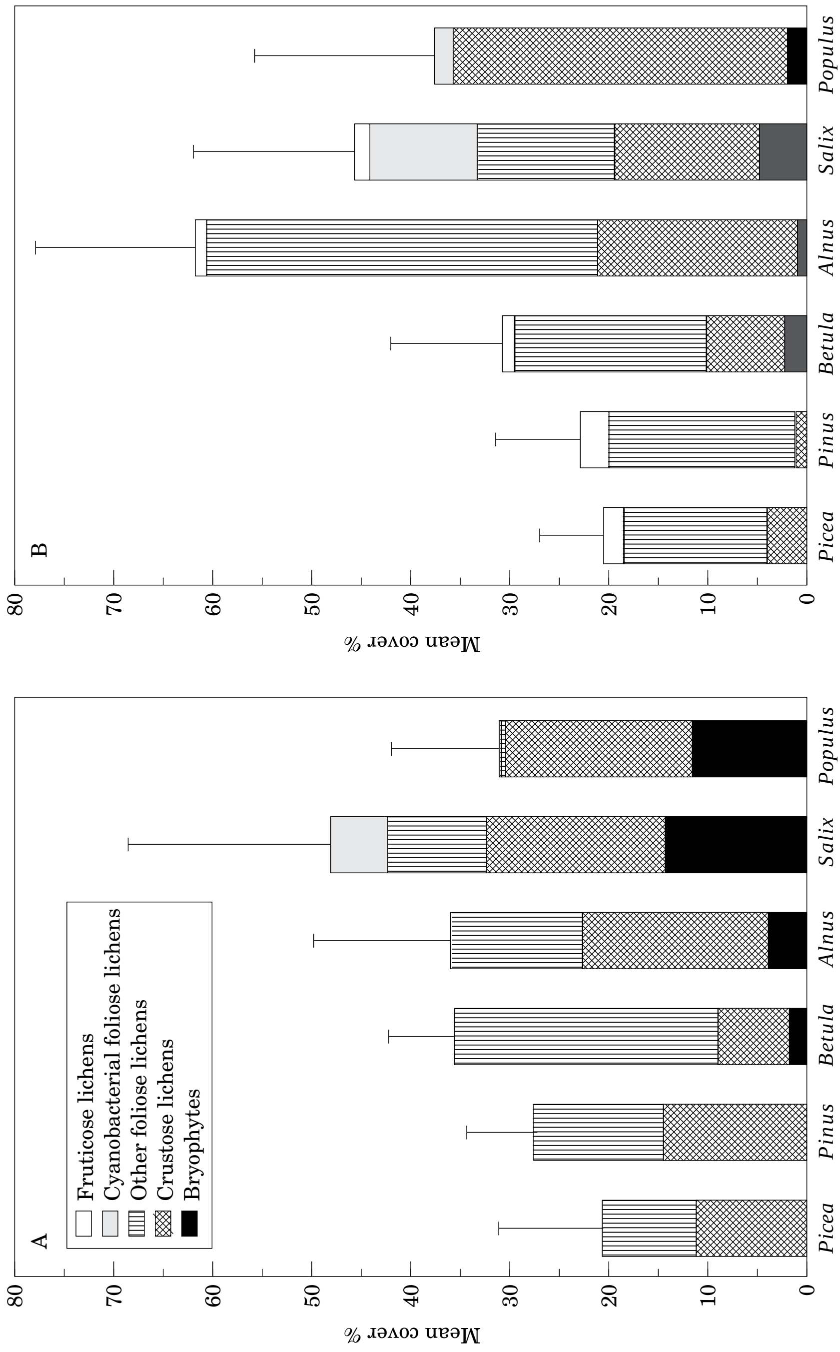


FIG. 2. Mean cover of bryophytes and different morphological groups of lichens on the six tree species in the two study areas. The error bars represent one S.D. of the total cover. A, Southern boreal area (Evo); B, Middle boreal area (Kuhmo): n=20, except 12 for *Salix* in Evo.

alpinus, *M. sanguinarius* and *Ochrolechia androgyna* were the most characteristic species.

The species composition of *Alnus* was closest related to *Salix* (Table 3, Fig. 1). The crustose lichen flora was especially well developed on *Alnus*. In particular, the smooth bark of young trunks was often covered by a patchy mosaic of small crustose lichens with thin thalli growing inside the uppermost layer of the bark. The most characteristic crustose lichens on *Alnus* were: *Biatora efflorescens*, *Buellia disciformis* coll., *Buellia griseovirens*, *Pertusaria amara*, *P. borealis*, *P. ophthalmiza* and *Ropalospora viridis*; in the middle boreal area characteristic species were also: *Caloplaca borealis*, *Fuscidea arboricola*, *Japewia tornoënsis*, *Lecidea pullata*, *Lecanora cateilea*, *L. circumborealis*, *Pertusaria carneopallida* and *P. leioplaca*. Many of these species were confined to *Alnus*.

The most distinctive feature of the epiphyte flora of *Salix* was the abundance of cyanobacterial lichens, especially *Lobaria pulmonaria* and *Nephroma* spp. (Table 3). Bryophytes were also most abundant on *Salix*: *Dicranum* spp., *Hylocomium splendens*, *Lophozia longidens* and *Ptilidium pulcherrimum* were the most typical species. Several infrequent crustose lichens, such as *Arthonia incarnata*, *Bacidia circumspecta*, *Lopadium disciforme*, *Pertusaria coccodes*, *Rinodina cinereovirens* and *R. degeliana*, were chiefly confined to *Salix*.

The composition of the epiphytic flora on *Populus* was quite distinct from the other tree species (Table 3, Fig. 1). It was dominated by crustose lichens and bryophytes while the widespread foliose lichens were scarce. The proportion of habitat specialist species was high on *Populus* and some of these species, such as *Bacidia subincompta*, *Biatora carneoalbida* and *B. epixanthoides* were very abundant.

Discussion

The epiphytic flora of most of the trees studied was dominated by a few widespread habitat-generalist species, such as the foliose lichens *Hypogymnia physodes*, *Parmeliopsis ambigua*, *Platismatia glauca* and the bryophyte *Ptilidium pulcherrimum*. Presumably, due to effective dispersal capacity and lack of specific habitat demands, these are the most common epiphyte species also in the managed forest landscape. The most significant differences between the phorophytes were observed in the occurrence and abundance of the rarer species.

Picea was the dominant tree species in the study areas, but supported the lowest total cover of epiphytes, which is most probably due to low levels of illumination and moisture on the basal trunks. The living canopy extends often very low on *Picea*, efficiently shading the lower trunk. In addition, the fairly strongly exfoliating bark prevents epiphytes from forming extensive cover on the trunks. Halonen *et al.* (1991) suggested that the small and often concave pieces of spruce bark could restrict the extension of foliose lichen thalli.

Pinus had relatively low species richness and diversity and only a few specific species. The often very strongly exfoliating bark is most probably the main explanation for the low total cover of epiphytes. The epiphyte flora of *Pinus* was most similar to the flora on *Picea*. According to Hyvärinen *et al.* (1992) the differences in species composition between these conifers could be partly related to the generally somewhat higher bark pH on *Pinus*. Koskinen (1955) and Barkman (1958), however, recorded in the 1950s higher bark pH values on *Picea* than on *Pinus*, which may indicate that *Pinus* bark is better buffered against acidification.

The epiphyte flora on *Betula* was rather poor and closely resembled that on the conifers; however, bryophytes, especially *Ptilidium pulcherrimum*, were most abundant on *Betula*. The similarity between *Betula* and the conifers in their epiphyte flora was also noticed by Koskinen (1955). Coppins (1984) reported a total of 235 lichen species on *Betula* in the British Isles, but hardly any of these was strictly confined to it. He also noted the general poorness of the epiphyte flora and its similarity to *Pinus* in the native woodlands of Scotland.

The bark of *Alnus* is the thinnest and smoothest of the six tree species studied. It seems also to be quite elastic and hardly at all exfoliating. The low level of disturbance by bark scaling would suggest a high total cover of epiphytes on *Alnus* trunks, but my data do not unambiguously support this hypothesis as the total cover values were not particularly high in the southern boreal area. Furthermore, the open, moist habitats of the *Alnus* trees, rather than the lack of bark scaling, may best explain the high total cover of epiphytes in the middle boreal area. Some photophilous species, such as *Hypogymnia tubulosa*, *Pseudevernia furfuracea* and *Vulpicida pinastri* were particularly common on the middle boreal *Alnus* trees. The high number of specific species is most probably also due to the habitat difference between *Alnus* and the other tree species. This view is supported by several studies emphasizing the importance of habitat type for the comparison of the epiphyte flora (Koskinen 1955; Sõmermaa 1972; Müller *et al.* 1981; Oksanen 1988).

The epiphyte species richness and diversity were highest on *Salix* in both study areas and also the number of specific species was high. Kuusinen (1994a) suggested that the high lichen species numbers on *Salix* could best be related to the combination of high microhabitat heterogeneity on the trunks, favourable bark structure and chemistry for epiphyte colonization and the humid habitats of the trees.

The uniqueness of the epiphyte flora on *Populus* is most probably related to the high bark pH and perhaps also to the abundance of nutrients available for epiphytes on the bark surface. Barkman (1958) and Brodo (1974) have discussed the important role of water relations of the bark to the epiphytic communities. According to my field observations the rather thick basal bark of old *Populus* trees may have a higher water capacity than the bark of other forest trees, which may partly explain the abundance of the generally hydrophilic bryophytes on *Populus* (Kuusinen 1994*b*). One potential explanation for the low lichen species numbers on *Populus* may be the low number of forest epiphyte species adapted to the high bark pH conditions prevailing on this tree species (Kuusinen 1995).

Several of the species classified as tree-specific occur most frequently in habitats other than the trunk bases of the trees studied, for example, those principally growing on the upper trunk and canopy (*Lecidella euphorea*, *Physcia* *aipolia*), on dry or decaying wood (several Caliciales) or on ground and rocks (several bryophytes and *Cladonia* species). Furthermore, although the number of sampled trees appears to have been adequate to reveal the typical features of the epiphytic flora on each tree species, a large proportion of the rarest species have most probably remained unobserved. It is, however, worth remarking that the proportion of specific species was especially low on the major commercial tree species, *Picea*, *Pinus*, and *Betula*.

Barkman (1958) reviewed potential explanations for the differences in epiphytic flora and species richness between different phorophytes. European trees fell into three major groups: *Picea*, *Pinus* and *Betula* were included in the first and *Alnus*, *Salix* and *Populus* in the second group. Barkman concluded that the major differences between these groups were in bark chemistry, especially in buffer capacity, acidity and electrolyte concentration. Trees in the first group generally have a lower buffer capacity, more acidic bark and lower electrolyte concentrations than trees in the second group. He concluded that habitat preferences of the tree species, canopy structure, scaling or hardness of the bark were of only secondary importance. The importance of bark structure and chemistry in structuring the epiphytic communities has also been emphasized by several other authors (Du Rietz 1945; Culberson 1955; Hale 1955; Koskinen 1955; Kalgutkar & Bird 1969; Brodo 1974; Gough 1975; Slack 1976; Studlar 1982; Eversman *et al.* 1987; Fos & Barreno 1994; Gauslaa 1995). Differences in bark chemistry, acidity and structure are also the most likely explanations for the observed differences in the epiphytic flora between the tree species in my study. In particular, the pH of the surface bark appears to predict fairly well the composition of the epiphytic flora.

Differences in methodology and taxonomic problems severely complicate the comparison of epiphyte species richness and diversity values reported by different authors. This is well illustrated in the summary tables of epiphyte species numbers observed on European trees produced by Barkman (1958: 130–132). For example, Koskinen (1955) reported 154 lichen species on *Picea abies*, 215 on *Pinus sylvestris*, 239 on *Betula* spp., 156 on *Alnus incana*, 165 on *Salix* spp. and 164 on *Populus tremula* in his data from Central Finland. These very high species numbers are not comparable with my data, as his data has been collected from a very large number of trees (though the figures are not given) in various habitats and it includes species on the whole trunk and branches. Furthermore, several of his species are of doubtful taxonomic status, such as many species of *Biatora* and *Usnea*.

Sõmermaa (1972) found that *Picea* and *Pinus* had the richest and *Betula* the poorest epiphytic lichen flora when she surveyed the flora on *Picea*, *Pinus*, *Betula* and *Alnus* in Estonia. The total lichen species numbers were generally somewhat higher in her data (46–74 species) than in my data (31–66 species), but her data was also more extensive: it included *c.* 8000 20 cm × 20 cm sample plots in various habitat types. Hyvärinen *et al.* (1992) reported a total of 48 epiphytic lichen species on basal trunks of *Pinus* and 38 on *Picea* from middle boreal forests of Finland. These species numbers are very similar to my data from the middle boreal area, although the number of trees was much larger in their survey: 225 *Pinus* and 135 *Picea* trees of varying age. This may indicate that increasing my sample size would not significantly increase the total number of species observed.

The higher lichen species richness on most tree species in the middle compared to the southern boreal area may be related to the more humid climate and longer continuity of the stands in the middle boreal area (Kuusinen 1994*a*). Species such as *Alectoria sarmentosa*, *Mycoblastus*, *Lobaria pulmonaria* and *Nephroma*, which were more common in the middle boreal area, thrive best in moist sheltered habitats of long continuity. On the other hand, the generally lower number and cover of epiphytic bryophytes on the middle boreal trees may best be explained by severity of the winter climate above the sheltering snow cover (Kuusinen 1994*b*).

The lower abundance of *Alectoria sarmentosa*, *Bryoria* spp., *Usnea* spp. and most of the cyanobacterial lichens in the southern boreal area may also be partly due to the long-term effects of air pollution, as these lichens are known to be very sensitive to acid deposition (Hawksworth & Rose 1970; Insarova *et al.* 1992). However, although the sulphur deposition values are slightly higher in the southern boreal than in the middle boreal area the only insignificant differences in the bark acidity values between the areas do not indicate the more severe influence of acid deposition in the former area.

Conclusions

This study confirms the suggestion by Kuusinen (1995) that *Salix* and *Populus* are the most important tree species for the conservation of epiphyte diversity in the boreal forests of Finland: the former for high species diversity, and the latter for high number of specific species. As old individuals of both tree species are currently rare in managed forest landscape, several epiphytes confined to these tree species are becoming threatened.

Alnus also supports a rich epiphyte flora, but it is likely that most of the species thrive well also in managed forest landscape. *Alnus* is most essentially a pioneer tree of the six species studied, is most abundant in clear-cuts and grows also along roadsides and in abandoned fields. According to my field observations the species composition on these ruderal trees is quite similar to trees growing in forests. Thus, there may not be as urgent a threat to the diverse epiphytic flora of *Alnus* as that on *Salix* and *Populus*.

Old *Picea* trees, particularly in moist habitats, also have several unique species (Kuusinen 1996) and there is considerable, yet poorly known, species richness on branches of this tree species (Koskinen 1955; Hilmo 1994; Kuusinen unpubl.). The few unique features of the epiphyte flora on *Pinus* and *Betula* will mostly be retained in the managed forests. However, old individuals of even these tree species, especially with inclined or unusually shaped basal trunks, may support an exceptionally diverse epiphyte flora.

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References

Adams, D. B. & Risser, P. G. (1971) Some factors influencing the frequency of bark lichens in north central Oklahoma. *American Journal of Botany* **58:** 752–757.

Ahti, T. (1977) Lichens of the boreal coniferous zone. In *Lichen Ecology* (M. R. D. Seaward, ed.): 145–181. London: Academic Press.

Ahti, T., Hämet-Ahti, L. & Jalas, J. (1968) Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici* **5:** 169–211.

Alalammi, P. (1987) *Atlas of Finland, Folio 131: Climate.* Helsinki: The National Board of Survey.

Barkman, J. J. (1958) *Phytosociology and Ecology of Cryptogamic Epiphytes.* Assen: Van Gorcum.

Bates, J. W. (1992) Influence of chemical and physical factors on *Quercus* and *Fraxinus* epiphytes at Loch Sunart, western Scotland: a multivariate analysis. *Journal of Ecology* **80:** 163–179.

Bates, J. W. & Brown, D. H. (1981) Epiphyte differentiation between *Quercus petraea* and *Fraxinus excelsior* trees in a maritime area of South West England. *Vegetatio* **48:** 61–70.

Bray, J. R. & Curtis, J. T. (1957) An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* **27:** 325–349.

Brodo, I. M. (1961) A study of lichen ecology in Central Long Island, New York. *American Midland Naturalist* **65:** 290–310.

Brodo, I. M. (1974) Substrate ecology. In *The Lichens* (V. Ahmadjian & M. E. Hale, eds): 401–441. New York: Academic Press.

Coppins, B. J. (1984) Epiphytes of birch. *Proceedings of the Royal Society of Edinburgh* **85B:** 115–128.

Culberson, W. L. (1955) The corticolous communities of lichens and bryophytes in the upland forests of Northern Wisconsin. *Ecological Monographs* **25:** 215–231.

Du Rietz, G. E. (1945) Om fattigbark-och rikbarksamhällen. *Svensk Botanisk Tidskrift* **39:** 147–150.

Esseen, P.-A. (1981) Host specificity and ecology of epiphytic macrolichens in some central Swedish spruce forests. *Wahlenbergia* **7:** 73–80.

Esseen, P.-A., Ehnström, B., Ericson, L. & Sjöberg, K. (1992) Boreal forests—the focal habitats of Fennoscandia. In *Ecological Principles of Nature Conservation* (L. Hansson, ed.): 252–325. London: Elsevier Applied Science.

Eversman, S., Johnson, C. & Gustafson, D. (1987) Vertical distribution of epiphytic lichens on three tree species in Yellowstone National Park. *Bryologist* **90:** 212–216.

Faith, D. P., Minchin, P. R. & Belbin, L. (1987) Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* **69:** 57–68.

Fos, S. & Barreno, E. (1994) Epiphytic lichens on *Quercus suber L.* and their relation to the quality of cork. *Cryptogamic Botany* **4:** 156–165.

Gauslaa, Y. (1995) The *Lobarion*, an epiphytic community of ancient forests threatened by acid rain. *Lichenologist* **27:** 59–76.

Gough, L. P. (1975) Cryptogam distribution on *Pseudotsuga menziesii* and *Abies lasiocarpa* in the Front Range, Boulder county, Colorado. *Bryologist* **78:** 124–145.

Hale, M. E. (1955) Phytosociology of corticolous cryptogams in the upland forests of Southern Wisconsin. *Ecology* **36:** 45–63.

Halonen, P., Hyvärinen, M. & Kauppi, M. (1991) Epiphytic lichens in relation to climate in mesic heath forests of the middle boreal subzone. *Lichenologist* **23:** 61–72.

Hawksworth, D. L. & Rose, R. (1970) Qualitative scale for estimating sulphur dioxide air pollution in England and Wales using epiphytic lichens. *Nature* **227:** 145–148.

Hilmo, O. (1994) Distribution and succession of epiphytic lichens on *Picea abies* branches in a boreal forest, central Norway. *Lichenologist* **26:** 149–169.

Hyvärinen, M., Halonen, P. & Kauppi, M. (1992) Influence of stand age and structure on the epiphytic lichen vegetation in the middle-boreal forests of Finland. *Lichenologist* **24:** 165–180.

Insarova, I. D., Insarov, G. E., Bråkenhielm, S., Hultengren, S., Martinsson, P.-O. & Semenov, S. M. (1992) *Lichen Sensitivity and Air Pollution—a Review of Literature Data.* Swedish Environmental Protection Agency, Report 4007.

Jesberger, J. A. & Sheard, J. W. (1973) A quantitative study and multivariate analysis of corticolous lichen communities in the southern boreal forest of Saskatchewan. *Canadian Journal of Bontany* **51:** 185–201.

Kalela, A. (1961) Waldvegetationszonen Finnlands und ihre klimatischen Paralleltypen. *Archivum Societatis Zoologicae Botanicae Fennicae Vanamo* **16**(Suppl.): 65–83.

Kalgutkar, R. M. & Bird, C. D. (1969) Lichens found on *Larix lyallii* and *Pinus albicaulis* in southwestern Alberta, Canada. *Canadian Journal of Botany* **47:** 627–648.

Koponen, T., Isoviita, P. & Lammes, T. (1977) The bryophytes of Finland: An annotated checklist. *Flora Fennica* **6:** 1–77.

Koskinen, A. (1955) *Über die Kryptogamen der Bäume, besonders die Flechten, im Gewässergebiet des Päijänne sowie an den Flüssen Kalajoki, Lestijoki und Pyhäjoki. Floristische, soziologische und ökologische Studie 1.* Helsinki: Mercator.

Kujala, V. (1926) Untersuchungen über die Waldvegetation in Süd—und Mittelfinnland. I. Zur Kenntnis des ökologisch—biologischen Charakters der Pflanzenarten unter spezieller Berücksichtigung der Bildung von Pflanzenvereinen. C. Flechten. *Communicationes ex Instituto Quaestionum Forestalium Finlandiae* **10**(5): 1–61.

Kuusinen, M. (1994*a*) Epiphytic lichen diversity on *Salix caprea* in old-growth southern and middle boreal forests of Finland. *Annales Botanici Fennici* **31:** 77–92.

Kuusinen, M. (1994*b*) Epiphytic lichen flora and diversity on *Populus tremula* in old-growth and managed forests of southern and middle boreal Finland. *Annales Botanici Fennici* **31:** 245–260.

Kuusinen, M. (1995) Epiphytic lichen diversity of *Salix caprea* and *Populus tremula* in old-growth forests of Finland. *Mitteilugen Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft* **70:** 125–132.

Kuusinen, M. (1996) Importance of spruce swamp-forests for epiphyte diversity and flora on *Picea abies* in southern and middle boreal Finland. *Ecography* **19:** 41–51.

McCune, B. (1993) Gradients in epiphyte biomass in three Pseudotsuga-Tsuga forests of different ages in western Oregon and Washington. *Bryologist* **96:** 405–411.

Minchin, P. R. (1989) *DECODA user's manual.* Canberra: Research School of Pacific Studies, Australian National University.

Müller, J., Schneider, K. & Kreeb, K. H. (1981) Zur Ökologischen Analyse des Flechtenvorkommens: Die Bedeutung von synergistische Wirkungen. *Angewandte Botanik* **55:** 227–236.

Oksanen, J. (1988) Impact of habitat, substrate and microsite classes on the epiphyte vegetation: Interpretation using exploratory and canonical correspondence analysis. *Annales Botanici Fennici* **25:** 59–71.

Palmer, M. W. (1986) Pattern in corticolous bryophyte communities of the North Carolina piedmont: Do mosses see the forest or the trees? *Bryologist* **89:** 59–65.

Rasmussen, L. (1975) The bryophytic epiphyte vegetation in the forest, Slotved Skov, Northern Jutland. *Lindbergia* **3:** 15–38.

Räsänen, V. (1927) Über Flechtenstandorte und Flechtenvegetation im westlichen Nordfinnland. *Annales Societatis Zoologicae-Botanicae Fennicae Vanamo* **7:** 1–202.

Routledge, R. D. (1980) Bias in estimating the diversity of large, uncensused communities. *Ecology* **61:** 276–281.

Santesson, R. (1993) *The Lichens and Lichenicolous Fungi of Sweden and Norway.* Lund: SBT-förlaget.

Slack, N. G. (1976) Host specificity of bryophytic epiphytes in eastern North America. *Journal of Hattori Botanical Laboratory* **41:** 107–132.

Sõmermaa, A. (1972) Ecology of epiphytic lichens in main Estonian forest types. *Scripta Mycologica* **4:** 1–117.

Studlar, S. M. (1982) Host specificity of epiphytic bryophytes near Mountain Lake, Virginia. *Bryologist* **85:** 37–50.

Trynoski, S. E. & Glime, J. M. (1982) Direction and height of bryophytes on four species of northern trees. *Bryologist* **85:** 281–300.

Tuovinen, J.-P., Kangas, L. & Nordlund, G. (1990) Model calculations of sulphur and nitrogen deposition in Finland. In *Acidification in Finland* (P. Kauppi, P. Anttila & K. Kenttämies, eds): 167–197. Berlin & Heidelberg: Springer-Verlag.

White, F. J. & James, P. W. (1985) A new guide to microchemical techniques for the identification of lichen substances. *British Lichen Society Bulletin* **57**(Suppl.): 1–41.

Zahl, S. (1977) Jackknifing an index of diversity. *Ecology* **58:** 907–913.

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