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Factors important for epiphytic lichen communities in wooded meadows of Estonia

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Abstract: The epiphytic lichen communities in open and overgrown wooded meadows in Estonia were examined. From 29 study stands, 179 taxa of lichens, lichenicolous and allied fungi were identified, 41 of them are nationally rare, red-listed or protected. Non-metric multidimensional scaling (NMS) was performed to examine the main gradients in species composition and to relate these gradients to environmental variables. The response of lichen species richness to the influence of the environmental variables was tested using a general linear mixed model (GLMM). We revealed that overgrowing of wooded meadows caused significant changes in lichen communities on trees: richness of lichen species decreased and the composition of species changed. Photophilous lichen communities with many species of macrolichens in open wooded meadows were replaced with associations of more shade-tolerant microlichen species. The composition of epiphytic lichen communities were also influenced by the tree species composition, diameter of trees and the geographical location of the stand.

Kokkuvõte: Eesti puisniitude epifüütseid samblikukooslusi mõjutavad tegurid

Epifüütseid samblikukooslusi uuriti Eesti avatud ja kinnikasvanud puisniitudel. 29 proovialalt registreeriti kokku 179 taksonit samblikke, lihhenikoolseid ja lähedasi seeneliike, millest 41 on kas haruldased, kuuluvad Eesti Punasesse Raamatusse või on riikliku kaitse all. Samblike liigilise koosseisu ja keskkonnaparameetrite vaheliste seoste analüüsimiseks kasutati ordinatsioonanalüüsi NMS (mittemeetriline mitmedimensionaalne skaleerimine). Keskkonnaparameetrite mõju samblike liigirikkusele analüüsiti kasutades üldist lineaarset segamudelit (GLMM). Leidsime, et puisniitude kinnikasvamine põhjustab epifüütsetes samblikukooslustes olulisi muutusi: samblike liigirikkus väheneb ning liigiline koosseis muutub. Avatud puisniitudel asenduvad suursamblike liigirikkad valguslembesed samblikukooslused rohkem varju taluvate pisisamblike kooslustega. Samblike liigilist koosseisu mõjutavad veel prooviala puuliigiline koosseis, puude läbimõõt ning prooviala geograafiline asukoht.

INTRODUCTION

Wooded meadows are mosaic vegetation complexes which consist of small copses of deciduous trees and shrubs alternating more or less irregularly with open regularly mowed meadow glades (Hæggström, 1983). Wooded meadows have been widespread in the countries around the Baltic Sea (e.g. Estonia, Sweden, southern part of Finland), particularly on the islands (Hæggström, 1983). These semi-natural man made habitats have very high diversity of vascular plants due to evolutional and historical reasons (Hæggström, 1983; Kull & Zobel, 1991; Pärtel et al., 2007).

Traditional management of wooded meadows includes raking and picking of fallen branches in spring, mowing in July, aftermath is grazed by cattle in autumn and clearings of trees and shrubs are carried out in late autumn or winter (Hæggström 1983, Kukk & Kull, 1997; Mitlacher et al., 2002). Pollarding of trees for winter fodder in wooded meadows was popular in Finland, Sweden and Norway (Hæggström, 1983; Austad, 1988; Moe & Botnen, 2000), but not in Estonia (Kukk & Kull, 1997).

In Estonia, wooded meadow-like ecosystems have existed around settlements approximately 7000–8000 years (Kukk, 2004). Mowed wooded meadows, however, were prevailing in the cultural landscape of Estonia in the 18th century, covering roughly 20% of Estonian area (about 850 000 ha) at their peak (Kukk & Kull, 1997). The area of managed wooded meadows in Estonia decreased after World War II, mostly due to the collectivization of farm land and rapid progress of intensive agriculture (Kukk & Kull, 1997). Some of the wooded meadows were cultivated, some afforested or left to overgrow. Today, the area of wooded meadows has decreased significantly, and probably only 1500–2000 ha are being managed (Kukk & Sammul, 2006), which forms 0.2% of the former territory of these habitats in Estonia.

Diversity of epiphytic lichens in wooded meadows is high with many rarities (Thor, 1998; Thor & Nordin, 1998; Leppik & Saag, 2005). It has been supposed, that most epiphytic lichens prefer an environment of 'open shade' (Stoutesdijk & Barkman, 1992; Renhorn et al., 1997), a combination of good illumination and some shelter from desiccative winds (Rose, 1992). Sparse and mosaic allocation of the trees in wooded meadows should offer favorable conditions. The question emerges, what will happen with the lichen community after these conditions change, management stops and wooded meadows grow over with deciduous wood?

The concern of future decline of these semi-natural habitats actuated us to study the epiphytic lichen community of wooded meadows. So far, only the lichen community of open wooded meadows in Estonia has been shortly described (Leppik & Saag, 2005). In this study, at the stand level, the effect of overgrowing, tree species composition, diameter of trees and geographical location of the stands on lichen species composition will be discussed.

MATERIALS AND METHODS

Study sites and environmental variables

Estonia is located in the hemiboreal sub-zone of the boreal forest zone, i.e. in the transitional area where the southern boreal forest sub-zone changes into the spruce-hardwood sub-zone (Laasimer & Masing, 1995). Characteristic tree species in wooded meadows of Estonia is *Quercus robur*, rather common are also *Betula pendula, B. pubescens, Populus tremula, Fraxinus excelsior* and *Alnus glutinosa,* the conifers *Picea abies* and *Pinus sylvestris* are more rare (Paal, 2007).

Historically the islands and western Estonia were the regions most rich in wooded meadows, while in central and eastern Estonia wooded meadows never were so widespread (Kukk & Kull, 1997). During 2004–2006, 29 stands were selected for the study according to the general distribution of wooded meadows in Estonia (Fig. 1). GIS (Geographic Information System) based database of Estonian Seminatural Community Conservation Association and Web map server of Estonian Land Board (Maainfosüsteemi avalik kaardiserver, 2005) were used for the selection of study sites and stands. In every study site, if available, a pair of open and overgrown

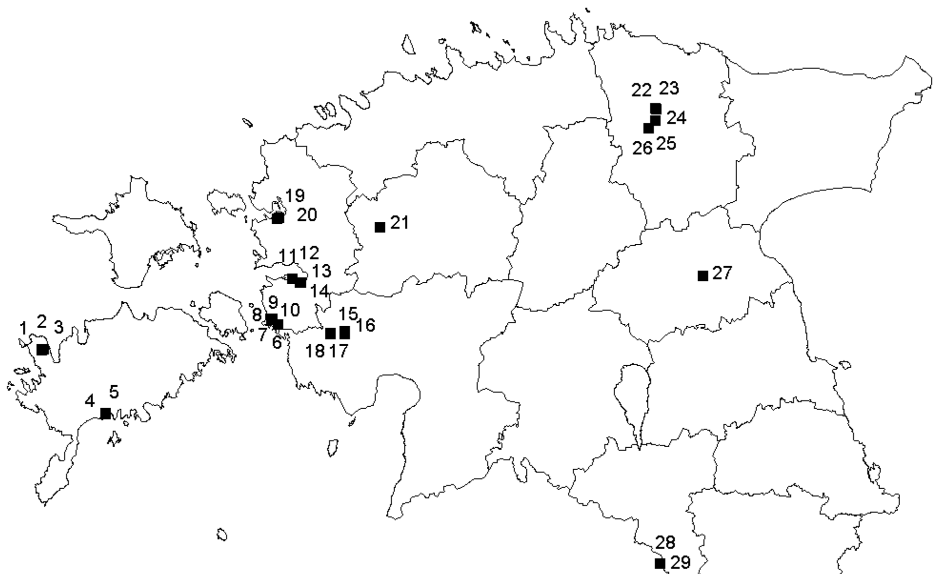

Fig. 1. Location of the studied wooded meadows in Estonia. Quadrate denotes the centre of the study site; the number indicates the study stand (n=29).

stands was selected for investigation. Most of the overgrown wooded meadows resembled deciduous forests and have not been mowed approximately for 50 years. Geographical coordinates of each study stand were recorded by means of GPS or were measured using the digital map of Estonia (Maainfosüsteemi avalik kaardiserver, 2008) (Table 1). Stands were located in three regions: western island (n=5), western part of the mainland (n=16) and eastern part of the mainland (n=8). In addition, every study stand was characterized by distance from the gravel road, canopy cover, the number and proportion of different tree species and mean diameter of studied trees (Table 1). The digital map of Estonia was used to measure the distance from the center of the stand to the nearest gravel road (log-transformed) and to estimate

Table 1. Main characteristics of the studied stands: No – number of a stand; Name – name of a stand, Habitat – open and overgrown stands (* restored recently, dense canopy; ** with the influence of sea; *** restored ten years ago; **** with young brushwood); Latitude – latitudinal coordinates of a stand (N); Longitude – longitudinal coordinates of a stand (E); Region – stands location in three regions: western island (Island of Saaremaa), western and eastern part of the mainland; Dist – distance from the nearest gravel road (km); Studied trees – tree species and the number of the studied trees (Ag – *Alnus glutinosa*; Ai – *Alnus incana*; B – *Betula* spp.; Fe – *Fraxinus excelsior*; Pa – *Picea abies*; Ps – *Pinus sylvestris*; Pt – *Populus tremula*; Qr – *Quercus robur*; Tc – *Tilia cordata*); Cov – canopy cover (%); DBH – mean diameter of studied trees at breast height (cm); Tot – total number of lichen species in a stand; Val – number of valuable lichen species in a stand.

No	Name	Habitat	Latitude	Longitude	Region	Dist	Studied trees	Cov	DBH	Tot	Val
1	Tagamõisa I	open	58°27’41”	22°0’22”	Island Saaremaa	0.17	6Qr3B2Fe1Tc	0.30	37	53	3
2	Tagamõisa II	overgrown	58°27’37”	21°59’51”	Island Saaremaa	0.57	4Qr4B2Fe2Pt	0.85	30	40	3
3	Tagamõisa III	overgrown*	58°27’42”	21°59’53”	Island Saaremaa	0.60	6Qr4B2Tc	0.65	35	52	2
4	Loode I	open	58°14’15”	22°26’27”	Island Saaremaa	0.03	9Qr3Fe	0.60	48	48	5
5	Loode II	overgrown	58°14’13”	22°26’34”	Island Saaremaa	0.11	9Qr3Fe	0.80	43	34	3
6	Pouli	open	58°34’	23°37’	West-Estonia	0.20	5Qr4Pt2B1Ai	0.15	41	46	1
7	Laelatu I	open	58°35’3”	23°34’17”	West-Estonia	0.06	4Fe4Qr2B2Pt	0.40	29	56	5
8	Laelatu II	overgrown	58°35’13”	23°34’36”	West-Estonia	0.09	4B4Fe2Pt2Qr	0.90	37	56	4
9	Laelatu III	open**	58°34’59”	23°34’15”	West-Estonia	0.08	5Qr4Fe2B1Pt	0.40	26	54	4
10	Laelatu IV	open***	58°35’9”	23°34’16”	West-Estonia	0.14	6Fe5Qr1B	0.45	26	54	5
11	Suuremõisa I	open	58°43’49”	23°42’28”	West-Estonia	0.07	6Qr3B2Fe1Ag	0.45	55	45	2
12	Suuremõisa II	overgrown	58°43’48”	23°42’36”	West-Estonia	0.20	5Qr4Ag2B1Pt	0.85	54	36	1
13	Allika I	open	58°43’2”	23°46’24”	West-Estonia	0.16	4Fe3B3Pt2Qr	0.40	34	43	2
14	Allika II	overgrown	58°43’3”	23°45’55”	West-Estonia	0.15	5Pt3Qr2Fe2Pb	0.75	43	36	2
15	Kalli-Nedrema I	open	58°32’13”	24°4’18”	West-Estonia	1.70	3Fe3Pt3Qr2B1Pa	0.50	44	49	3
16	Kalli-Nedrema II	overgrown	58°32’31”	24°4’22”	West-Estonia	1.34	4Pt4Qr3B1Ps	0.70	43	36	2
17	Peantse I	open	58°32’5”	23°58’14”	West-Estonia	0.07	7Pt2B2Ps1Qr	0.40	28	39	4
18	Peantse II	open****	58°31’58”	23°58’17”	West-Estonia	0.22	6Ps3B3Pt	0.50	28	38	6
19	Uuemõisa I	open	58°56’58”	23°37’5”	West-Estonia	0.11	12Qr	0.20	54	53	3
20	Uuemõisa II	overgrown	58°56’46”	23°36’9”	West-Estonia	0.36	12Qr	0.60	63	37	2
21	Sipa	open	58°55’	24°19’	West-Estonia	0.05	5B3Pt2Ps1Pab1Qr	0.25	42	50	2
22	Mädapea I	open	59°19’17”	26°15’45”	East-Estonia	0.50	6Qr6B	0.35	66	53	4
23	Mädapea II	overgrown	59°19’30”	26°15’28”	East-Estonia	0.33	7Qr5B	0.70	53	31	2
24	Järni	open	59°16’53”	26°15’10”	East-Estonia	0.11	12Qr	0.25	55	55	5
25	Lasila I	open	59°15’15”	26°12’16”	East-Estonia	0.91	12Qr	0.25	49	53	4
26	Lasila II	overgrown	59°15’19”	26°12’20”	East-Estonia	0.93	12Qr	0.80	44	37	2
27	Tammemetsa	open	58°43’	26°33’	East-Estonia	0.17	4B4Ag2Pt1Pab1Qr	0.40	41	48	2
28	Koiva I	open	57°41’20”	26°11’11”	East-Estonia	2.04	8Qr2B1Pa1Tc	0.20	57	59	8
29	Koiva II	overgrown	57°41’21”	26°11’16”	East-Estonia	1.91	8QrB2B1Pa1Tc	0.70	50	42	3

the percent of canopy cover of each study stand. The number of tree species and the proportion of different tree species were evaluated per study stand. Proportion of neutral-barked trees in a stand was a percent of trees with slightly acid to sub-neutral bark (average pH≥5 according to Barkman 1958, i.e. *Alnus incana*, *Fraxinus excelsior*, *Populus tremula* and *Tilia cordata*) from all studied trees in a stand. Proportion of acid-barked trees in a stand was a percent of trees with more acid bark (average pH<5 according to Barkman 1958, i.e. *Alnus glutinosa*, *Betula* spp., *Picea abies* and *Pinus sylvestris*). *Quercus robur* was considered separately since the bark pH of oak is known to be more acid (average pH=4.5) than that of other temperate broad-leaved trees (Barkman, 1958; Watson et al., 1988). The diameter of each sample tree (DBH) was measured at 1.2 m above ground level and the mean DBH of all studied trees per study stand was used in the statistical analyses.

Lichen sampling

In every stand, 12 sample trees in the area of one ha were selected according to the composition and proportion of tree species in a stand (Table 1). Epiphytic lichen communities were investigated on temperate broad-leaved trees (*Fraxinus excelsior*, *Quercus robur* and *Tilia cordata*), on other deciduous tree species (*Alnus glutinosa*, *A. incana*, *Betula* spp. and *Populus tremula*), and on conifers (*Picea abies* and *Pinus sylvestris*).

On every sample tree, the occurrence of lichen species on the stem up to two meters above ground level was recorded. In addition to lichenized fungi, lichenicolous and allied fungi were examined. Hereafter, all these taxa will be mentioned as 'lichens'. The species list of lichens per study stand was compiled, considering the recorded taxa on all twelve sample trees.

The specimens which were hard to identify in the field were collected for indoor investigation. Stereomicroscope, light microscope, UV light and standardized thin-layer chromatography (TLC) were used for identification of lichens in the laboratory. The reference material is deposited in the lichen herbarium at the Natural History Museum of the University of Tartu (TU).

The total number of lichen species and the number of valuable species (protected, red-listed and rare species with up to 10 localities in Estonia) per stand were considered in data analyses. The nomenclature of lichens, lichenicolous and allied fungi follows Randlane et al. (2007). Data about the species frequency are derived from Randlane and Saag (1999) and updated according to the Database of Estonian lichens *eSamba* (2008) and Atlas of the Estonian lichens (2008). The list of protected lichen species is presented according to the official decrees (Keskkonnaministri määrus nr 51, 2004; Vabariigi Valitsuse määrus nr 195, 2004) and the red-listed lichen species are according to Randlane et al. (2008).

Statistical analyses

The influence of environmental variables on the lichen species richness and the number of valuable lichens was tested using a general linear mixed model (GLMM; Littell et al., 1996) with the stepwise selection procedure, implemented in the program package SAS ver. 8.2 (proc MIXED; SAS Institute Inc., 1989). The categorical factor 'Region' was considered fixed factor and the pair of open and overgrown stands in a study site was treated as repeated observations per study site.

Non-metric multidimensional scaling (NMS; Kruskal, 1964a, b; Mather, 1976) with Sørensen distance was used in PC-ORD version 4.25 (McCune & Mefford, 1999) to examine the main gradients in species composition and to relate these gradients to the environmental variables. To reduce noise, the species appearing only in three study stands were removed from the data set prior to ordination. The frequency of lichen species on twelve sampled trees were used in data analyses. NMS analysis was run in autopilot mode, using slow and thorough settings (comparing 1 to 6-dimensional solutions, 40 runs with real data, 50 runs with randomized data, instability criterion 0.00001 and maximum number of iterations 400). Pearson correlations (r) with ordination axes for all quantitative variables and species were calculated. Pearson squared correlations (r^2) were calculated for the axes to express total variation in lichen community composition and for the environmental variables and axes to express strength of correlations of ordination axes with environmental variables (McCune & Mefford, 1999).

RESULTS

In total, 179 species and infraspecific taxa of lichens, lichenicolous and allied fungi were identified during this study (Appendix). Three lichen species were identified as new to Estonia: *Biatoridium delitescens*, *Leucocarpia dictyospora* and *Lecanora thysanophora* (Suija et al., 2006, 2007). All these species were found to inhabit oak trees in overgrown wooded meadows. *Lecanora thysanophora* has also been found on other tree species in deciduous forests of Estonia (Suija et al., 2007).

Most of the recorded lichen species are frequent in Estonia, except 33 species which are categorized as rare (Appendix). Ten of all recorded species are either red-listed or protected by the law in Estonia (Appendix). The overall number of valuable lichen species recorded in studied wooded meadows was 41.

On average, 46 epiphytic lichen species per wooded meadow were recorded; the highest number of species was 59 and the lowest 31 (Table 1). According to the stepwise model, the total number and the number of valuable lichen species were both negatively influenced by the variable 'Canopy cover' (Table 2, Fig. 2). The other considered variables did not influence the species richness of lichens significantly.

Analyzing the composition of lichen species with NMS, the best solution was a three dimensional configuration (final stress 11.3, number of iteration 118). Proportion of variance in lichen community composition represented by those three axes was 88%. Pearson squared correlation coefficients (r^2) were 0.39, 0.18 and 0.30 for the first, second and third axis, respectively. Correlations of environmental variables with ordination axes are presented in Table 3.

The variation of the data along the first axis is mainly determined by canopy cover. Open wooded meadows with low canopy cover are mostly on the right side and overgrown stands with high canopy cover are on the left side of the ordination plot (Figs 3, 5). According to the ordination scores of the lichen species, the lichens associated with open wooded meadows are located mostly in the positive side of the first axis (e.g. *Candelariella xanthostigma*, *Lecidella flavosorediata*, *Evernia prunastri, Ramalina fastigiata* and *R. fraxinea*; Figs 4, 6) and the lichens associated with overgrown habitats are located mostly in the negative side of the first axis (e.g. *Chaenotheca ferruginea*, *Dimerella pineti*, *Lepraria eburnea*, *L. lobificans* and *Micarea prasina*; Figs 4, 6).

The gradient directed along the second ordination axis is mainly related to the composition of tree species in wooded meadows (Fig. 3; Table 3). On the lower part of the ordination plot are the stands with many tree species and higher amount of sub-neutral barked trees in a stand, and on the upper part are the stands dominated mainly by large-diameter oak trees. The lichens characteristic to the trees with sub-neutral bark are located in the negative side of the second axis (e.g. *Lecidella subviridis* and *Lecanora rugosella*; Fig. 4) and the lichens predominately found on oak trees (e.g. *Calicium salicinum*, *Chaenotheca trichialis*, *Chaenothecopsis vainioana*, *Lobaria pulmonaria* and *Physconia perisidiosa*) are in the positive side of the second axis (Fig. 4). Also the third axis demonstrates the gradient associated with the composition of tree species in a wooded meadow, the variable acid-barked trees has the highest correlation with the third axis (Fig. 5, Table 3).

The importance of the geographical location of the stand (variable 'Longitude'; Fig. 5; Table 3) is observable in the ordination plot of the first and third axes: the stands from western Estonia are on the upper left side of the ordination plot and the stands from eastern Estonia are on the lower right side of the ordination plot.

Other considered environmental variables ('Latitude' and 'Distance from gravel road') did not provide reliable information for data interpretation (Table 3).

Table 2. The results of general linear mixed model analysis (GLMM) for the total number of lichen species and for the number of valuable lichen species. Abbreviations: df – degrees of freedom; Slope – slope of the regression line; SE – standard error; p – significance value.

	Total no. of lichen species			No. of valuable lichen species		
Factor	df	Slope (±SE)	p	df	Slope (±SE)	p
Intercept	1; 16		<0.0001	1; 18		<0.0001
Canopy cover	1; 11	-23.416 (±4.898)	0.0006	1; 9	-2.767 (±1.042)	0.026

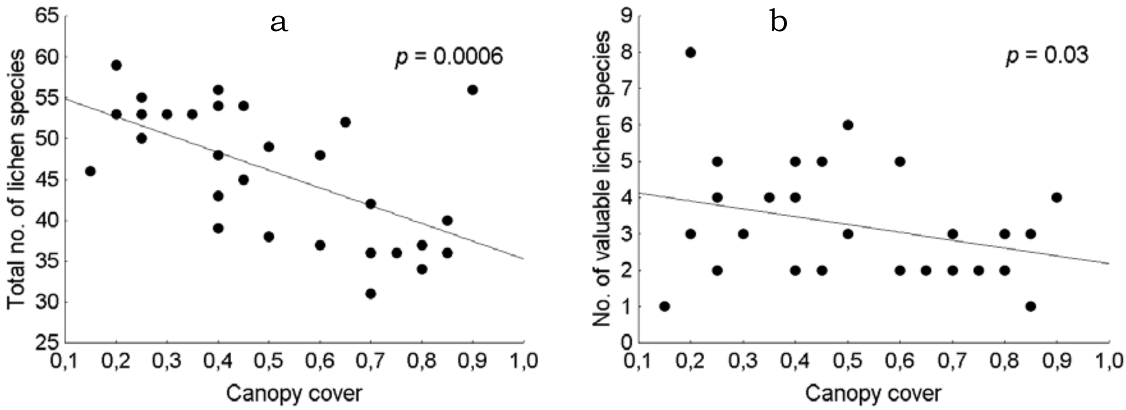

Fig. 2. Relationship between canopy cover and total number of lichen species (a) and the number of valuable lichen species (b) according to general linear mixed model (see Table 2).

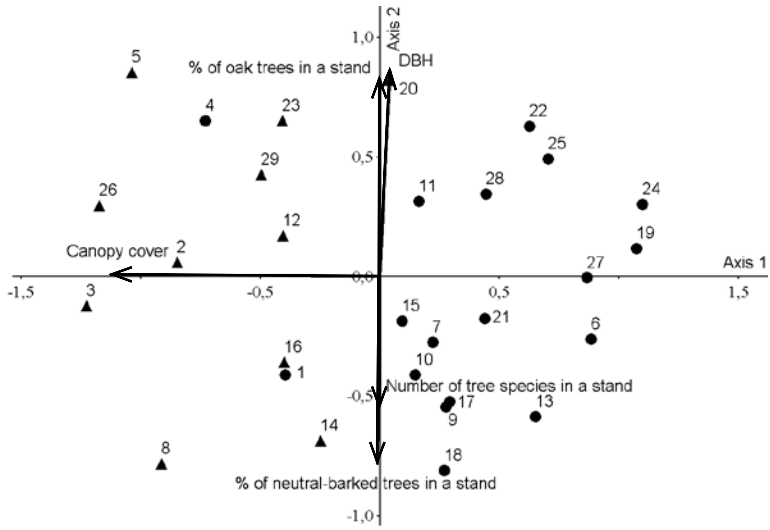

Fig. 3. NMS ordination (axes 1 vs 2) of stands in species space with joint plot overlays of environmental variables and habitat type: open (●) and overgrown (▲) stands (see Table 1). Pearson correlations (r) for quantitative environmental variables are presented in Table 3, variables are shown if $r^2 \geq 0.2$.

DISCUSSION

Overgrowing of semi-natural open wooded meadows influences drastically the composition and richness of vascular plants (Kull & Zobel, 1991; Wahlman & Milberg, 2002; Mitlacher et al., 2002) and, according to our study, causes also significant changes in the lichen communities on trees. The cessation of traditional management (hay mowing) and succession of meadows to deciduous woods result in impoverishing of lichen communities: both the total number and the number of valuable lichen species decrease with increasing canopy cover. This result is in accordance with earlier study by Arup et al. (2003) who detected slight decrease in species richness of lichens in similar habitats on the Island of Öland, south-eastern part of Sweden.

Furthermore, the composition of epiphytic lichens also changes with increasing density of the tree canopies in wooded meadows (Figs 3, 5). Some recorded crustose lichens (e.g., *Caloplaca flavorubescens*, *Candelariella xanthostigma*, *Lecidella flavosorediata* and *Ochrolechia arborea*) prefer open wooded meadows with sparse canopy cover (Figs 4, 6). Simultaneously, more lichens of foliose and fruticose growth forms occurred in the open habitats than in the

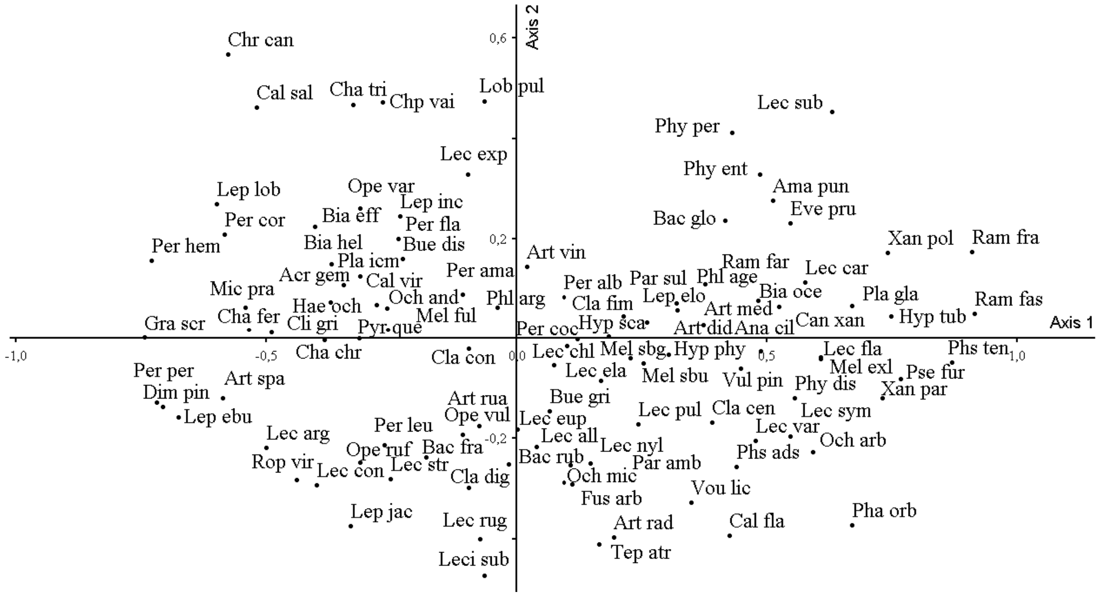

Fig. 4. NMS ordination (axes 1 vs 2) of lichen species. Abbreviations of species names are given in Appendix.

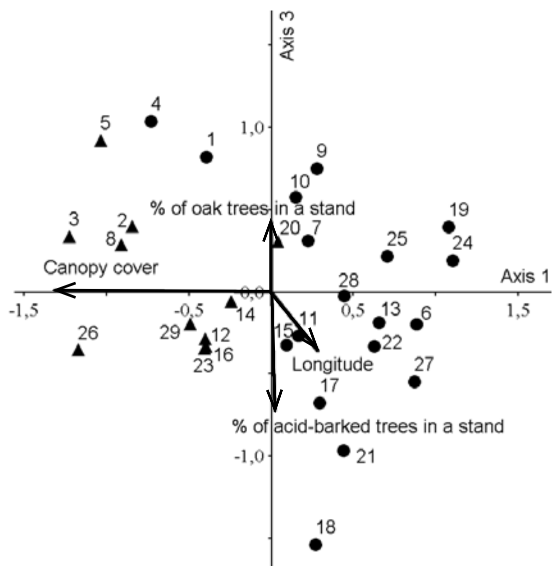

Fig. 5. NMS ordination (axes 1 vs 3) of stands in species space with joint plot overlays of environmental variables and habitat type: open (●) and overgrown (▲) stands (see Table 1). Pearson correlations (r) for quantitative environmental variables are presented in Table 3, variables are shown if $r^2 \geq 0.2$

overgrown stands (Figs 4, 6). Barkman (1958) has declared that most of foliose and fruticose lichens are photophilous. In wooded meadows, during the development of denser tree canopy, the photophilous lichen communities with many species of macrolichens are replaced with associations of more shade-tolerant microlichen species (e.g. *Chaenotheca trichialis*, *Lepraria eburnea* and *Micarea prasina*; Figs 4, 6). Similar changes in the composition of epiphytic communities on *Fraxinus excelsior* between open meadow and overgrown stands have been detected also in western Norway (Moe & Botnen, 1997, 2000).

At the stand level, similarly to high forest (Oksanen, 1988; Jüriado et al., 2003; Will-Wolf et al., 2006), the composition of tree species determined the composition of lichen species in wooded meadows. In boreal forest region, the epiphytic vegetation on the trees with most acid bark, i.e. *Picea abies*, *Pinus sylvestris* and *Betula* spp., is very different from the lichen vegetation on the trees with sub-neutral bark, mainly *Populus tremula* and temperate broad-leaved trees (Barkman, 1958; Cieśliński, 1996). In this study, the wooded meadows with mostly large-diameter oak trees supported assemblages of lichen species different from stands domi-

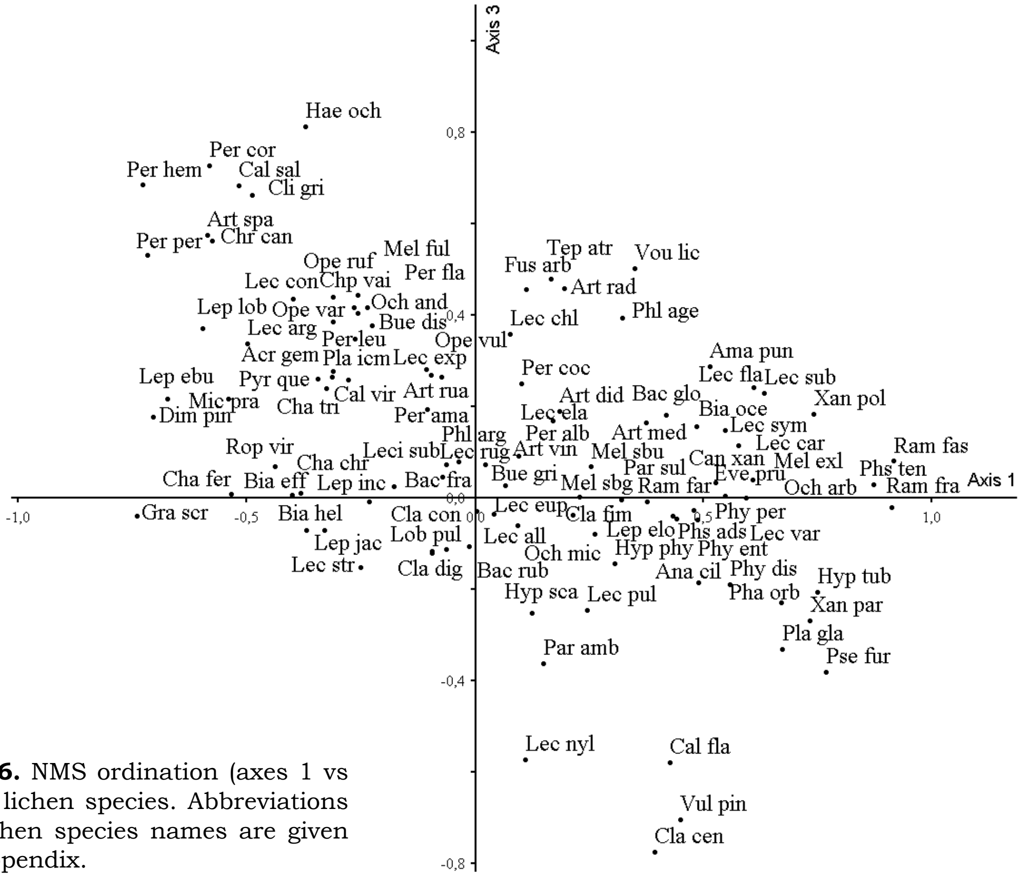

Fig. 6. NMS ordination (axes 1 vs 3) of lichen species. Abbreviations of lichen species names are given in Appendix.

Table 3. Pearson correlations (r) of quantitative environmental variables with the NMS ordination axes. An environmental variable is considered important (*) if $r^2 \geq 0.20$ with at least one ordination axis.

Environmental variable	Axis 1	Axis 2	Axis 3
Latitude	0.29	0.14	-0.19
Longitude*	0.41	0.31	-0.45
Distance from gravel road	-0.16	0.22	-0.20
Number of tree species in a stand*	-0.01	-0.60	-0.29
% of neutral-barked trees in a stand*	-0.08	-0.72	-0.05
% of acid-barked trees in a stand*	0.11	-0.37	-0.64
% of oak trees in a stand*	-0.02	0.74	0.49
DBH (mean diameter of studied trees)*	0.17	0.76	-0.03
Canopy cover*	-0.87	0.05	0.09

nated by acid- or by subneutral-barked trees. The large diameter of trees is also known to be an important factor to support high species richness of lichens and occurrence or abundance of specific lichen species (Lyons et al., 2000; Hedenås & Ericson, 2000; Gustafsson et al., 1992; Benson & Coxson, 2002). Difference of the oak-dominated stands from the stands dominated by other tree species is apparently related also to the properties of oak bark. Bark of oak trees has generally higher porosity and absorptive capacity than bark of other tree species (Rose, 1974).

In the composition of lichens in wooded meadows, similarly to high forests (Jüriado et al., 2003), we can detect the distinction of the stands between western and eastern part of Estonia. Several lichen species i.e. *Pertusaria coronata*, *P. hemisphaerica* and *P. pertusa* (Fig. 6), probably favoured by milder coastal climate (Tønsberg, 1992; Wirth, 1995), are more characteristic to the wooded meadows in the western part of Estonia, particularly western Island of Saaremaa, than to the wooded meadows in the eastern part of Estonia.

We can conclude that open wooded meadows are important habitats for epiphytic lichens and the composition of lichen species is influenced by similar factors as in high forests. Overgrowing of wooded meadows change the composition of lichen communities and decreases the species richness of lichens. Therefore, the structure of the remaining stands of wooded meadows should be maintained by hay mowing or cutting to conserve the peculiar biodiversity of semi-natural habitats.

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Appendix. List of the recorded lichenized, lichenicolous (#) and non-lichenized (+) fungi in wooded meadows of Estonia. Abbrev – abbreviations of species names used in Figs 4 and 6 (macrolichens are in bold). Freq – frequency classes in Estonia: rr – very rare, 1–2 localities; r – rare, 3–5 localities; st r – rather rare, 6–10 localities; st fq – rather frequent, 11–20 localities; fq – frequent, 21–50 localities; fqq – very frequent, 51 or more localities (Randlane & Saag 1999); rare frequency classes are in bold. Red-listed – Red-listed and protected lichen species in Estonia: NT – Near threatened, VU – Vulnerable; PC II, III – protection categories.

	Species	Abbrev	Freq	Red-listed
	Acrocordia cavata (Ach.) R. C. Harris		st fq	
	Acrocordia gemmata (Ach.) A. Massal.	Acr_gem	fq	
	Amandinea punctata (Hoffm.) Coppins & Scheid.	Ama_pun	fqq	
	Anaptychia ciliaris (L.) Körb.	**Ana_cil**	fqq	
	Arthonia didyma Körb.	Art_did	st fq	NT
	Arthonia leucopellaea (Ach.) Almq.		fqq	
	Arthonia mediella Nyl.	Art_med	st fq	
	Arthonia radiata (Pers.) Ach.	Art_rad	fq	
#	*Arthonia ruana* A. Massal.	Art_rua	fq	
	Arthonia spadicea Leight.	Art_spa	fq	
	Arthonia vinosa Leight.	Art_vin	st fq	
	Bacidia arceutina (Ach.) Arnold		fq	
	Bacidia fraxinea Lönnr.	Bac_fra	fqq	
	Bacidia rubella (Hoffm.) A. Massal.	Bac_rub	fq	
	Bacidia subincompta (Nyl.) Arnold		st fq	
	Bactrospora dryina (Ach.) A. Massal.		**r**	
	Biatora chrysantha (Zahlbr.) Printzen		**r**	
	Biatora efflorescens (Hedl.) Räsänen	Bia_eff	fq	
	Biatora globulosa (Flörke) Fr.	Bac_glo	st fq	
	Biatora helvola Körb.	Bia_hel	fq	
	Biatora ocelliformis (Nyl.) Arnold	Bia_oce	st fq	
	Biatoridium delitescens Arnold & Hafellner		**rr**	
	Bilimbia sabuletorum (Schreb.) Arnold		fq	
	Bryoria fuscescens (Gyeln.) Brodo & D. Hawksw.		fqq	
	Buellia arnoldii Servít		**st r**	
	Buellia disciformis (Fr.) Mudd	Bue_dis	fqq	
	Buellia griseovirens (Turner & Borrer ex Sm.) Almb.	Bue_gri	fqq	
	Buellia schaereri De Not.		st fq	
	Calicium abietinum Pers.		fqq	
	Calicium adspersum Pers.		**st r**	
	Calicium glaucellum Ach.		fqq	
	Calicium pinastri Tibell		**r**	
	Calicium salicinum Pers.	Cal_sal	fq	
	Calicium viride Pers.	Cal_vir	fqq	
	Caloplaca cerina (Ehrh. ex Hedw.) Th. Fr.		fqq	
	Caloplaca chrysophthalma Degel.		**st r**	
	Caloplaca flavorubescens (Huds.) J. R. Laundon	Cal_fla	fqq	
	Caloplaca lucifuga G. Thor		**r**	NT
	Candelaria concolor (Dicks.) Stein		**st r**	
	Candelariella xanthostigma (Ach.) Lettau	Can_xan	fq	
	Chaenotheca brachypoda (Ach.) Tibell		fq	
	Chaenotheca chlorella (Ach.) Müll. Arg.		fq	
	Chaenotheca chrysocephala (Turner ex Ach.) Th. Fr.	Cha_chr	fqq	
	Chaenotheca ferruginea (Turner & Borrer) Mig.	Cha_fer	fqq	
	Chaenotheca furfuracea (L.) Tibell		fqq	
	Chaenotheca phaeocephala (Turner) Th. Fr.		fq	
	Chaenotheca stemonea (Ach.) Müll. Arg.		fq	
	Chaenotheca trichialis (Ach.) Th. Fr.	Cha_tri	fqq	
+	*Chaenothecopsis pusiola* (Ach.) Vain.		st fq	
#	*Chaenothecopsis vainioana* (Nádv.) Tibell	Chp_vai	**st r**	
	Chrysotrix candelaris (L.) J. R. Laundon	Chr_can	fq	
	Cladonia cenotea (Ach.) Schaer.	**Cla_cen**	fqq	
	Cladonia coniocraea (Flörke) Spreng.	**Cla_con**	fqq	
	Cladonia digitata (L.) Hoffm.	**Cla_dig**	fqq	
	Cladonia fimbriata (L.) Fr.	**Cla_fim**	fqq	

	Cliostomum flavidulum Hafellner & Kalb		**rr**	
	Cliostomum griffithii (Sm.) Coppins	Cli_gri	st fq	
	Cyphelium inquinans (Sm.) Trevis.		st fq	NT, PC III
#	*Cyphelium sessile* (Pers.) Trevis.		**r**	
	Dimerella pineti (Ach.) Vězda	Dim_pin	fq	
	Evernia prunastri (L.) Ach.	**Eve_pru**	fqq	
	Fuscidea arboricola Coppins & Tønsberg	Fus_arb	st fq	
	Fuscidea praeruptorum (Du Rietz & H. Magn.) Wirth & Vězda		**r**	
	Fuscidea pusilla Tønsberg		**st r**	
	Graphis scripta (L.) Ach.	Gra_scr	fqq	
	Haematomma ochroleucum (Neck.) J. R. Laundon	Hae_och	st fq	
	Hypocenomyce scalaris (Ach.) M. Choisy	**Hyp_sca**	fqq	
	Hypogymnia physodes (L.) Nyl.	**Hyp_phy**	fqq	
	Hypogymnia tubulosa (Schaer.) Hav.	**Hyp_tub**	fqq	
	Imshaugia aleurites (Ach.) S. L. F. Meyer		fqq	
	Lecania cyrtella (Ach.) Th. Fr.		fq	
	Lecania naegelii (Hepp) Diederich & Van den Boom		fq	
	Lecanora allophana Nyl.	Lec_all	fqq	
	Lecanora argentata (Ach.) Malme	Lec_arg	fqq	
	Lecanora cadubriae (A. Massal.) Hedl.		**st r**	
	Lecanora carpinea (L.) Vain.	Lec_car	fqq	
	Lecanora chlarotera Nyl.	Lec_chl	fqq	
	Lecanora conizaeoides Nyl. ex Cromb.	Lec_con	st fq	
	Lecanora expallens Ach.	Lec_exp	fq	
	Lecanora hagenii (Ach.) Ach.		fqq	
	Lecanora norvegica Tønsberg		st fq	
	Lecanora pulicaris (Pers.) Ach.	Lec_pul	fqq	
	Lecanora rugosella Zahlbr.	Lec_rug	fqq	
	Lecanora saligna (Schrad.) Zahlbr.		fq	
	Lecanora sambuci (Pers.) Nyl.		st fq	
	Lecanora strobilina (Spreng.) Kieff.	Lec_str	st fq	
	Lecanora subintricata (Nyl.) Th. Fr.	Lec_sub	**st r**	
	Lecanora symmicta (Ach.) Ach.	Lec_sym	fqq	
	Lecanora thysanophora R.C. Harris		**r**	
	Lecanora varia (Hoffm.) Ach.	Lec_var	fqq	
	Lecidea nylanderi (Anzi) Th. Fr.	Lec_nyl	fqq	
	Lecidella elaeochroma (Ach.) M. Choisy	Lec_ela	fqq	
	Lecidella euphorea (Flörke) Hertel	Lec_eup	fqq	
	Lecidella flavosorediata (Vězda) Hertel & Leuckert	Lec_fla	**st r**	
	Lecidella subviridis Tønsberg	Leci_sub	**st r**	
	Lepraria eburnea J. R. Laundon	Lep_ebu	fq	
	Lepraria elobata Tønsberg	Lep_elo	st fq	
	Lepraria incana (L.) Ach.	Lep_inc	fqq	
	Lepraria jackii Tønsberg	Lep_jac	fq	
	Lepraria lobificans Nyl.	Lep_lob	fq	
	Lepraria vouauxii (Hue) R. C. Harris		**rr**	
	Leucocarpia dictyospora (Orange) R. Sant.		**rr**	
	Lobaria pulmonaria (L.) Hoffm.	**Lob_pul**	fqq	NT, PC III
	Megalaria grossa (Pers. ex Nyl.) Hafellner		st fq	NT, PC III
	Melanelia exasperatula (Nyl.) Essl.	**Mel_exl**	fqq	
	Melanelia fuliginosa (Fr. ex Duby) Essl.	**Mel_ful**	fqq	
	Melanelia olivacea (L.) Essl.		fqq	
	Melanelia subargentifera (Nyl.) Essl.	**Mel_sbg**	fq	
	Melanelia subaurifera (Nyl.) Essl.	**Mel_sbu**	fqq	
	Micarea melanobola (Nyl.) Coppins		**r**	
	Micarea prasina Fr.	Mic_pra	fqq	
	Mycoblastus fucatus (Stirt.) Zahlbr.		st fq	
+	*Mycomicrothelia confusa* D. Hawksw.		**st r**	
	Naetrocymbe punctiformis (Pers.) R. C. Harris		st fq	
	Nephroma parile (Ach.) Ach.		st fq	VU, PC III
	Ochrolechia androgyna (Hoffm.) Arnold	Och_and	fqq	
	Ochrolechia arborea (Kreyer) Almb.	Och_arb	st fq	
	Ochrolechia microstictoides Räsänen	Och_mic	fq	
	Ochrolechia szatalaënsis Verseghy		**st r**	
	Ochrolechia turneri (Sm.) Hasselrot		**r**	
	Opegrapha atra Pers.		st fq	NT

	Opegrapha rufescens Pers.	Ope_ruf	fq	
	Opegrapha varia Pers.	Ope_var	fq	
	Opegrapha vulgata Pers.	Ope_vul	st fq	
	Pachyphiale fagicola (Hepp) Zwackh.		**st r**	
	Parmelia saxatilis (L.) Ach.		fqq	
	Parmelia sulcata Taylor	**Par_sul**	fqq	
	Parmeliopsis ambigua (Wulfen) Nyl.	**Par_amb**	fqq	
	Peltigera membranacea (Ach.) Nyl.		st fq	
	Peltigera praetextata (Flörke ex Sommerf.) *Zopf*		fqq	
	Pertusaria albescens (Huds.) M. Choisy & Werner	Per_alb	fqq	
	Pertusaria amara (Ach.) Nyl.	Per_ama	fqq	
	Pertusaria coccodes (Ach.) Nyl.	Per_coc	fqq	
	Pertusaria coronata (Ach.) Th. Fr.	Per_cor	st fq	
	Pertusaria flavida (DC.) J. R. Laundon	Per_fla	**r**	
	Pertusaria hemisphaerica (Flörke) Erichsen	Per_hem	st fq	
	Perusaria leucostoma A. Massal.	Per_leu	st fq	
	Pertusaria pertusa (Weigel) Tuck.	Per_per	st fq	
	Phaeophyscia ciliata (Hoffm.) Moberg		fq	
	Phaeophyscia orbicularis (Neck.) Moberg	**Pha_orb**	fqq	
	Phlyctis agelaea (Ach.) Flot.	Phl_age	fq	
	Phlyctis argena (Spreng.) Flot.	Phl_arg	fqq	
	Physcia adscendens (Fr.) H. Olivier	**Phs_ads**	fqq	
	Physcia aipolia (Ehrh. ex Humb.) Fürnr.		fqq	
	Physcia dubia (Hoffm.) Lettau		fqq	
	Physcia stellaris (L.) Nyl.		fqq	
	Physcia tenella (Scop.) DC.	**Phs_ten**	fq	
	Physconia detersa (Nyl.) Poelt		st r	NT
	Physconia distorta (With.) J. R. Laundon	**Phy_dis**	fqq	
	Physconia enteroxantha (Nyl.) Poelt	**Phy_ent**	fqq	
	Physconia perisidiosa (Erichsen) Moberg	**Phy_per**	fq	
	Placynthiella icmalea (Ach.) Coppins & P. James	Pla_icm	fqq	
	Platismatia glauca (L.) W. L. Culb. & C. F. Culb.	**Pla_gla**	fqq	
	Pseudevernia furfuracea (L.) Zopf	**Pse_fur**	fqq	
	Pycnora sorophora (Vain.) Hafellner		fq	
	Pyrrhospora quernea (Dicks.) Körb.	Pyr_que	fq	
	Ramalina baltica Lettau		fq	
	Ramalina farinacea (L.) Ach.	**Ram_far**	fqq	
	Ramalina fastigiata (Pers.) Ach.	**Ram_fas**	fqq	
	Ramalina fraxinea (L.) Ach.	**Ram_fra**	fqq	
	Ramalina pollinaria (Westr.) Ach.		fqq	
	Rinodina efflorescens Malme		**st r**	
	Rinodina exigua Gray		fq	
	Ropalospora viridis (Tønsberg) Tønsberg	Rop_vir	st fq	
+	*Sarea difformis* (Fr.) Fr.		**r**	
	Sclerophora coniophaea (Norman) J. Mattsson & Middelb.		st fq	NT, PC II
	Sclerophora pallida (Pers.) Y. I. Yao & Spooner		fq	PC III
	Scoliciosporum chlorococcum (Stenh.) Vězda		fq	
	Strangospora moriformis (Ach.) Stein		**st r**	
	Strangospora pinicola (A. Massal.) Körb.		**r**	
	Tephromela atra (Huds.) Hafellner ex Kalb	Tep_atr	fqq	
	Tuckermannopsis chlorophylla (Willd.) Hale		fqq	
	Usnea hirta (L.) F. H . Wigg.		fqq	
#	*Vouauxiella lichenicola* (Linds.) Petr. & Syd.	Vou_lic	fq	
	Vulpicida pinastri (Scop.) J. -E. Mattsson & M. J. Lai	**Vul_pin**	fqq	
	Xanthoria candelaria (L.) Th. Fr.		fqq	
	Xanthoria fulva (Hoffm.) Poelt & Petutschnig		**st r**	
	Xanthoria parietina (L.) Th. Fr.	**Xan_par**	fqq	
	Xanthoria polycarpa (Hoffm.) Th. Fr. ex Rieber	**Xan_pol**	fqq	