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LIIS MARMOR

Ecology and bioindicative value of epiphytic lichens in relation to air pollution and forest continuity

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LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following publications that are referred in the further text by the Roman numerals:

I Marmor, L., Randlane, T., 2007. Effects of road traffic on bark pH and epiphytic lichens in Tallinn. Folia Cryptogamica Estonica 43, 23–37.

II Marmor, L., Tõrra, T., Randlane, T., 2010. The vertical gradient of bark pH and epiphytic macrolichen biota in relation to alkaline air pollution. Ecological Indicators 6, 1137–1143.

III Marmor, L., Tõrra, T., Saag, L., Randlane, T., 2011. Effects of forest continuity and tree age on epiphytic lichen biota in coniferous forests in Estonia. Ecological Indicators 11, 1270–1276.

IV Marmor, L., Tõrra, T., Leppik, E., Saag, L., Randlane, T., 2011. Epiphytic lichen diversity in Estonian and Fennoscandian old coniferous forests. Folia Cryptogamica Estonica 48, xx–xx. (accepted for publication)

Author's contribution to each paper (%)

	I	**II**	**III**	**IV**
Idea and design	70	70	70	70
Fieldwork	100	50	50	40
Species identification	80	80	60	60
Data analyses	100	100	100	90
Writing	70	80	80	80

1. INTRODUCTION

Lichens (systematically lichenized fungi) are among the most widely used bioindicators in the terrestrial environment. Lichens are perennial organisms available for monitoring throughout the year. Due to their physiological and metabolic peculiarities, like the lack of cuticle, lichens are, as a rule, more sensitive to air pollution than for example vascular plants (Nimis and Purvis, 2002; Nash, 2008). Pollution data from lichen indicators are well correlated with direct measurements of air pollutants (Nimis et al., 1990; van Herk, 1999). Lichens are also used as indicators of forest sites with high conservation value. Although individual lichen species are often characterized by high habitat specificity, lichens in general are widespread in a great range of environmental conditions. They may be found on very different types of substrata such as trees, rocks, and soil, allowing their use as bioindicators in both urban and rural environments (Nimis et al., 2002). Epiphytic lichens growing on trees are usually used in bioindication because of the wide availability of substrata, allowing a high density of sampling points.

The combination of various natural and anthropogenic factors determines which lichen species can be found on a tree. The effects of human related changes in habitat qualities on epiphytic lichen biota have been rather well studied as the results have a high practical value in the field of bioindication (e.g. Cislaghi and Nimis, 1997). Poor air quality can be regarded as the most important anthropogenic factor limiting epiphytic lichen diversity in urban, industrial and other polluted areas. As a result of numerous studies a strong effect of various pollutants on lichen communities has been revealed. The sensitivity to different types of air pollution varies between lichen species, leading to changes in lichen species richness and species composition in polluted areas. For example, there is a well-known negative relationship between epiphytic lichen diversity and atmospheric SO_2 concentration; but in case of NH_3 and NO_2 pollution the abundance of nitrophytic lichen species increases (van Dobben and ter Braak, 1999; van Herk, 2001; Gadsdon et al., 2010). In addition to the direct effects on lichen physiology, pollutants can affect epiphytic lichens also indirectly through the changes in substrate qualities, foremost in bark acidity, leading to the altering species composition (Wirth, 1995; van Herk, 2001; van Haluwyn and van Herk, 2002; Nash, 2008).

As atmospheric pollutant concentrations in Europe have changed, the focus in lichenological studies has shifted from SO_2 pollution (e.g. Gilbert, 1970; Hawksworth and Rose, 1970; Trass, 1973; Türk and Wirth, 1975) to NH_3 and NO_x (e.g. van Herk, 1999; van Herk et al., 2003; Wolseley et al., 2006; Davies et al., 2007; Frati et al., 2007; Larsen et al., 2007); a review on this subject has been provided by Purvis (2010). The effects of alkaline dust pollution on lichen biota have been comparatively less studied. Still, existing studies have demonstrated that alkaline dust from limestone quarries and cement industries can affect lichen physiology, element content and species composition (Gilbert, 1976; Zaharopoulou et al., 1993; Loppi and Pirintsos, 2000; Branquinho et al., 2008). Because of the high traffic contribution to dust pollution in many European cities (Querol et al., 2004; Hak et al., 2010) and severe health risks related to road dust (Nel, 2005; Pope and Dockery, 2006; WHO, 2006; Orru et al., 2009), information about most suitable lichen species and their phorophyte species for bioindication of traffic pollution and road dust is necessary. Another topic that certainly requires further research in connection with air pollution is the vertical distribution of lichens on trees. It is known that lichen species richness and composition change vertically in tree canopies (e.g. McCune et al., 2000; Campbell and Coxson, 2001; Ellyson and Sillett, 2003; Fritz, 2009), whereas the effects of air pollution on the vertical gradient of lichens have not been studied so far.

Besides air pollution a significant anthropogenic impact on epiphytic lichens is caused by forest management. It is known that epiphytic lichens are responsive to forest history and continuity (e.g. Tibell, 1992; Josefsson et al., 2005; Ellis and Coppins, 2009; Fritz et al., 2008). Lichen diversity is clearly higher in old-growth forests compared to young managed forests (Kuusinen and Siitonen, 1998; Nascimbene et al., 2010). Restricted dispersal ability is one important factor explaining species scarcity in younger stands (Sillett et al., 2000; Hilmo and Såstad, 2001). Tree age is also affecting epiphytic lichen communities. Several species prefer to grow on older trees, the fact which can be caused by changing bark qualities, increasing tree size and longer time available for colonisation (Nascimbene et al., 2008; Ranius et al., 2008; Fritz et al., 2009). In addition, forest management directly affects the availability of different phorophyte species and woody substrates. Lichen diversity in forest stands is increasing with increasing availability of different microhabitats (Gignac and Dale, 2005; McMullin et al., 2010). Many species are related to old-forest specific substrates, like snags and logs (Ohlson et al., 1997; Lõhmus and Lõhmus, 2008). Lichen species that prefer to grow in old-growth forests have been used as indicators of woodland key habitats (WKHs), forest stands that are likely to harbor endangered species (Timonen et al., 2010). The importance of old forests and old trees on epiphytic lichen diversity has been emphasized in several studies, but the relative effect of these and other factors limiting the occurrence of old-forest lichen species needs further research. In addition, the large-scale differences in lichen diversity and the importance of geographical location and scale on the indicative value of species are rather poorly studied.

As lichens respond to different habitat qualities, it is often difficult to distinguish between the effects of various variables on lichen biota. However, prior knowledge about the major factors affecting the occurrence of lichen species is necessary for distinguishing most suitable species for bioindication of environmental qualities. Moreover, the information about factors affecting endangered species can be used in species conservation. The objective of present study is to contribute to the knowledge about the ecology and bio-indicative value of epiphytic lichens, focusing on species growing on coniferous trees. The study aims to answer to the following main questions,

- In relation to air pollution: (1) how does traffic pollution affect bark pH and epiphytic lichen communities on tree species with different natural bark acidity? (2) which are the most suitable indicator lichens of road dust in Estonia? (3) does the proportion of dust indicators change vertically in coniferous forest canopies?
- In relation to old forests: (1) are forest continuity and tree age affecting epiphytic lichen diversity in Estonian coniferous forests? (2) which are the most suitable indicator lichens of old coniferous forests in Estonia? (3) are there any distinct differences in lichen species composition between Estonian and Fennoscandian old coniferous forests?

2. MATERIALS AND METHODS

2.1. Study area

Most of the studies were conducted in Estonia, but some sample plots were located also in Finland, Sweden and Norway (Fig. 1). The monthly mean temperature in Estonia varies from –5°C to +17°C (annual mean ca 5°C), southern and western winds prevail (EMHI). The mean temperature is decreasing northwards; the 0°C annual 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). The vegetation zone in the study area 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 and Masing, 1995). Conifers *Pinus sylvestris* L. and *Picea abies* (L.) H. Karst. are dominating tree species in whole study area, *Betula pendula* Roth being the most abundant deciduous tree species. 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).

Air pollution is a problem in Estonia mainly in bigger cities and in north-eastern part of the country. Industrial air pollution has decreased in Estonia during the last decades, contributing to a significant reduction in SO_2 pollution. However, a large part of many pollutants, including 56% of solid particles, emitted into the air from stationary sources in Estonia are still produced in Ida-Viru county in north-eastern corner of the country, an area with most industrial activity in Estonia (Statistics Estonia). The major part of electricity production of the country is based on burning of oil shale, emitting alkaline particulate matter (oil shale ash; caused by the carbonate content in local oil shale), SO_2, NO_X, CO_2, CO, HCl, heavy metals etc.; the two main power plants are located in north-eastern Estonia. In Tallinn, the capital city of Estonia with a registered population ca 400 000, air quality is mainly influenced by road traffic. The measured concentrations of several pollutants, including particulate matter (PM_{10}) and NO_2 are highest during working days, especially the rush hours (EERC, 2010). Fine dust particles are the most problematic pollutants in Tallinn as the PM_{10} level in the city centre occasionally exceeds the 24h limit value 50 µg/m^3 (48 occasions in 2007, 35 in 2008, 10 in 2009, 9 in 2010; EEIC). Traffic flow causes air turbulences that resuspend road and soil dust near the roadways. Traffic is also a direct source of dust through fuel burning, tire and break wear and road abrasion.

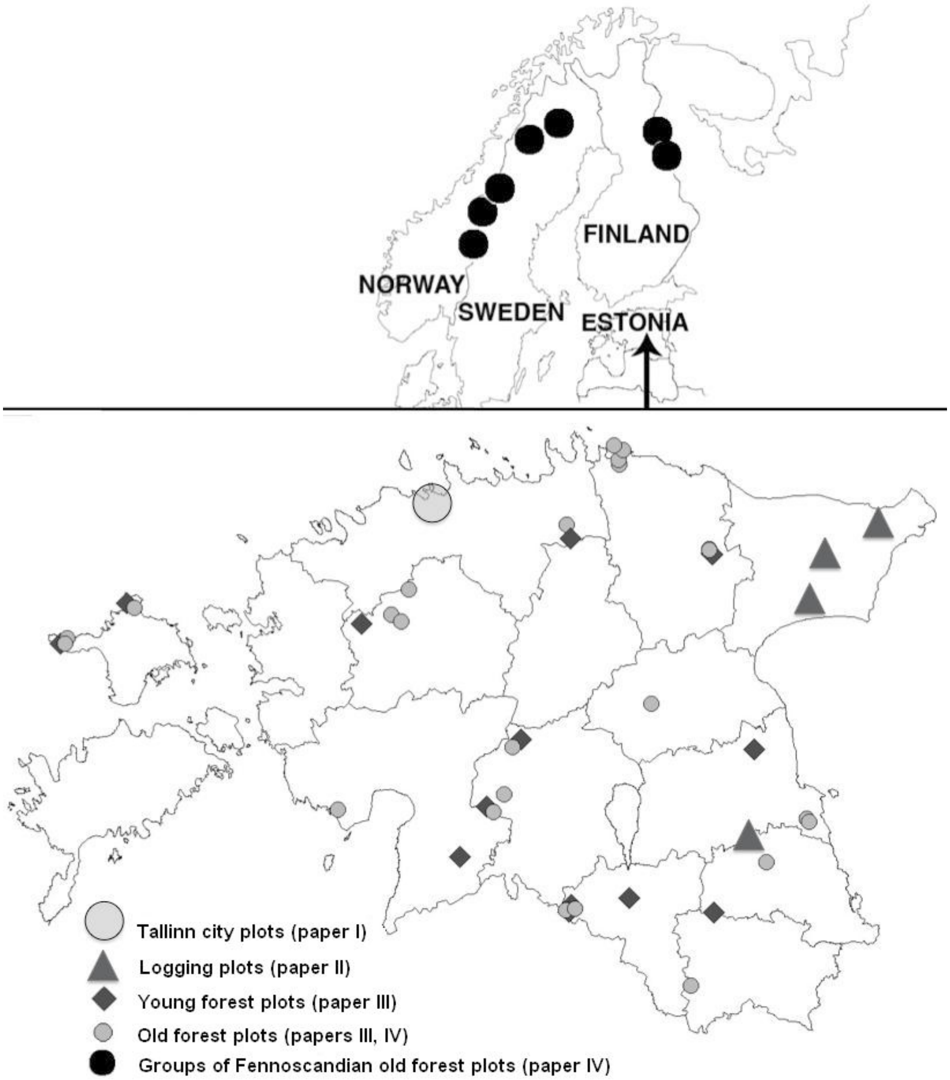

Figure 1. Study area and location of sample plots (paper I in Tallinn; paper II mainly in north-eastern Estonia; papers III and IV in different parts of Estonia; additional sample plots for paper IV in Fennoscandia).

2.2. Field methods

Fieldwork for **paper I** was carried out in Tallinn, for **papers II, III and IV** in different forest sites in Estonia, and for **paper IV** additionally in the forests in Finland, Sweden and Norway (Fig. 1). *Pinus sylvestris* L. (hereafter pine) and *Picea abies* (L.) H. Karst. (hereafter spruce) were chosen as main phorophyte species for the study. In addition, lichens growing on *Tilia cordata* Mill.

(hereafter lime), that is among the most common deciduous tree species in Estonian cities, were studied in Tallinn. Every studied sample plot comprised five trees of the same species. The sample plots for **paper I**, dealing with the effects of traffic pollution on epiphytic lichens, were situated in city parks and nature reserves of Tallinn. Altogether 39 pine and 18 lime sample plots were studied in the city. Distance from the nearest road was measured for every tree. Distance from the road of every sample plot was calculated as the arithmetic mean of five trees. Presence or absence of 60 selected lichen species (list in **paper I**), including very common species and species with predicted indicative value, was recorded on tree trunks at a height of 0.5–2 m. For bark pH measurements two bark pieces were collected from every tree at a height of 1.5 m from opposite sides of trunk. Bark pH measurements for **papers I and II** were done in the laboratory using a flathead pH meter. To allow rapid solution of hydrogen ions 0.5 ml of 0.1 M KCl was placed on the bark one minute before measuring the pH as previously employed in lichenological studies (Farmer et al., 1990; Kricke, 2002; Schmidt et al., 2001). Calculations of mean bark pH were based on mean hydrogen ion concentrations.

Studies for **paper II**, dealing with the effects of dust pollution on the vertical gradient of lichens in tree canopies, comprised four sample plots. Three sample plots were located in north-eastern Estonia in the area with highest alkaline dust pollution in Estonia, at different distances from oil shale power plants. The fourth plot was located in southern Estonia, in a relatively unpolluted area. Five spruce and five pine trees were cut down for the study in every sample plot, i.e. altogether 40 trees. For studying the vertical gradient of lichens all trees were divided into height ranges, first range extending from the ground up to 2 m (the height reachable without additional equipment or logging) and all next ranges being 4 m long. The treetops which were ≤2 m long were included into the previous height range, and treetops which were >2 m long into the next height range. Presence or absence of all macrolichen species on tree trunk and branches was recorded separately for every height range. Ten recorded lichen species were regarded as dust indicators for spruce and pine (list in **paper II**); the division was carried out according to the preferred bark acidity and tree species of lichen species, based on **paper I** and literature data (Smith et al., 2009; van Herk, 2001; Wirth, 1995). Two bark pieces were collected from every height range for pH measurements.

Studies for **paper III** comprised 33 spruce and 33 pine sample plots. In most cases spruce and pine sample plots were located in the same forest stand. Twenty-one plots of both tree species were located in old and 12 plots in young forests. Sample plots were divided into two groups according to the forest continuity which was studied using the historical maps from 17th century and from the end of 19th/beginning of 20th century. All old forest sample plots, except for island Hiiumaa (oldest maps unavailable), were located in areas which have been marked as forest on both historical maps, and thus have been forest land already at least 350 years. Most old forest sample plots were located in nature protection areas or WKHs and were surrounded by differently aged managed stands. Young forest sample plots were located in forest stands which have been marked as arable field or grassland on ca 100 year old maps; these were first-generation forests that have colonised above habitats after their abandonment. All studied trees were selected randomly within 50 m radius from plot centre; only trees with >50 cm circumference were included. Presence of all lichen species growing on selected trees on the first two meters from the ground was recorded separately for tree trunk and branches. 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 trees was determined with an increment borer; core samples were taken at the height of 1.3 m.

All sample plots for **paper IV** were located in old forests: Estonian plots in above-named old forests with long continuity, and Fennoscandian plots in large old forests (over 500 km^2; Greenpeace, 2006), many of them close to or in nature protection areas. 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. The random selection of trees, recording of lichen species, and measuring of tree age were done as described in previous paragraph. 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 1 m in every four cardinal direction, with back towards the tree. Mean canopy openness was calculated for every tree and sample plot.

2.3. Statistical analyses

Software applications R, STATISTICA 7 and PC-ORD 5 were used for the statistical analyses. Data were analysed separately according to the tree species. Most analyses were carried out in the sample plot level. Spearman's rank correlation coefficient was used for describing the relationships between (1) distance from the road, bark pH and lichen species richness in Tallinn (**paper I**), (2) height in the canopy, bark pH, lichen species richness and proportion of dust indicators in north-eastern Estonia **(paper II)**, and (3) max tree age, mean canopy openness and lichen species richness in old forests, separately for Estonian and Fennoscandian sample plots (paper IV). Pearson's correlation coefficient was used in tree level analyses for finding the correlations between lichen species richness on tree trunk and tree age in Estonian forests (**paper III**). Logistic regression was used in tree level analyses for describing the presence of lichen species on tree trunk in relation to (1) bark pH (**paper I**), and (2) tree age (**paper III**). Kruskal-Wallis test was carried out for comparing lichen species richness on tree trunks between young and old forest sample plots (**paper III**). T-test was used for comparing species richness on tree trunks between Estonian and Fennoscandian sample plots (**paper IV**). Analysis of variance (ANOVA, type III) was used for estimating the effects of sample plot (distance from the dust pollution source) and height in the canopy on lichen species richness (**paper II**). Analysis of covariance (ANCOVA, type III) was used for estimating (1) the effects of sample plot and height in the canopy on bark pH (**paper II**), and (2) the effects of forest continuity and tree age on lichen species richness and species composition (**paper III**). Principal component analysis (PCA; **paper III**) and detrended correspondence analysis (DCA; **paper IV**) were used for describing species composition in the sample plots; analyses were based on covariance of species (presence/absence in the sample plots). PCA Factor 1 coordinates of sample plots were used as measures of species composition in ANCOVA for analysing the effect of forest continuity on lichen species composition (**paper III**).

3. RESULTS

3.1. Effects of air pollution and bark pH on lichens (papers I, II)

The correlations between distance from the nearest road, bark pH and epiphytic lichen composition were studied in Tallinn (**paper I**). The mean bark pH in the sample plots varied between 3.0–5.3 in pines, and between 4.1–5.5 in limes. Distance of the nearest road affected mean bark pH in case of pines, its values being significantly higher near the roads (R_s = –0.59; n = 39; p < 0.0001). In case of limes the correlation was insignificant (R_s = –0.31; n = 18; p = 0.21). An opposite effect of distance of the nearest road on lichen species richness was found between the sample plots of different tree species. Number of lichen species on pines was significantly higher near the roads, whereas species richness on limes was significantly lower (Figs 2, 3).

Altogether 45 lichen species were recorded on the studied pines and 42 species on limes in Tallinn. According to the results of logistic regression analyses, 11 species (e.g. *Lecanora hagenii*, *Phaeophyscia orbicularis*, *Rinodina pyrina*, *Xanthoria parietina*) preferred higher bark pH on pines, and 4 species (*Lecanora carpinea*, *Physcia stellaris*, *Ramalina fraxinea*, and *Xanthoria parietina*) on limes. Another 11 species (e.g. *Bryoria fuscescens*, *Parmeliopsis ambigua*, *Platismatia glauca*, and *Usnea hirta*) preferred lower bark pH on pines, and only one taxon (*Lepraria* spp.) was found to prefer lower pH on limes. Number of lichen species that preferred higher bark pH increased significantly near the roads in case of pines (R_s = –0.55; n = 39; p = 0.0003; Fig. 4); there was no such correlation in case of limes (R_s = 0.10; n = 18; p = 0.68).

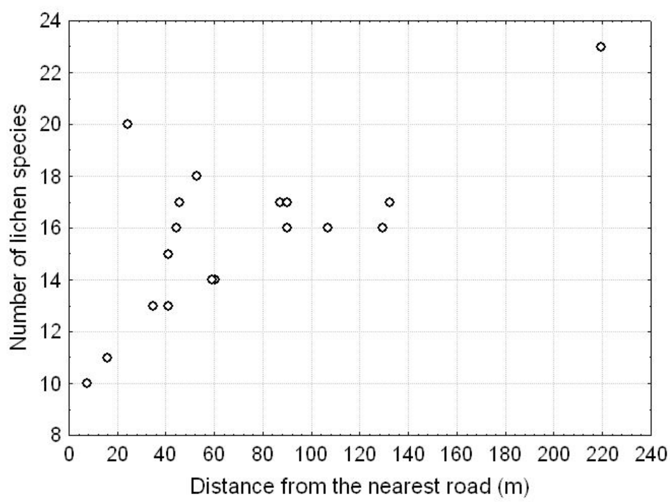

Figure 2. Correlation between distance of the nearest road and number of recorded lichen species in *T. cordata* sample plots in Tallinn (R_s = 0.54; n = 18; p = 0.021).

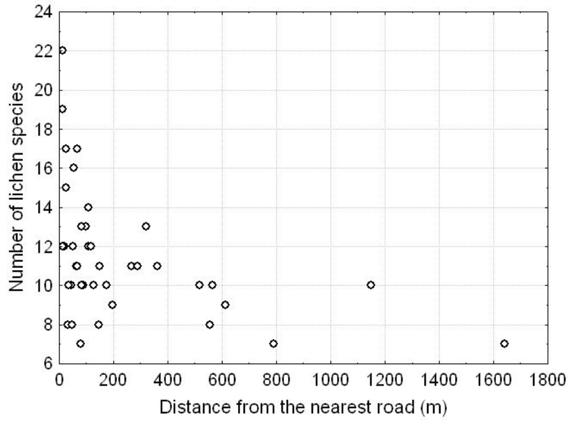

Figure 3. Correlation between distance of the nearest road and number of recorded lichen species in *P. sylvestris* sample plots in Tallinn ($R_s = –0.50$; $n = 39$; $p = 0.0013$).

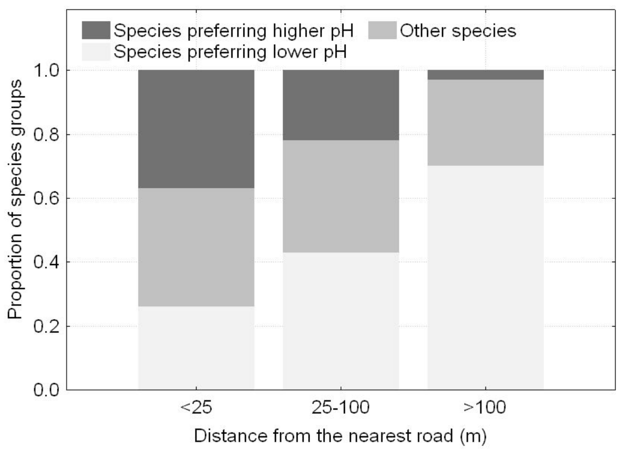

Figure 4. Proportion of lichen species groups with different bark pH preferences in *P. sylvestris* sample plots in Tallinn in different distances from the nearest road.

The impact of alkaline dust pollution on bark pH and epiphytic macrolichens in forest canopies was studied in north-eastern Estonia, in different distances from oil shale power plants. According to the results of ANCOVA and ANOVA, bark pH and lichen species richness depended on both sample plot (distance from the pollution source) and height in the canopy (results in **paper II**). Spearman's rank correlation analysis verified that pH values increased with height in all four sample plots in case of pines, and in three sample plots in case of spruces (results in **paper II**). Mean bark pH in the highest height range varied between 3.6–4.9 on spruces, and between 3.7–4.4 on pines, whereas the highest values were recorded in the sample plot located closest to the oil shale power plants (Narva).

The total number of recorded lichen species was highest in the presumably least polluted sample plot (Kiidjärve) and lowest in the most polluted plot (Narva) in both tree species (Table 1). Number of lichen species increased significantly with height in the canopy in the most polluted plots, Narva (R_s = 0.71, $p < 0.001$ in spruces; R_s = 0.55, $p < 0.001$ in pines) and Ahtme (R_s = 0.72, $p < 0.001$ in spruces; R_s = 0.67, $p < 0.001$ in pines). In Kiidjärve, a statistically significant correlation between the number of lichen species and height in the canopy was found only in case of spruces (R_s = 0.53, $p < 0.001$); there was no significant correlation in Iisaku. Only one species regarded as a dust indicator in present study, *Physcia tenella*, was recorded in all four sample plots. Most dust indicators, e.g. *Phaeophyscia orbicularis*, *Physcia dubia*, *P. stellaris*, and *Xanthoria parietina*, were found only in Narva or Ahtme, whereas the number of indicator species was highest in Narva (7 on spruces, 5 on pines). The proportion of dust indicators increased with height from 0.0 in the lowest height range (first two meters near the ground) to 0.8 in the ultimate height range in both tree species in Narva. There were no dust indicators growing in the lowest height range in any of the sample plots (Table 1).

Table 1. Number of macrolichen species and proportion of dust indicators in the sample plots at different distances from alkaline pollution sources (Kiidjärve farthest → Narva closest)

	Number of lichen species in the lowest height range/total number of lichen species		Proportion of dust indicators in the lowest/highest height range	
Sample plot	*P. abies*	*P. sylvestris*	*P. abies*	*P. sylvestris*
Kiidjärve	8/28	11/23	0/0,1	0/0
Iisaku	11/25	10/18	0/0,1	0/0
Ahtme	2/23	3/17	0/0,3	0/0,1
Narva	2/20	4/15	0/0,8	0/0,8

3.2. Effects of forest continuity and tree age on lichens (paper III)

The effects of forest continuity and tree age on lichen biota in Estonian coniferous forests were studied. As the young first-generation forests had established only within the 20th century, the mean and maximum age of trees were higher in old forests with long continuity. The mean age of spruces was 56 in young and 123 in old forests, the mean age of pines was 63 in young and 167 in old forests; the max age of trees in young forests was 93 in spruce and 106 in pine sample plots. Altogether, 72 lichen species were recorded on spruce and pine in young forests, and 93 species in old forests in this study. Results of Kruskal-Wallis test verified that the number of lichen species on tree trunks was significantly higher in old forest sample plots in case of both spruces (KW-H = 10.64; p = 0.001) and pines (KW-H = 6.39; p = 0.012). Lichen species composition in the sample plots (PCA Factor 1 coordinates) was affected by both forest age and max tree age (results of ANCOVA in **paper III**). Altogether 31 lichen species were found only in old forests, including all seven red listed and protected species and seven out of eight recorded WKH indicator species. Several species could be associated with old forests as they were comparatively frequent in old forest sample plots and were not found in young forests; among them, *Arthonia leucopellaea* and *Lecanactis abietina* were found in at least every second old spruce or pine forest.

The effect of tree age on the number of epiphytic lichen species was analysed separately in young and old forest sample plots. According to the results of Pearson's correlation analysis lichen species richness on tree trunks increased with increasing tree age in young and old spruce forests (Fig. 5), and in young pine forests (r = 0.31; n = 60; p = 0.015). Logistic regression was used for analysing the effect of tree age on the presence of lichen species growing on tree trunks in old forests; the results indicated that ten species (e.g. *Arthonia leucopellaea*, *Calicium viride*, *Chrysothrix chlorina*, *Cladonia cenotea*, and *Lecanactis abietina*) preferred to grow on older trees in case of spruces, and five species (*Chaenotheca stemonea*, *Cladonia ochrochlora*, *Hypocenomyce friesii*, *H. scalaris*, and *Lepraria incana*) in case of pines.

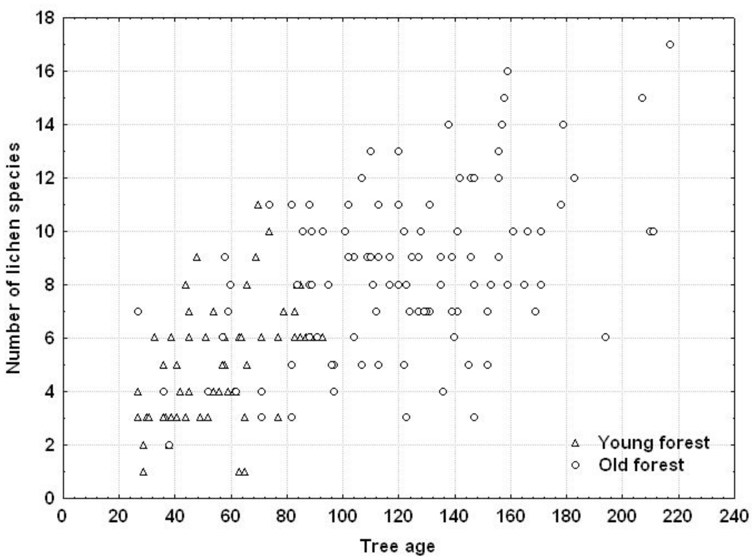

Figure 5. Correlations between tree age and number of lichen species on tree trunks in young (r = 0.50; n = 60; p = 0.00004) and old (r = 0.47; n = 104; p < 0.00001) *P. abies* forests in Estonia.

3.3. Geographical differences in lichen communities (paper IV)

The differences in epiphytic lichen communities between Estonian and Fennoscandian old coniferous forests were studied. Tree age and canopy openness were measured for describing habitat conditions. Altogether, 151 lichen species were recorded in the study. Some taxa were very frequent in both regions; but the occurrence and frequency of many species differed between Estonia and Fennoscandia. Sixty lichen species were found only in Fennoscandia, six of them have never been found in Estonia; thirty species were recorded only in Estonia in this study (species list in **paper IV**). The occurrence of nearly all recorded WKH indicator species (Nitare, 2000; RTL, 2009; Stenroos et al., 2011) differed between Estonian and Fennoscandian sample plots. Rather many indicator species were recorded only in one or two plots. *Arthonia leucopellaea* and *Lecanactis abietina* were most frequent indicators in Estonia and not found in studied Fennoscandian sample plots; several indicator species, *Alectoria sarmentosa*, *Bryoria fremontii*, *B. furcellata*, *Chaenotheca subroscida*, *Hypogymnia bitteri* and *Sclerophora coniophaea*, were quite frequent in Fennoscandian old forests and not recorded in Estonia (among them only *C. subroscida* and *S. coniophaea* are regarded as WKH indicators in Estonia).

The results of DCA verified the strong differences in lichen species composition between Estonia and Fennoscandia in case of both spruces (Fig. 6) and pines. In addition to species composition, species richness also differed between Estonian and Fennoscandian sample plots, its mean values being significantly higher in Fennoscandia (Fig. 7). Max tree age in the sample plots had a significant positive effect on lichen species richness on tree trunks only in Estonian spruces ($R_s = 0.64$; $n = 21$; $p = 0.002$), and mean canopy openness in Estonian pines ($R_s = 0.53$; $n = 21$; $p = 0.013$). The mean age of sampled spruces was higher in Fennoscandia compared to Estonia, whereas the mean age of pines was higher in Estonia; the mean percentage of canopy openness by the sampled trees was higher in Fennoscandia in both tree species (mean values in **paper IV**).

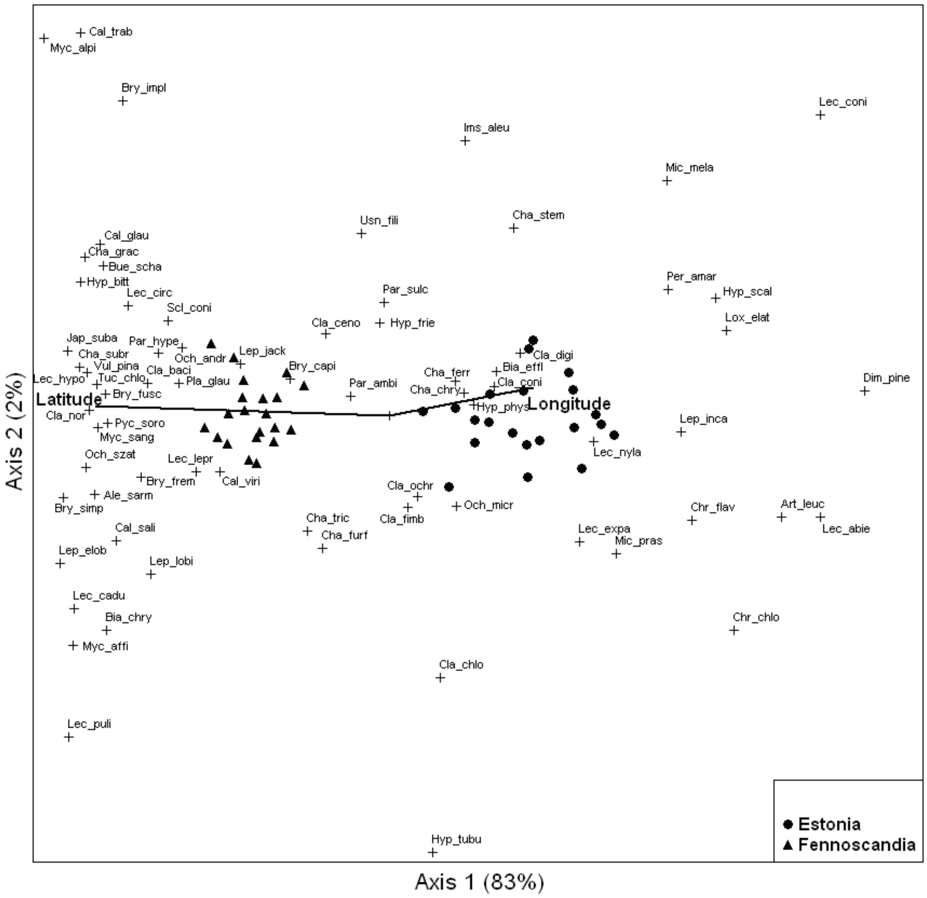

Figure 6. Fennoscandian and Estonian *P. abies* sample plots on DCA joint-plot (only lichens growing on tree trunks have been included in the analysis).

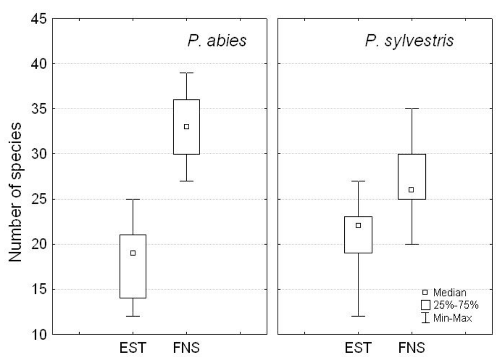

Figure 7. Number of lichen species on tree trunks in *P. abies* ($t = -13.6$; $n = 42$; $p < 0.0001$) and *P. sylvestris* ($t = -5.0$; $n = 40$; $p < 0.0001$) sample plots in Estonian (EST) and Fennoscandian (FNS) old forests.

4. DISCUSSION

4.1. Effects of air pollution on epiphytic lichen communities

Previous studies have confirmed that the combined effect of different drivers, like air pollution, forest management and climate, is affecting epiphytic lichen communities (Ellis and Coppins, 2010; Giordani, 2006). Poor air quality has a predominant effect on epiphytic lichen diversity in urban and industrial areas (Giordani, 2007). Clear alterations in lichen communities in case of traffic and industrial dust pollution were found in present study; in both cases lichen species composition proved to be a good indicator of air pollution. In Tallinn, the number of lichen species that preferred higher bark pH increased significantly near the roads on pines. In coniferous forests in north-eastern Estonia, where the vertical distribution of lichens was studied, the proportion of dust indicators was evidently highest in the treetops, which can be associated with the highest direct impact of dust deposition from the atmosphere. The effect of dust pollution on epiphytic lichen biota can be at least partially explained by the changes in bark acidity. Dust increases bark pH, which is confirmed by a significant correlation between pH level and distance from the pollution source – distance from the nearest road in **paper I**, and distance from oil shale power plants in **paper II**. As the pH preferences vary between lichen species (e.g. Wirth, 1995), the changes in bark acidity bring about clear changes in epiphytic lichen communities. There are rather few previous studies concerning the effects of dust pollution on lichen species composition (e.g. Gilbert, 1976; Loppi and Printsos, 2000; Martin and Martin, 2000), whereas the effects of nitrogen pollution have been quite well studied in Europe (e.g. van Dobben and ter Braak, 1999; Davies et al., 2007; Sparrius, 2007; Gadsdon et al., 2010). In Tallinn, other pollutants, like nitrogen oxides, are also likely to affect lichens besides fine dust particles. Several species that are regarded as dust indicators in present study are also known to be favored by increased nitrogen levels (Hauck, 2010). However, the changes in lichen composition and bark acidity of roadside trees indicate the predominant effect of dust pollution on lichen communities near the roads in Tallinn. Altered lichen species composition on roadside trees has been related to particle pollution also by Madl et al. (2010). The suitability of different phorophyte species for dust pollution bioindication has not been compared previously.

Although as a rule lichen diversity decreases in polluted areas due to the decrease of more sensitive species (Hawksworth and Rose, 1970), correlations between species richness and pollution level are not straightforward in all cases because of the addition of species facilitated by pollution. An opposite effect of distance of the nearest road on lichen species richness was found between the sample plots of different tree species in Tallinn (**paper I**). Number of recorded lichen species on pines was significantly higher near the roads, whereas species richness on limes was significantly lower (Figs 2, 3). This can be explained by the naturally different bark qualities of these two tree species. Lime bark is already naturally subneutral, whereas the originally acid pine bark was modified to subneutral near the roadways. In case of pines the decreasing number of acidophilic lichen species near the roads was compensated by the addition of neutro/nitrophilic species that usually do not grow on this phorophyte, leading to the increase in species richness. For example, *Candelariella xanthostigma*, *Phaeophyscia orbicularis*, *Physcia dubia*, *P. tenella*, *Xanthoria parietina* and *X. polycarpa*, were found on pine trunks near the major roads in Tallinn, and their presence on this phorophyte can be regarded as a good indicator of traffic pollution and road dust. The proportion of species with different pH requirements on pines seems to be a useful illustrative method for demonstrating dust pollution levels (Fig. 4). Similarly Gadsdon et al. (2010) have recommended using the proportion of nitrophilic species in lichen community for estimating nitrogen pollution, concluding that the total number of lichen species is not a suitable measure of air pollution in case some species are facilitated by higher pollution levels.

Results in **paper II** indicate that in relatively dense coniferous forests lichens growing in upper canopy are more affected by alkaline dust depositions from atmosphere compared to lichens growing in lower canopy. Vertical changes in lichen diversity and abundance of species have been reported already previously (e.g. McCune et al., 2000; Campbell and Coxson, 2001; Ellyson and Sillett, 2003; Fritz, 2009), but not in relation to dust pollution. According to our results not only the number of lichen species but also the proportion of dust indicators change vertically in spruce and pine canopies. The number of lichen species increased with height in the canopy in most sample plots, which can be explained by vertically improving light conditions and increasing abundance of different substrata, like branches and deadwood (Sillet and Antoine, 2004). Bark pH of studied trees was highest in the treetops in the most polluted sample plot (both spruce and pine have naturally acidic bark). The addition of species that were facilitated by dust pollution, e.g. *Physcia dubia*, *Xanthoria parietina*, *X. polycarpa*, certainly added to the higher species richness in upper canopy in polluted sample plots. There were no dust indicators in the lowest height range in any of the sample plots. In the highest height range in the most polluted sample plot the proportion of indicator species was 0.8 (Table 1), proving that treetop lichens are informative indicators of dust pollution in relatively dense forests where less pollution will reach lower canopy. For practical reasons, planned logging sites could be used for biomonitoring of air pollution in forest landscapes. Few neutro/nitrophilic species (*Physcia adscendens*, *P. tenella*) were found in upper canopy also in the presumably unpolluted sample plot. Previously, an unusual lichen composition with the dominance of *Melanohalea exasperatula* has been recorded in the spruce tops in an unpolluted area in Norway (Kermit and Gauslaa, 2001). Such peculiarities might be related to natural origin dust particles in the air or long-distance air pollution. Nutrients delivered by birds may also favor the presence of nitrophilic species in some treetops (McCune et al., 2000).

4.2. Effects of habitat continuity and other factors on lichens in coniferous forests

In relatively unpolluted areas the effects of other variables than air pollution on lichen biota become prevailing. The negative effects of forest management on lichen diversity have been emphasized in several studies (e.g. Dettki and Esseen, 1998, 2003; Kuusinen, 1996; Kuusinen and Siitonen, 1998; Nascimbene et al., 2010). According to our results (in **paper III**) forest continuity is a major factor affecting epiphytic lichens in Estonian coniferous forests. The occurrence of many species differed between first-generation forests and forests with long historical continuity, resulting in significantly higher species richness in old forests. Although both forest groups contained unmanaged stands and the oldest trees in young forests reached ca 100 years, all red-listed and protected lichen species, and almost all WKH indicator species were exclusively found in old forests. This clearly indicates the importance of old forests for high lichen diversity in landscape level, and the need to preserve forest stands with high species richness and presence of endangered species. In only few previous studies forest history and continuity data have been used for explaining lichen diversity and presence of species with conservation value (Josefsson et al., 2005; Fritz et al., 2008). Ellis and Coppins (2007) showed that species richness in aspen stands is better explained by historic woodland structure compared to the present one, demonstrating the strong effect of forest history on lichen biota. In addition, the occurrence probability of several epiphytic lichen species is found to increase with increasing tree age (Rolstad et al., 2001; Nascimbene et al., 2008; Ranius et al., 2008; Fritz et al., 2009). In the present study a positive effect of increasing tree age on lichen species richness was detected in young and old spruce forests (Fig. 5) and in young pine forests. Higher lichen diversity on older spruces has been recorded also previously (Lie et al., 2009; Nascimbene et al., 2009).

The limited dispersal ability of many species can be regarded as one important reason explaining the varying diversity of epiphytic lichens and presence of rare species between forest stands. It has been proven experimentally that some lichen species which are restricted to old-growth forests, like *Lobaria oregana* and *L. scrobiculata*, are capable of establishing and growing also in young forests, demonstrating that dispersal difficulties may explain the lack of these species in younger stands (Sillett et al., 2000; Hilmo and Såstad, 2001; Hilmo, 2002). The patchy distribution of *Lobaria pulmonaria* also suggests colonization from nearby sources (Kalwij et al., 2005). The sparseness of many old-forest lichens is presumably not only due to the low historical continuity of many forests but also due to the low connectivity of suitable old forests at the landscape scale, both aspects being associated with forest management and land-use changes. The negative effects of fragmentation on lichen populations have been demonstrated in case of *Lobaria pulmonaria* (Gu et al., 2001; Öckinger and Nilsson, 2010). Hedenås and Ericson (2008) have stated that the predictions of species occurrences at the stand level have to take into account the amount of suitable habitats at the landscape scale.

When Estonian coniferous forests were compared with Fennoscandian ones, great differences in epiphytic lichen communities were revealed (Fig. 6). The reasons behind the significant differences in lichen species richness (Fig. 7) between the two areas remain unclear. It can be hypothesized that the relatively small size of old-growth forest stands may have led to the sparseness of more sensitive old-forest lichen species in Estonian coniferous forests. Of course, climatic gradients can be regarded as a major factor affecting the distribution of lichen species in large-scale studies. The impact of climate on lichen species composition has been found previously in several studies (e.g. Halonen et al., 1991; Werth et al., 2005; Giordani, 2006; Ellis and Coppins, 2010). Many lichen species that were absent in Estonian sample plots were rather frequent in Fennoscandia, whereas some species were more frequent in Estonia. Rather many WKH indicator species were infrequent on sampled trees in whole study area; the relatively frequent indicators differed between Estonia and Fennoscandia (species list in **paper IV**). The differences in the occurrence and frequency of many species, including WKH indicators, between the studied areas 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 lichen species are not equally suitable as ecological indicators across wide geographical scale. In some cases the indicative value of species may vary significantly between regions. For example, some lichens (e.g. *Bryoria capillaris*, *Chaenotheca chrysocephala*, *Cladonia cenotea*) that are used as indicators of native pinewoods in UK (Coppins and Coppins, 2002) are quite frequent in Estonia even in young forests (**paper III**). Considering that easily applicable indicator species should be rather frequent in the habitats that meet their requirements, *Arthonia leucopellaea* and *Lecanactis abietina* are recommended as best indicator lichens of old coniferous forests in Estonia. These species tend to be rather abundant in suitable forest stands in Estonia and are easily identifiable in the field. Another taxon, *Chrysothrix* spp., is also relatively frequent in Estonian old forests and lacking in young ones (**paper III**), and could be used as an old forest indicator at the genus level as the identification of *Chrysothrix* species may be difficult in the field.

Finally, it should be taken into account that other factors, like unsuitable microclimate and lack of suitable microhabitats, may limit the presence of lichen species in forest stands. Transplantation experiments have proven the contrasting response of selected lichen species to the increased light availability in forest edges (Stevenson and Coxson, 2008; Jansson et al., 2009), which can be associated with varying light and humidity preferences between species. According to Gauslaa et al. (2007) poor light conditions may cause the absence of some lichen species in dense spruce stands. In present study the effect of canopy openness on epiphytic lichen biota on tree trunks was revealed in Estonian pine sample plots (on the studied first meters near the ground; **paper IV**). Microclimate conditions vary significantly between forest types and may affect the distribution of species in forest stands. Whereas air pollution studies are often carried out in city parks and alleys where microclimate tends to be less varying and light availability is usually rather high. It can be concluded that various environmental factors affect the distribution of epiphytic lichens. Our results highlight the importance of human-induced changes in lichen communities. The effects of air pollution are prevailing in the cities and industrial regions, while habitat continuity is one of the major factors affecting lichens in the forests.

CONCLUSIONS

1. Particulate matter pollution from road traffic is a problem in many cities, but there are very few studies dealing with the effects of road dust on epiphytic lichen communities and no previous studies comparing the suitability of different phorophyte species for dust pollution bioindication. In Tallinn, the alterations in lichen species composition on roadside trees proved to be more evident in case of pines compared to lime trees. The normal acidophilic lichen biota on pines was replaced with neutro/nitrophilic species near the roads. Bark pH of pines increased significantly with decreasing distance from the roads, evidently due to road dust. The presence of lichen species that prefer higher bark pH on pines can be recommended as a good indicator of dust pollution. Several such indicator species, e.g. *Phaeophyscia orbicularis*, *Physcia dubia*, *Xanthoria parietina*, have been proposed in present study.
2. It is known that lichen communities change vertically in tree canopies, but so far these changes have not been studied in relation to air pollution. Present results revealed a strong impact of alkaline dust pollution on canopy lichens near the oil shale power plants in north-eastern Estonia. The vertical changes in lichen communities on spruce and pine demonstrate that lichens growing in upper canopy are much more affected by dust depositions from atmosphere compared to lower canopy lichens in relatively dense coniferous forests. In polluted forests the proportion of dust indicator species was clearly highest in the treetops, whereas there were no dust indicators in the lowest height range. The results indicate that treetop lichens, recorded for example in logging sites, could be used as air pollution indicators in forest landscapes.
3. The importance of old forests and old trees on epiphytic lichen diversity has been emphasized in several studies, but there are rather few studies were forest history and continuity data have been used for explaining the differences in lichen species richness between forest stands. According to present results forest continuity has a strong effect on lichen diversity in Estonian coniferous forests. The number of lichen species was higher in old forests with long continuity compared to first-generation forests. Several lichen species, including protected and red listed species, were associated with old forests, demonstrating the high conservational value of old forests. Few relatively frequent old-forest species, *Arthonia leucopellaea* and *Lecanactis abietina*, have been recommended as best indicator lichens of old coniferous forests in Estonia.
4. When Estonian old coniferous forests were compared with Fennoscandian ones, clear differences in epiphytic lichen diversity were revealed. The occurrence of many lichen species, including majority of recorded WKH indicator species, differed between Estonian and Fennoscandian sample plots. The results confirm that the local context has to be taken into account when choosing indicator lichens of valuable forest habitats.

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SUMMARY IN ESTONIAN

Epifüütsete samblike ökoloogia ja bioindikatsiooniline väärtus seoses õhusaaste ja metsa järjepidevusega

Samblikud kui kahest osapoolest koosnevad sümbiootilised organismid on tundlikud kasvukeskkonna erinevatele omadustele ning seetõttu kasutusel bioindikaatoritena. Linnades ja tööstuspiirkondades kasutatakse samblikke õhusaaste hindamiseks, metsamaastikel looduskaitseliselt väärtuslike vanade metsaeraldiste eristamiseks. Kuna samblikuliikide tundlikkus erinevatele keskkonnateguritele varieerub, võivad keskkonnatingimuste muutumisega kaasneda muutused nii samblike liigirikkuses kui liigilises koosseisus. Õhu kehv kvaliteet on peamiseks samblike liigirikkust piiravaks teguriks saastatud piirkondades. Kuigi õhusaaste ja samblike vahelisi seoseid on uuritud juba aastakümneid, on saaste koostise muutumise tõttu jätkuvalt vajalik bioindikatsiooniliste meetodite edasiarendamine ning päevakajaliste saasteainete hindamiseks sobivate indikaatorliikide väljaselgitamine. Seejuures on võrdlemisi vähe informatsiooni just tolmusaaste kohta, kuigi peened tolmuosakesed on kujunenud paljudes Euroopa linnades peamiseks õhusaaste probleemiks. Lisaks õhusaastele mõjutab inimtegevus epifüütseid samblikke olulisel määral metsamajanduse kaudu, muutes nii kasvukohtade kvaliteeti, pindala kui sidusust maastikus. Varasemad uuringud on näidanud, et majandusmetsades on samblike liigirikkus väiksem võrreldes vanade majandamata metsadega. Paljud samblikuliigid on seotud spetsiifiliste substraatidega, nagu püstised puutüükad ning laialehised puud; mitmed liigid on sagedasemad vanadel puudel. Vaid vähesed uurimused on seni vaadelnud epifüütsete samblike mitmekesisuse erinevusi seoses metsa ajalise järjepidevusega. Olemasolevad tulemused näitavad, et osad liigid on sagedasemad pika järjepidevusega metsades. Kindlasti on vajalikud täiendavad uuringud, et hinnata metsa järjepidevuse ja puu vanuse olulisust eri samblikuliikide esinemise jaoks okasmetsades.

Käesoleva töö käigus uuriti samblike liigirikkuse ja liigilise koosseisu erinevusi seoses õhusaaste ning metsa järjepidevusega, keskendudes okaspuudel kasvavatele liikidele. Töö põhieesmärgiks oli välja selgitada õhusaaste ja metsa järjepidevuse mõju samblike kooslustele ning leida sobivad indikaatorliigid esiteks tolmusaaste hindamiseks ja teiseks vanade pika järjepidevusega okasmetsade eristamiseks. Järgnevalt on välja toodud peamised läbi viidud uurimused, samas järjekorras doktoritöös esitatud artiklitega. (1) Tallinnas läbi viidud uuringute raames hinnati liiklussaaste mõju samblike kooslustele ning puukoore pH tasemele. Muuhulgas leiti seosed samblike liigirikkuse ning lähima autotee kauguse vahel ning eri liikide esinemise ja puukoore pH vahel. (2) Ida-Virumaal uuriti samblike liigilise koosseisu vertikaalseid muutusi puuvõras seoses tolmusaastega, erinevatel kaugustel põlevkivi soojuselektrijaamadest. Põhitähelepanu pöörati tolmusaaste indikaatorliikide esinemise erinevustele tüve alumises osas ja ladvas. (3) Metsa järjepidevuse olulisuse välja selgitamiseks võrreldi samblike kooslusi esimese põlvkonna majandamata metsades ja pika järjepidevusega vanades majandamata metsades üle Eesti. Metsa järjepidevuse andmed saadi kuni ca 350 aasta vanustelt ajaloolistelt kaartidelt. Lisaks määrati uuritud puude vanus. (4) Lõpetuseks võrreldi samblike liigirikkust ja liigilist koosseisu Eesti vanades okasmetsades ja Fennoskandia suurtes vana metsa massiivides. Lisateguritena mõõdeti võra katvus ning uuritud puude vanus.

Tulemused kinnitavad, et õhusaaste on oluline samblike koosseisu mõjutav tegur linnades ja tööstuspiirkondades. Tallinnas muutusid samblike kooslused koos kaugusega teedest, tõendades liiklussaaste suurt osatähtsust linnaõhu saastes. Puukoore pH taseme oluline tõus ning kaasnevad muutused samblike kooslustes teeäärsetel puudel viitavad selgelt liiklusega seotud tolmusaaste olulisusele Tallinnas, kuigi samblikke võivad mõjutada ka teised saasteühendid, näiteks lämmastikoksiidid. Liiklussaaste mõju samblikele sõltus vaadeldud puuliigist. Subneutraalse koorega pärnade puhul avaldus saaste mõju eelkõige samblikuliikide arvu vähenemises, happelise koorega mändide puhul liigilise koosseisu muutumises. Varasemates uurimustes on tugeva tolmusaate korral täheldatud selgeid muutusi samblike koosseisus ka lehtpuudel, kuid seni ei ole võrreldud eri puuliikide sobivust tolmusaaste hindamiseks. Mitmed samblikuliigid, mis tavaliselt mändidel ei kasva, asustasid Tallinnas teeäärseid mände. Selle põhjuseks võib pidada puukoore pH tõusu teede lähedal, mis on tingitud liiklusega seotud tolmusaastest. Paljude liikide puhul avastati oluline seos liigi esinemise ning puukoore pH taseme vahel. Kõrgemat pH taset eelistavate liikide esinemist männil võib pidada heaks tolmusaaste indikaatoriks. Käesolevas töös on välja toodud mitmed taolised indikaatorliigid, näiteks *Candelariella xanthostigma* (tera-sädesamblik), *Phaeophyscia orbicularis* (hägu-tõmmusamblik), *Physcia dubia* (kahtlane rosettsamblik), *Xanthoria parietina* (harilik korpsamblik) ja *Xanthoria polycarpa* (viljakas korpsamblik). Ida-Virumaal läbi viidud uuringute käigus selgus, et võrdlemisi tihedates okasmetsades mõjutab tolmusaaste eelkõige puulatvades kasvavaid samblikke. Nii mändidel kui koore sarnase happesusega kuuskedel domineerisid latvades tolmusaaste indikaatorliigid, kusjuures alumistel meetritel ei leitud ühtegi indikaatorliiki. Seega võiks puulatvades kasvavaid samblikke kasutada õhusaaste hindamiseks metsaaladel, valides praktilistel põhjustel proovipunktid näiteks planeeritud raielankidel. Olukorras, kus osad liigid lisanduvad saaste korral, on samblike liigiline koosseis ning indikaatorliikide esinemine saaste hindamiseks kindlasti sobivam kui liigirikkus.

Eesti vanade ja noorte okasmetsade võrdlemisel selgus, et epifüütsete samblike liigirikkus on suurem vanades pika järjepidevusega metsades võrreldes nooremate esimese põlvkonna metsadega (seejuures leidus ka noortes metsades ligi 100 aasta vanuseid puid). Lisaks erinevustele metsa järjepidevuses, eelistasid mõned liigid kasvada vanematel puudel. Võrdlemisi väikese liigirikkuse üheks oluliseks põhjuseks noortes metsades peetakse osade samblikuliikide kehva levikuvõimet. Käesolevad tulemused kinnitavad metsa ajaloo olulist mõju looduskaitselise väärtusega liikide esinemisele. Paljusid liike, sh kaitsealuseid liike, leiti vaid vanades metsades, mis tõendab selgelt vanade metsade olulisust looduskaitse seisukohast. Samas olid vaid vähesed noores metsas puuduvad liigid vanades metsades niivõrd sagedased, et neid võiks pidada väga headeks vanade järjepidevate okasmetsade indikaatorliikideks Eestis. Esile tõstmist väärivad eelkõige kaks lihtsalt määratavat vanas metsas sagedast liiki, *Arthonia leucopellaea* (valkjas tähnsamblik) ja *Lecanactis abietina* (kuuse-nublusamblik). Eesti ja Fennoskandia vanade okasmetsade omavahelisel võrdlemisel selgusid olulised piirkondade vahelised erinevused paljude samblikuliikide, sh enamiku leitud vääriselupaiga indikaatorliikide, esinemises. Lisaks erinevustele liigilises koosseisus leiti olulised erinevused ka samblike liigirikkuses. Samblikuliikide arv oli väiksem Eesti proovipunktides, mille konkreetsed põhjused jäävad ebaselgeks. Klimaatilised erinevused mõjutavad kindlasti liikide esinemist uuritud alal. Võimalik, et liigirikkuse erinevust põhjustavad lisaks mõned teised tegurid, nagu vanade metsade suurem fragmenteeritus Eestis. Taolised suureskaalalised uuringud on seni võrdlemisi harvad. Saadud tulemuste ja ka varasemate tööde põhjal võib järeldada, et konkreetse piirkonna jaoks sobivate indikaatorliikide valikul tuleb kindlasti arvestada piirkondlike eripäradega liikide arvukuses. Kirjandusandmete põhjal võib oletada, et erinevused on suuremad just vana metsa liikide puhul ning suhteliselt väiksemad õhusaaste indikaatorliikide puhul.

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