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Epiphytic lichen diversity in Estonian and Fennoscandian old coniferous forests

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Abstract: Lichen species richness and species composition were compared between Estonian and Fennoscandian old coniferous forests, with a special emphasis on woodland key habitat indicator species. Altogether 42 *Picea abies* and 40 *Pinus sylvestris* sample plots were studied in Estonia, Finland, Sweden and Norway. In every plot lichens were recorded on five randomly selected trees; in addition, tree age and canopy openness by the sampled trees were measured. The results revealed clear differences in lichen species composition; the occurrence of many species differed between Estonia and Fennoscandia. Several indicator species were recorded only in one or two sample plots; the relatively frequent indicators differed between the two studied areas. The number of lichen species per sample plot was significantly higher in Fennoscandia compared to Estonia. Maximum tree age was positively correlated with species richness in Estonian spruce sample plots, and mean canopy openness with species richness in Estonian pine sample plots.

Kokkuvõte: Epifüütsete samblike mitmekesisus Eesti ja Fennoskandia vanades okasmetsades

Töös võrreldi samblike liigirikkust ja liigilist koosseisu Eesti ja Fennoskandia vanades okasmetsades, pöörates muuhulgas tähelepanu vääriselupaiga indikaatorliikidele. Kokku hõlmas uurimus 42 hariliku kuuse ja 40 hariliku männi proovipunkti, mis asusid Eestis, Soomes, Rootsis ja Norras. Igas punktis registreeriti samblikud viiel juhuslikult valitud puul, lisaks mõõdeti puude vanus ja võra avatus uuritud puude juures. Töö tulemusena leiti selged erinevused samblike liigilises koosseisus; paljude samblikuliikide esinemine erines Eesti ja Fennoskandia vahel. Mitmeid indikaatorliike leiti vaid üksikutes proovipunktides; sagedasemad indikaatorliigid erinesid uuritud alade vahel. Samblike liigirikkus oli oluliselt suurem Fennoskandia proovipunktides. Proovipunkti vanima puu vanus oli samblike liigirikkusega positiivselt seotud Eesti kuuse proovipunktides ning keskmine võra avatus Eesti männi proovipunktides.

INTRODUCTION

Various factors may limit the occurrence of lichen species in a forest stand. On a large geographical scale climatic gradients are affecting the distribution patterns of species. On the scale of a single tree the microhabitat quality may be crucial. Many species have been associated with old forests (e.g. Coppins & Coppins, 2002; Josefsson et al., 2005; Fritz et al., 2008; Nascimbene et al., 2008), highlighting the great importance of this habitat for lichen diversity in landscape level. Forest management and related changes in forest landscape and stand structure have strong effects on epiphytic lichens; a review about the consequences of disturbance on boreal forest lichens has been provided by Johansson (2008). Lichen diversity is clearly higher in old-growth forests compared to young managed forests (Kuusinen & Siitonen, 1998; Nascimbene et al., 2010), and several species are more frequent on older trees (e.g. Nascimbene et al., 2009; Ranius et al., 2008; Fritz et al., 2009; Lie et al., 2009). It is also known that lichens are responsive to habitat history and continuity (e.g. Tibell, 1992; Josefsson et al., 2005; Ellis & Coppins, 2009; Fritz et al., 2008; Marmor et al., 2011).

Despite the fact that coniferous forests are widely spread in boreal Europe, *Picea abies* (L.) H. Karst (hereafter spruce) and *Pinus sylvestris* L. (hereafter pine) being the most common tree species, many lichen species that are associated with these phorophytes are rather rare in the region. Several species with conservation value and also several woodland key habitat (WKH) indicator species are relatively infrequent in Estonia even in old coniferous forests with long continuity (Marmor et al., 2011). In present study epiphytic lichen diversity in Estonian old coniferous forests is compared with the one in Fennoscandian large old coniferous forests. The main aim is to find out if there are any distinct differences in lichen species composition and species richness between these two areas; a special emphasis has been given to WKH indicators, species that are regarded as indicators of the quality of forest habitats (Nitare, 2000; RTL, 2009; Timonen et al., 2010). Tree age and canopy openness have been included in the study as additional variables.

MATERIALS AND METHODS

Study area

The study comprises coniferous forests in Estonia, Finland, Sweden and Norway (Fig. 1). The annual mean temperature is decreasing northwards, being 4–6°C in Estonia (EMHI); the 0°C mean limit runs slightly to the south of the Arctic Circle (FMI). In the Scandinavian mountains the annual mean temperature is below 0°C (NMI). The mean precipitation is ca 650 mm in Estonia (EMHI) and ca 600 mm in northern Finland (FMI); in Scandinavia the precipitation levels are varying and may be twice as high or even higher in some areas compared to Estonia and Finland (NMI). Vegetation zone varies from hemiboreal to northern boreal; Fennoscandian sample plots are located in northern taiga with strong conifer dominance in forests (Ahti et al., 1968). Estonia is located in hemiboreal subzone of boreal forest zone, in the transitional area where southern taiga forest changes into spruce-hardwood forest (Ahti et al., 1968; Laasimer & Masing, 1995). Spruce and pine are dominating tree species in whole study area, birch (*Betula pendula* Roth) being the most abundant deciduous tree species. Forest stands with long forest continuity and without any signs of management have been preferred in the study. Fennoscandian sample plots are located in large old forests (over 500 km^2; Greenpeace, 2006); many of them close to or in nature protection areas, e.g. Vålådalen, Oulanka and Martinselkonen. Estonian plots are located in comparatively small old forests mainly in nature protection areas and WKHs (and are surrounded by differently aged managed stands) as large old-forest areas are lacking in the country. Estonian sample plots are located in areas that have been mapped as forest on the maps from 17th century and the end of 19th/beginning of 20th century (the 17th century maps were unavailable for four plots), and might have been managed historically. About half of Estonian territory is covered with forests; whereas only ca 6% of forests is over 100 years old, including 1000 km^2 pine and 160 km^2 spruce forests (EEIC, 2010).

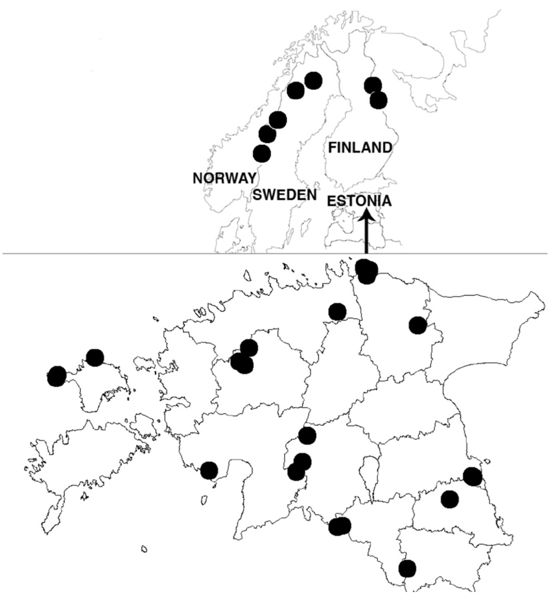

Fig. 1. Location of sample plots (dots in Fennoscandia represent sample plot groups).

Field methods

Fieldwork was carried out in 2008–2009. Altogether 42 spruce and 40 pine sample plots were studied. The spruce sample plots were divided between the countries as follows, 21 in Estonia, 5 in Finland, 13 in Sweden and 3 in Norway; and pine sample plots as follows, 21 in Estonia, 7 in Finland, 10 in Sweden and 2 in Norway. In most cases spruce and pine sample plots were located in the same forest stand. Minimum distance between the plots of same tree species was ca one km. Each sample plot contained five trees of the same species i.e. altogether 410 trees were sampled. All trees were selected randomly within 50 m radius from plot centre; only trees with >50 cm circumference were included in the study. Presence of all lichen species growing on tree trunk, branches and twigs on the first two meters from the ground was recorded on every selected tree. Some specimens were collected for later identification with microscope and spot tests. Thin layer chromatography with solvent A (Orange et al., 2001) was used for identifying secondary compounds, if necessary. The age of all selected trees was determined with an increment borer; core samples were taken at the height of 1.3 m. The max length of sampled branches was measured for every tree. A spherical densiometer was used for estimating light conditions by the studied trees. Canopy openness (percentage of open sky) was measured 0.8 m from tree trunk at the height of ca one meter in every four cardinal direction, with back towards the tree. Mean canopy openness was calculated for every tree and sample plot.

Statistical analyses

Software applications STATISTICA 7 and PC-ORD 5 were used for the statistical analyses. Only lichen species that were recorded on tree trunks were included in analyses, because the length and presence of branches on the first meters near the ground differed between study areas. T-test was used for describing the differences in lichen species richness between Estonian and Fennoscandian sample plots; it was also used for comparing tree age and canopy openness between Estonian and Fennoscandian sampled trees. Spearman's correlation analysis was used for finding the relationships between max tree age, mean canopy openness and lichen species richness in the sample plots, separately for Estonia and Fennoscandia. Detrended correspondence analysis (DCA) was used for describing lichen species composition on tree trunks in the sample plots. DCA was based on covariance of species (presence/absence data); species that were recorded on tree trunks in only 1–2 sample plots were excluded from analysis. The following variables were included in DCA joint plots: latitude, longitude, mean canopy openness and maximum tree age of the sample plots; 0.300 being the cutoff r^2 value. Frequency of lichen species was calculated as the percentage of occurrence in the sample plots, together for tree trunks and branches (Table 1).

RESULTS

Altogether, 151 lichen species were recorded in the study: 130 on spruces and 105 on pines. The occurrence and frequency of many species differed between Estonia and Fennoscandia (Table 1). Sixty species were found only in Fennoscandia, *Alectoria sarmentosa*, *Japewia subaurifera*, *Lecidea hypopta*, and *Mycoblastus affinis* being most frequent among them; only six of these sixty species have never been found in Estonia (Table 1; Randlane et al., 2009). One species, *Lecidea leprarioides*, was recorded for the first time for Estonia during these studies (Suija et al., 2010). Thirty species were recorded only in Estonia, *Arthonia leucopellaea*, *Dimerella pineti*, *Evernia prunastri*, *Lecanactis abietina*, and *Phlyctis argena* being the most frequent ones among them. Some taxa, e.g. *Bryoria capillaris*, *Chaenotheca ferruginea*, *Cladonia digitata*, *Hypogymnia physodes*, and *Parmeliopsis ambigua*, were very frequent in both regions. The occurrence of nearly all found WKH indicator species differed between Estonia and Fennoscandia (only one common indicator species, *Ramalina thrausta*, was recorded in both Estonia and Fennoscandia in present study; *Mycoblastus sanguinarius* is not regarded as a WKH indicator in Fennoscandia; Table 1).

The results of DCA verified the strong differences in lichen species composition between Estonia and Fennoscandia in case of both spruces (Fig. 2) and pines (Fig. 3). In addition to species composition, species richness also differed between Estonia and Fennoscandia, its mean values being significantly higher in Fennoscandia (Fig. 4). According to the results of Spearman's correlation analyses max tree age in the sample plots had a significant positive effect on lichen species richness on tree trunks only in Estonian spruces (Fig. 5), and mean canopy openness in Estonian pines (Fig. 6).

The mean age of sampled spruces was higher in Fennoscandia (mean value 143) compared to Estonia (mean value 123; $t = 3.82$; $df = 206$; $p = 0.0002$), whereas the mean age of pines was higher in Estonia (mean value 167) compared to Fennoscandia (mean value 153; $t = -2.16$; $df = 196$; $p = 0.032$). The mean percentage of canopy openness was significantly higher in Fennoscandia compared to Estonia in both spruces (mean values 26 and 21; $t = -3.55$; $df = 208$; $p < 0.001$) and pines (mean values 45 and 27; $t = -11.31$; $df = 198$; $p < 0.00001$). The mean branch length of spruces was 1.7 m in Estonia and 2.5 m in Fennoscandia; the mean branch length of Fennoscandian pines was 0.6 m, whereas Estonian pines had almost no branches at the first meters from the ground (trees with branch length 0 m have been included in calculations).

Table 1. The frequency (percentage of occurrences) of lichen species in Fennoscandian (FNS) and Estonian (EST) sample plots; species that were found only on branches have been marked with (B); species that have not been reported from Estonia are marked with*; species that are regrded as WKH indicators in Estonia (RTL 2009), Sweden (Nitare 2000) and/or Finland (indicator species of old forests; Stenroos et al., 2011) are underlined, and the abbrevations of countries added (EST for Estonia, FIN for Finland and SWE for Sweden)

Lichen species	*P. abies*		*P. sylvestris*	
	FNS	EST	FNS	EST
Alectoria sarmentosa (Ach.) Ach. FIN. SWE	95	0	68	0
Arthonia leucopellaea (Ach.) Almq. EST, FIN, SWE	0	57	0	38
Arthonia mediella Nyl.	0	5	0	0
Arthonia vinosa Leight. EST, SWE	0	5	0	5
Biatora chrysantha (Zahlbr.) Printzen	38	0	0	0
Biatora efflorescens (Hedl.) Räsänen	52	38	5	10
Biatora helvola Körb.	0	19	0	5
Bryoria capillaris (Ach.) Brodo & D. Hawksw.	100	86	84	48
Bryoria fremontii (Tuck.) Brodo & D. Hawksw. FIN *	43	0	63	0
Bryoria furcellata (Fr.) Brodo & D. Hawksw. SWE	10	0	37	0
Bryoria fuscesens (Gyeln.) Brodo & D. Hawksw.	100	38	100	10
Bryoria implexa (Hoffm.) Brodo & D. Hawksw.	24	5	5	0
Bryoria nadvornikiana (Gyeln.) Brodo & D. Hawksw. SWE (B)	5	0	0	0
Bryoria simplicior (Vain.) Brodo & D. Hawksw.	38	0	53	0
Bryoria subcana (Nyl. ex Stizenb.) Brodo & D. Hawksw. (B)	0	14	0	0
Buellia disciformis (Fr.) Mudd	5	0	5	0
Buellia griseovirens (Turner & Borrer ex Sm.) Almb.	5	10	0	0
Buellia schaereri De Not.	24	0	0	0
Calicium glaucellum Ach.	33	0	16	0
Calicium parvum Tibell SWE	0	0	5	0
Calicium salicinum Pers.	29	0	0	0
Calicium trabinellum (Ach.) Ach.	24	0	5	0
Calicium viride Pers.	100	24	5	0
Cetraria sepincola (Ehrh.) Ach.	5	0	21	0
Chaenotheca chrysocephala (Turner ex Ach.) Th. Fr.	100	95	32	86
Chaenotheca ferruginea (Turner & Borrer) Mig.	86	81	11	95
Chaenotheca furfuracea (L.) Tibell	71	33	0	0
Chaenotheca gracilenta (Ach.) Mattsson & Middelb. FIN, SWE	5	0	0	0
Chaenotheca gracillima (Vain.) Tibell FIN, SWE	14	0	0	0
Chaenotheca sphaerocephala Nádv.*	5	0	0	0
Chaenotheca stemonea (Ach.) Müll. Arg.	24	24	0	10
Chaenotheca subroscida (Eitner) Zahlbr. EST, FIN, SWE	52	0	0	0
Chaenotheca trichialis (Ach.) Th. Fr.	52	19	5	5
Chrysothrix chlorina (Ach.) J. R. Laundon	0	19	0	0
Chrysothrix flavovirens Tønsberg	10	24	0	33

Table 1. (continued)

Lichen species	*P. abies*		*P. sylvestris*	
	FNS	EST	FNS	EST
Cladonia bacillaris (Leight.) Arnold	0	0	11	0
Cladonia bacilliformis (Nyl.) Glück	71	5	68	10
Cladonia cenotea (Ach.) Schaer.	76	43	95	95
Cladonia chlorophaea (Flörke ex Sommerf.) Spreng.	19	19	21	19
Cladonia coniocraea (Flörke) Spreng.	90	100	58	95
Cladonia cornuta (L.) Hoffm.	5	5	0	5
Cladonia crispata (Ach.) Flot.	0	0	21	0
Cladonia deformis (L.) Hoffm.	0	0	16	0
Cladonia digitata (L.) Hoffm.	76	100	100	100
Cladonia fimbriata (L.) Fr.	86	67	89	81
Cladonia furcata (Huds.) Schrad.	0	0	5	0
Cladonia grayi G. Merr. ex Sandst.	0	0	21	0
Cladonia mitis Sandst.	0	0	26	0
Cladonia norvegica Tønsberg & Holien	52	0	84	19
Cladonia ochrochlora Flörke	57	38	11	52
Cladonia parasitica (Hoffm.) Hoffm. $_{SWE}$	0	0	0	5
Cladonia pleurota (Flörke) Schaer.	5	0	16	0
Cladonia polydactyla (Flörke) Spreng.	0	10	0	5
Cladonia rangiferina (L.) Weber ex F. H. Wigg.	0	0	16	0
Cladonia squamosa Hoffm.	0	0	11	0
Cladonia sulphurina (Michx.) Fr.	10	0	58	0
Cliostomum griffithii (Sm.) Coppins	10	24	5	5
Cliostomum leprosum (Räsänen) Holien & Tønsberg $_{FIN}$	0	0	0	14
Cyphelium inquinans (Sm.) Trevis. $_{EST, FIN, SWE}$	10	0	0	0
Cyphelium tigillare (Ach.) Ach. $_{SWE}$ (B)	0	0	5	0
Dimerella pineti (Ach.) Vězda	0	38	0	38
Evernia divaricata (L.) Ach. $_{EST, FIN, SWE}$	0	5	0	0
Evernia mesomorpha Nyl. $_{EST, FIN, SWE}$ (B)	5	0	5	0
Evernia prunastri (L.) Ach.	0	52	0	0
Fellhanera subtilis (Vězda) Diederich & Serus. (B)	0	5	0	0
Fuscidea pusilla Tønsberg (B)	5	0	0	0
Haematomma ochroleucum (Neck.) J.R. Laundon	0	0	0	5
Hypocenomyce anthracophila (Nyl.) P. James & Gotth. Schneid. $_{SWE}$	0	0	0	5
Hypocenomyce friesii (Ach.) P. James & Gotth. Schneid.	14	10	37	29
Hypocenomyce scalaris (Ach.) M. Choisy	0	19	58	71
Hypogymnia bitteri (Lynge) Ahti $_{SWE}$ *	48	0	26	0
Hypogymnia farinacea Zopf $_{EST}$	0	0	0	5
Hypogymnia physodes (L.) Nyl.	100	100	100	100
Hypogymnia tubulosa (Schaer.) Hav.	90	71	53	14

Table 1. (continued)

Lichen species	*P. abies*		*P. sylvestris*	
	FNS	EST	FNS	EST
Imshaugia aleurites (Ach.) S.L.F. Meyer	29	29	100	43
Japewia subaurifera Muhr & Tønsberg	100	0	89	0
Japewia tornoënsis (Nyl.) Tønsberg*	52	0	16	0
Lecanactis abietina (Ach.) Körb. EST, FIN	0	57	0	24
Lecanora cadubriae (A. Massal.) Hedl.	29	0	26	0
Lecanora circumborealis Brodo & Vitik.	62	0	32	0
Lecanora conizaeoides Nyl. ex Cromb.	0	29	0	5
Lecanora expallens Ach.	19	48	0	0
Lecanora norvegica Tønsberg	0	0	0	5
Lecanora pulicaris (Pers.) Ach.	48	14	26	0
Lecanora symmicta (Ach.) Ach. (B)	5	0	0	0
Lecidea hypopta Ach.	95	0	95	0
Lecidea leprarioides Tønsberg	76	10	5	0
Lecidea nylanderi (Anzi) Th. Fr.	62	81	53	90
Lecidea turgidula Fr.	10	10	42	14
Lepraria elobata Tønsberg	38	0	0	0
Lepraria incana (L.) Ach.	14	100	11	100
Lepraria jackii Tønsberg s.lat.	100	29	32	67
Lepraria lobificans Nyl.	57	5	0	0
Letharia vulpina (L.) Hue SWE *	0	0	5	0
Loxospora elatina (Ach.) A. Massal.	5	95	11	90
Melanelixia subaurifera (Nyl.) O. Blanco et al. (B)	0	14	0	0
Melanohalea exasperatula (Nyl.) O. Blanco et al. (B)	0	38	0	0
Melanohalea olivacea (L.) O. Blanco et al.	24	0	5	0
Micarea elachista (Körb.) Coppins & R. Sant.	0	5	0	29
Micarea hedlundii Coppins	0	0	0	10
Micarea melaena (Nyl.) Hedl.	5	24	26	90
Micarea prasina Fr. s.lat.	29	86	0	57
Mycoblastus affinis (Schaer.) T. Schauer*	90	0	32	0
Mycoblastus alpinus (Fr.) Th. Fr. ex Hellb.	43	0	37	0
Mycoblastus fucatus (Stirt.) Zahlbr.	24	0	16	0
Mycoblastus sanguinarius (L.) Norman EST	100	5	89	10
Ochrolechia alboflavescens (Wulfen) Zahlbr.	19	10	11	5
Ochrolechia androgyna (Hoffm.) Arnold	100	19	100	0
Ochrolechia arborea (Kreyer) Almb.	5	5	0	0
Ochrolechia frigida (Sw.) Lynge	10	0	5	0
Ochrolechia microstictoides Räsänen	90	71	32	24
Ochrolechia szatalaënsis Verseghy	67	0	32	0
Opegrapha vulgata Ach. EST	0	5	0	0

Table 1. (continued)

Lichen species	*P. abies*		*P. sylvestris*	
	FNS	EST	FNS	EST
Parmelia ernstiae Feuerer & A. Thell (B)	0	5	0	0
Parmelia saxatilis (L.) Ach.	5	33	0	5
Parmelia sulcata Taylor	95	95	58	19
Parmeliopsis ambigua (Wulfen) Nyl.	100	67	100	100
Parmeliopsis hyperopta (Ach.) Arnold	100	14	100	90
Pertusaria amara (Ach.) Nyl.	24	86	0	0
Pertusaria borealis Erichsen	71	0	21	0
Pertusaria coccodes (Ach.) Nyl.	0	29	0	0
Phlyctis argena (Spreng.) Flot. (B)	0	48	0	0
Physcia tenella (Scop.) DC. var. tenella (B)	0	10	0	0
Placynthiella dasaea (Stirt.) Tønsberg	5	0	0	0
Placynthiella icmalea (Ach.) Coppins & P. James	0	0	5	0
Platismatia glauca (L.) W.L. Culb. & C.F. Culb.	100	100	63	57
Pseudevernia furfuracea (L.) Zopf	19	86	26	5
Pycnora sorophora (Vain.) Hafellner	86	0	95	5
Pyrrhospora cinnabarina (Sommerf.) M. Choisy $_{SWE}$	5	0	0	0
Pyrrhospora quernea (Dicks.) Körb.	0	14	0	0
Ramalina dilacerata (Hoffm.) Hoffm. $_{FIN, SWE}$ (B)	14	0	0	0
Ramalina farinacea (L.) Ach. (B)	5	29	0	0
Ramalina thrausta (Ach.) Nyl. $_{EST, FIN, SWE}$	10	5	0	0
Sclerophora coniophaea (Norman) Mattsson & Middelb. $_{EST, FIN, SWE}$	29	0	0	0
Scoliciosporum chlorococcum (Stenh.) Vězda (B)	0	0	5	0
Strangospora moriformis (Ach.) Stein	0	0	11	0
Trapeliopsis flexuosa (Fr.) Coppins & P. James	5	5	11	14
Tuckermannopsis chlorophylla (Willd.) Hale	100	57	100	0
Usnea barbata (L.) Weber ex F.H. Wigg. (B)	24	0	0	0
Usnea chaetophora Stirt. (B)	29	5	0	0
Usnea diplotypus Vain. (B)	5	0	0	0
Usnea filipendula Stirt.	76	62	26	5
Usnea glabrescens (Vain.) Vain. (B)	29	0	0	0
Usnea hirta (L.) F.H. Wigg.	14	67	11	5
Usnea lapponica Vain. (B)	24	0	0	0
Usnea subfloridana Stirt.	52	52	5	0
Usnea substerilis Motyka (B)	5	0	0	0
Usnea wasmuthii Räsänen (B)	5	5	0	0
Vulpicida pinastri (Scop.) J.-E. Mattsson & M.J. Lai	95	38	89	38
Xanthoria polycarpa (Hoffm.) Th. Fr. ex Rieber (B)	0	5	0	0
Xylographa vitiligo (Ach.) J.R. Laundon (B)	5	0	21	0

DISCUSSION

There were clear differences in lichen species composition between Fennoscandian and Estonian sample plots (Figs 2, 3). Species richness was significantly higher in Fennoscandia in case of both spruces and pines (Fig. 4). Some species, relatively frequent in studied Fennoscandian old forests, have not been reported from Estonia at all or are rather rare in Estonia. There were also some species that were recorded only in Estonia in this study (for example, *Evernia prunastri*, *Melanohalea exasperatula* and *Phlyctis argena* that are common on deciduous trees in the whole study area; Santesson et al., 2004). There was a difference in the occurrence of almost all WKH indicator lichens between Estonia and Fennoscandia (Table 1). Many indicators were infrequent on sampled trees across the study area. Two indicator species, *Arthonia leucopellaea* and *Lecanactis abietina*, were quite frequent in Estonia and not found in studied Fennoscandian plots (both are common in WKHs, and *L. abietina* also in production forests, in southern Sweden; Johansson & Gustafsson, 2001). Several indicator species, *Alectoria sarmentosa*, *Bryoria fremontii*, *B. furcellata*, *Chaenotheca subroscida*, *Hypogymnia bitteri*, and *Sclerophora coniophaea*, were rather frequent in Fennoscandian old forests (the last one is associated mainly with old broad leaved trees in Estonia).

Several simultaneously changing variables may affect lichen communities in wide geographical scale. Climatic conditions certainly affect the distribution trends of lichen species (e.g. Giordani, 2006; Will-Wolf et al., 2006; Ellis & Coppins, 2010). The varying lichen species composition in northern Norway has been associated with climatic gradients (Werth et al., 2005). The abundance of some epiphytic lichen species in Finnish coniferous forests changes on east-to-west gradient, and has been associated with the continentality gradient (Halonen et al., 1991). Longitudinal differences in the abundance of several lichen species have been noticed also in Estonia (Randlane et al., 2002; Jüriado et al., 2003). Based on a study conducted by Ellis & Coppins (2009) in juniper scrubs across Britain, climate is affecting species composition but not species richness of epiphytic lichens. Therefore, the significant differences in the number of lichen species between Estonian and Fennoscandian sample plots (Fig. 4) may be due to some additional factors.

Concerning the variables included in present study, the effects of both light availability and tree age should be considered. Canopy openness was positively correlated with lichen species richness in Estonian pine sample plots (on the studied first two meters from the ground; Fig. 6); mean canopy openness was significantly higher in Fennoscandia compared to Estonia. It has been suggested previously that poor light conditions may cause lower lichen cover and limit the presence of some lichen species in dense spruce stands (Gauslaa et al., 2007; Hilmo et al., 2009). Maximum tree age had a positive effect on the number of lichen species in Estonian spruce sample plots (Fig. 5). Higher lichen diversity on older spruces has been recorded also previously (Lie et al., 2009; Nascimbene et al., 2009). Longer time available for tree colonisation has been regarded as one important reason facilitating the addition of species with low dispersal ability on older trees (Ranius et al., 2008). However, the number of lichen species on tree trunks was lower in all Estonian spruce sample plots compared to Fennoscandian ones, although the age ranges of studied trees overlapped (Fig. 5).

It can be hypothesised that the long-term impact of forest management on Estonian forest landscapes and the consequent relatively small size of old-growth forest stands may have led to the rareness of more sensitive old-forest lichen species in Estonia. Fennoscandian sample plots were located in large old-forest areas (Greenpeace, 2006), whereas Estonian plots were located in comparatively small old-forest patches. Previously Lommi et al. (2010) have suggested that longer history of forest management might be behind the lower lichen species richness in southern compared to middle Finland pine forests. The importance of habitat history and connectivity on the diversity of epiphytic lichens and presence of species of conservation concern has been emphasised in several studies, and in relation to this, an extinction debt in small fragmented old-forest patches has been suggested (e.g. Berglund & Jonsson, 2005; Ellis & Coppins, 2007; Ranius et al., 2008). Hedenås & Ericson (2008) have concluded that predictions of species occurrences at the stand level have to take

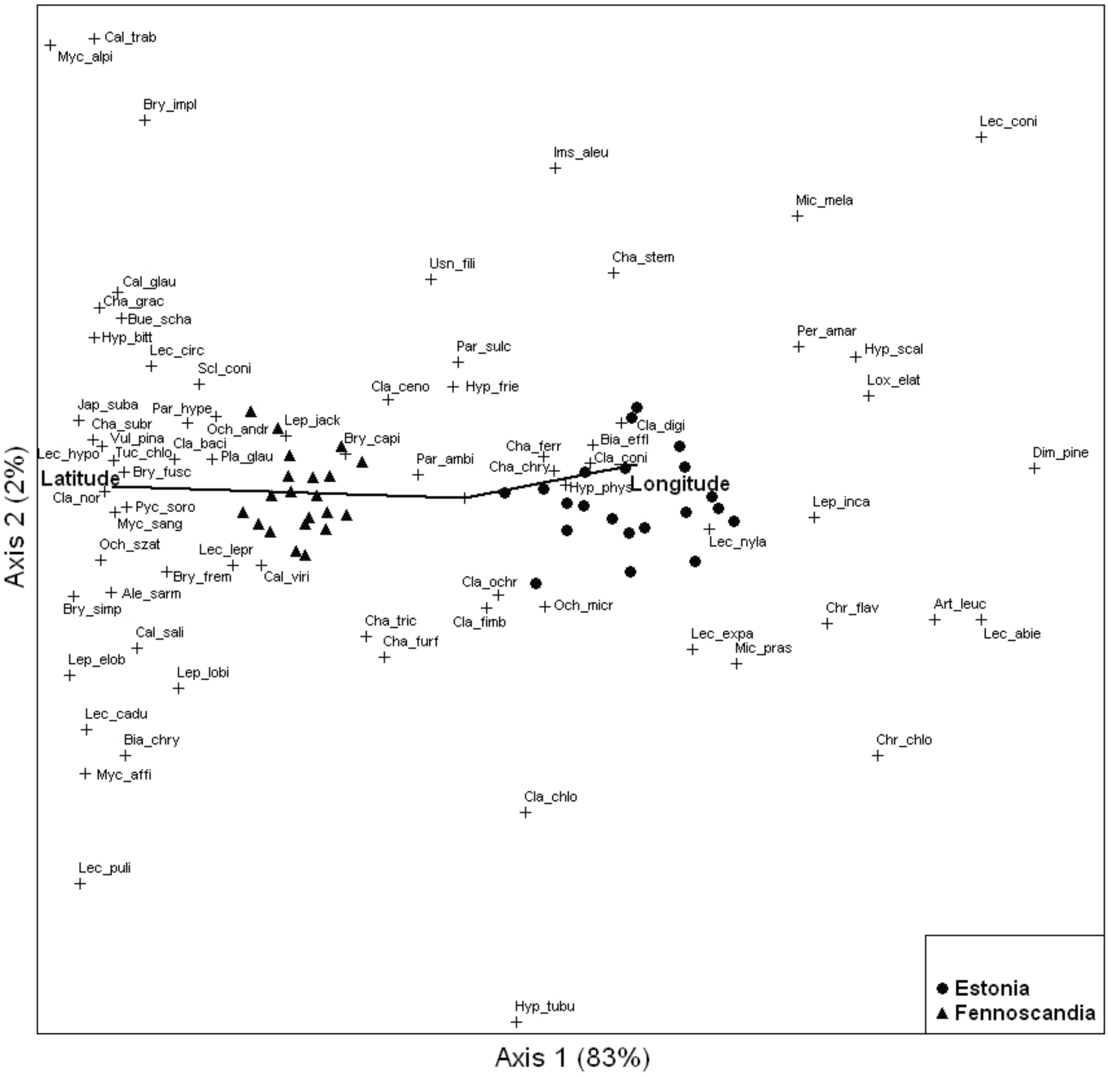

Fig. 2. Estonian and Fennoscandian spruce sample plots on DCA joint-plot.

into account the amount of suitable habitats at the landscape scale.

It can be concluded that lichen species composition differed significantly between Estonia and Fennoscandia, species richness being lower in Estonia. Climatic gradients certainly affect the general distribution trends of lichen species across the studied area, whereas the importance of various factors behind the difference in lichen species richness between Estonian and Fennoscandian sample plots remains unclear. The differences in the occurrence and frequency of many species, including WKH indicators, between Estonia and Fennoscandia confirm that the local context has to be taken into account when choosing indicator species of valuable forest habitats. Previously Will-Wolf et al. (2006) have stated that the importance of different variables may depend on geographical scale and lichen species are not equally suitable as ecological indicators across a wide scale. The further information about the biogeography of lichens and limiting factors at different scales would be highly helpful for evaluating the bioindicational and conservational value of species in different regions.

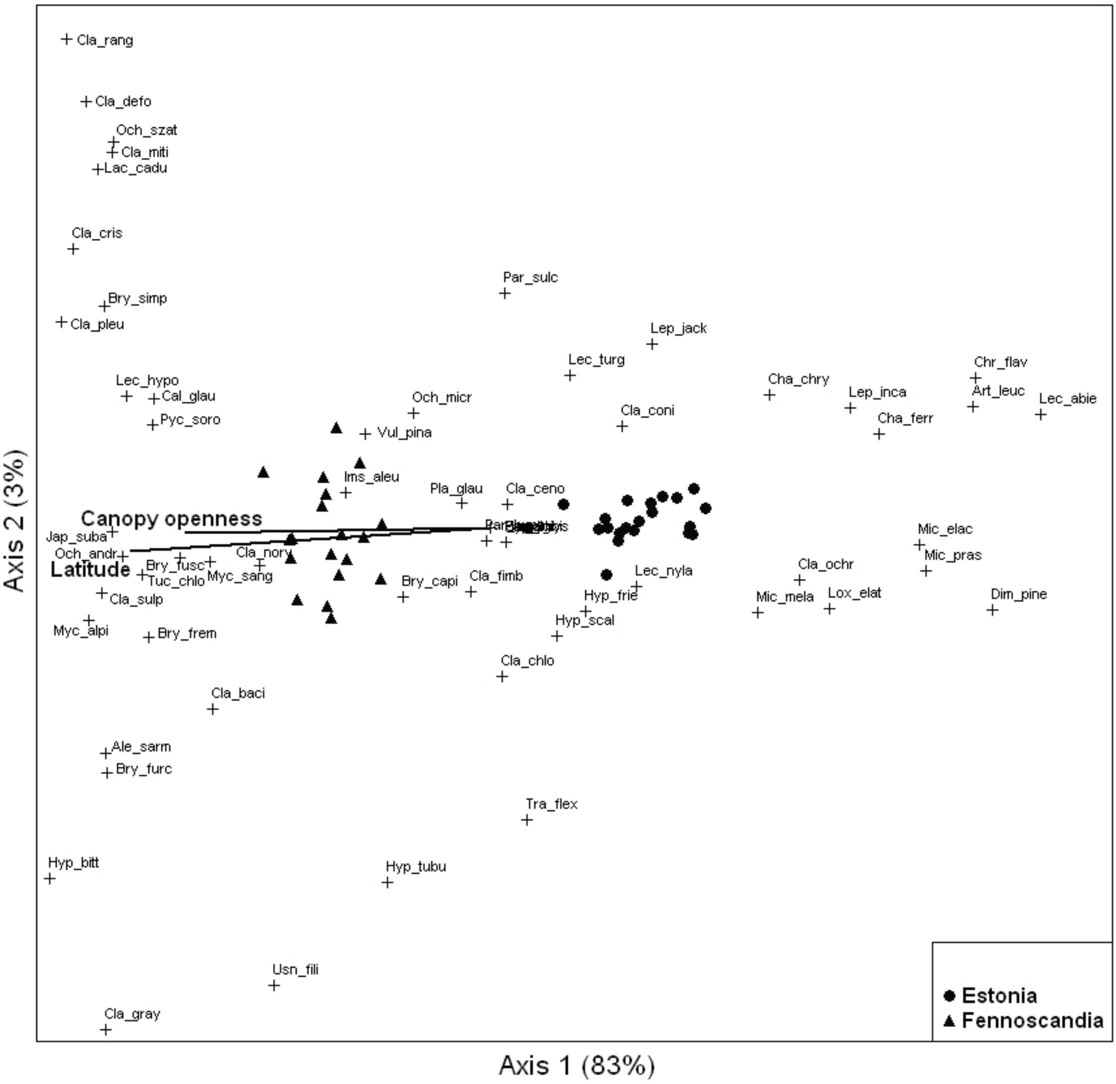

Fig. 3. Estonian and Fennoscandian pine sample plots on DCA joint-plot.

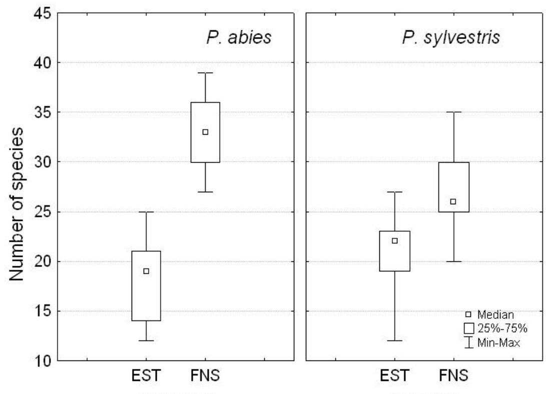

Fig. 4. Number of lichen species on tree trunks in Estonian (EST) and Fennoscandian (FNS) spruce ($t = -13.6$; $n = 42$; $p < 0.0001$) and pine ($t = -5.0$; $n = 40$; $p < 0.0001$) sample plots.

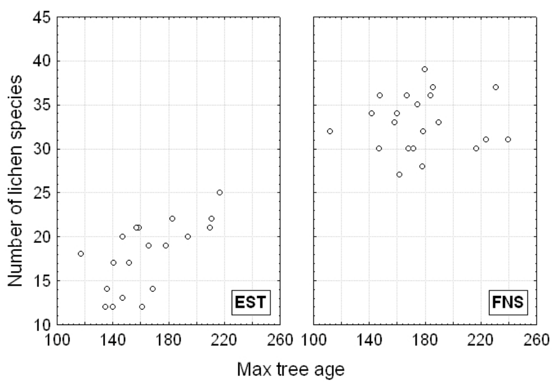

Fig. 5. Correlations between maximum tree age and number of lichen species on tree trunks in Estonian ($R_s = 0.64$; $n = 21$; $p = 0.002$) and Fennoscandian ($R_s = 0.11$; $n = 21$; $p = 0.64$) spruce sample plots.

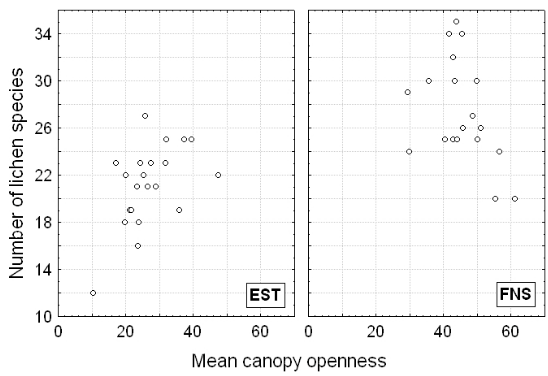

Fig. 6. Correlations between mean canopy openness and number of lichen species on tree trunks in Estonian ($R_s = 0.53$; $n = 21$; $p = 0.013$) and Fennoscandian ($R_s = -0.39$; $n = 19$; $p = 0.10$) pine sample plots.

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