

POLINA DEGTJARENKO

Impacts of alkaline dust pollution on
biodiversity of plants and lichens:
from communities to genetic diversity



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from communities to genetic diversity



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LIST OF ORIGINAL PUBLICATIONS

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

- I** Paal, J., **Degtjarenko, P.**, Suija, A. & Liira, J. (2013) Vegetation responses to long-term alkaline cement dust pollution in *Pinus sylvestris*-dominated boreal forests – niche breadth along the soil pH gradient. *Applied Vegetation Science* 16: 248–259. doi: 10.1111/j.1654-109X.2012.01224.
- II** Marmor, L. & **Degtjarenko, P** (2014) *Trentepohlia umbrina* on Scots pine as a bioindicator of alkaline dust pollution. *Ecological Indicators* 45: 717–720. doi: 10.1016/j.ecolind.2014.06.008.
- III** **Degtjarenko, P.**, Marmor, L. & Randlane, T. (2016) Changes in bryophyte and lichen communities on Scots pines along an alkaline dust pollution gradient. *Environmental Science and Pollution Research* 23: 17413–17425. doi: 10.1007/s11356-016-6933-5.
- IV** **Degtjarenko, P.**, Marmor, L., Tõrra, T., Lerch, M., Saag, A., Randlane, T. & Scheidegger, C. (2016) Impact of alkaline dust pollution on genetic variation of *Usnea subfloridana* populations. *Fungal Biology* 120: 1165–1174. doi: 10.1016/j.funbio.2016.05.010.

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Author's contribution to the publications:

- I.** participated in developing the idea, had the main responsibility in data collection, participated in data analysis and manuscript preparation;
- II.** participated in developing the idea, participated in data collection and analysis, and manuscript preparation;
- III.** had the main responsibility in developing the idea, data collection and analysis, as well as manuscript preparation;
- IV.** had the main responsibility in developing the idea, data collection and analysis, as well as manuscript preparation.

1. INTRODUCTION

1.1. General introduction

Environmental pollution (including air pollution) is a consequential global threat to overall biodiversity. Air pollution impacts on all levels of biological organization, from individuals to ecosystems (Grantz et al. 2003; Lovett et al. 2009). For instance, changes induced by air pollution can disturb the composition, function and structure of ecosystems (Vitousek et al. 1997), triggering the loss of sensitive species or inducing the succession by pollutant-tolerant species. Moreover, environmental pollution could influence the genes and genetic diversity of organisms from different species groups (DiBattista 2008; Holloway et al. 2012). Therefore, there are multiple tasks for air pollution management. In order to control, monitor and, consequently, mitigate damages caused by air pollution, the influence of air pollution on different levels of biodiversity should be estimated and the potential sources of pollution and their extension detected (Guerreiro et al. 2015). Additionally, it is required to improve the mitigation technologies and set the new possible methods for complementing the data from air monitoring stations.

The total emission and concentrations of many air pollutants (e.g., SO₂, CO, C₆H₆) have decreased and, generally, air quality has improved in Europe for now, while particulate matter (PM) is still an acute and problematic pollutant as EU limits for PM have continued to be exceeded in large parts of Europe (Guerreiro et al. 2015). PM is air pollutant, which represents the heterogeneous mixture of solid particles, differing in size (ca. 0.1–10 µm), origin and chemical composition, and has been suspended in the air (Grantz et al. 2003). PM pollution is usually defined by size fraction (Grantz et al. 2003). Coarse PM (or larger dust particles, hereafter dust pollution) is released to the environment e.g., through rock quarrying, combustion processes, kiln grinding, directly from surfaces of unpaved roads by intensive traffic or from biogenic sources e.g., from surfaces of deserts or from wildfires. Anthropogenic dust pollution usually disperses by the wind and, therefore, deposits generally in the vicinity of emission sources, e.g., power plants, cement industries, limestone quarries, and unpaved roads (e.g., Farmer 1993; Mandre 1995; Paoli et al. 2014; Rai 2016). The chemical composition of dust pollution is variable, depending on properties of raw material and particular source of emission. In general, dust emission from aforementioned industrial pollution sources contains a high amount of CaCO₃, MgO, K₂O, small amount of SiO₂, Al₂O₃, Fe₂O₃, and heavy metals like Mn, Zn, Cu (Mandre 2000; Reinsalu 2008), and is extremely alkaline. For instance, the pH of cement dust in water suspension is 12.3–12.6 (Mandre 2000). The alkaline dust pollution has always been essential environmental issue in Estonia since over the years the large part of industrial pollution was formed by alkaline dust, and remarkable changes of local environment have been detected in northern region of Estonia due to high presence of alkaline dust pollution (e.g., Laasimer 1958; Annuka 1995; Kask et al. 2008; Reintam et al. 2011).

The effects of alkaline PM on biodiversity have been less studied (Farmer 1993; Zvereva et al. 2008; Rai 2016) in comparison with the effects of acidifying pollutants (i.e., SO₂, NO_x, NH₃). Dust emission can effect vegetation directly, causing negative changes in physiology and biochemistry or indirectly, through the environment. Considerable dust pollution causes visible injuries of plant tissue (Farmer 1993) or necrotic disrupt of lichen thalli (Józwiak and Józwiak 2009), damages spruce needles (Mandre et al. 2002; Ots et al. 2009; Lukjanova et al. 2013), disturbs stomatal function (Siqueira-Silva et al. 2016), reduces transpiration and degrades photosynthetic pigments that results in inhibition of photosynthetic activity (Zaharopoulou et al. 1993; Lepeduš et al. 2003; Maletsika et al. 2015), consequently causing cell plasmolysis and death of entire plants (Saha and Padhy 2011; Siqueira-Silva et al. 2016). Dust pollution can also change element concentration of vascular plants (Mandre and Korsjukov 2007; Kupcinskiene et al. 2008), mosses (Liiv and Kaasik 2004), and lichens (Kortesharju and Kortesharju 1989) or decrease the level of carbohydrates leading to decrease of plant biomass (Mandre and Klõšeiko 2000; Klõšeiko 2005; Ade-Ademiula and Obalola 2008). Moreover, dust pollution can disturb the radial increment and height growth of conifers, and cause defoliation of trees (Mandre et al. 1998; Ots and Rauk, 2000; 2001; Ots et al. 2009). However, the negative effect of dust pollution on vegetation could be counterbalanced to some extent through a fertilizing effect on plants (Annuka and Rauk 1990; Kask et al. 2008; Rizvi and Khan 2009); for example, dust increases the graminoid biomass closer to the calcareous dusty roads (Auerbach et al. 1997).

Indirect effects through the increasing pH and hypertrophication of habitats (changes in chemical properties of soil) provoke the alteration of nutrient cycling and, thus, imbalance nutrient uptake or cause deficiencies (Farmer 1993; Nanos and Ilias 2007) and damage soil biota, e.g., mycorrhizal and bacterial communities involved in nutrient cycling of plants (Grantz et al. 2003; Bilen 2010). The response to dust pollution of individual species consequently leads to the changes at population, community and, finally, at ecosystem level. Those indirect impacts can alter the total species richness, abundance and community structure, changing species composition (e.g., Marmor et al. 2010; Stravinskienė 2011; Vellak et al. 2014). For example, the soil long-term alkalization provokes the successional changes in forest communities (Brandt and Rhoades 1972) or induces the disappearance of *Sphagnum* mosses from sensitive to alkaline dust bogs (Paal et al. 2010) and tundras (Auerbach et al. 1997). Several studies have shown the replacement of acidophytic lichens by basiphytic and neutrophytic lichenized taxa along a dust pollution gradient (e.g., Gilbert 1976; Loppi and Pirintsos 2000; Paoli et al. 2014). The impact intensity of dust pollution depends on the distance from pollution sources, frequency and continuation of emission, dominant wind direction, the amount of deposited dust particles, and particular responses of species groups (Farmer 2000; Grantz et al. 2003). Among other items, PM pollution poses a remarkable harm to human health, particularly in urban areas, provoking the respiratory and cardiovascular diseases and increasing risks of mortality (Brook et al. 2010; World

Health Organization 2013; Yorifuji et al. 2016). For instance, traffic-released PM can cause damage of airway epithelial cells that lead to the production of pro-inflammatory cytokines (Kumar et al. 2015) playing important role in pathogenesis of asthma (Barnes 2008).

Air monitoring stations can provide the real-time information about pollutant concentrations in the surrounding area; however, such data collection is usually performed in a limited number of monitoring stations. Bioindication is a potential tool for complementing the data from air monitoring stations, supplying information about the pollution status and its cumulative impacts in areas that are not covered with direct measurements (Conti and Cecchetti 2001; Sujetovienė 2015). Bryophytes and lichens are widely used as effective indicators for monitoring air quality and surrounding environment (e.g., Gilbert 1968; Hawksworth and Rose 1970; Nimis et al. 2002) due to their particular physiology (e.g., lack of a root system and protective waxy cuticles), metabolic peculiarities (e.g., poikilohydry) and distinctive sensitivity to particular air pollutants (Barkman 1958; Nash 2008; Zvereva and Kozlov 2011). Several studies consider indicator values of lichens and bryophytes for monitoring the atmospheric deposition of different pollutants (e.g., Pakarinen and Hasanen 1983; Branquinho et al. 2008; Sujetovienė 2015); however, simultaneous changes in abundance and species richness or possibilities to use other organisms, for instance epiphytic algae, as bioindicators of dust pollution are poorly investigated.

The majority of studies considering the effects of environmental pollution (including PM pollution) on vegetation have concentrated on responses of individual species or communities (Smith 1990; Farmer 1993; Ellenberg 2009; Rai 2016), while pollution impact on genetic diversity of species has received much less attention (van Straalen and Timmermans 2002). The genetic diversity within populations results from cumulative effects of both historical and present processes (Hewitt 2000; Frankham 2010). Present processes include changes in environmental conditions and, finally, in species habitat, which may influence growth, dispersal and vitality of species. The variation at the genetic level is important part of biodiversity as it initiates evolutionary processes, provides the raw material for adaptation to changing environments, and ensures healthy populations (Lacy 1997; Helm et al. 2009; Frankham et al. 2010). Therefore, the changes in genetic structure and loss of genetic diversity, caused by anthropogenic disturbances, could be a serious threat to natural populations. Moreover, the knowledge of changes or declines in genetic diversity of populations may be used as a warning to vulnerability and sustainability of populations to environmental changes (Bickham et al. 2000).

1.2. Objectives of the thesis

The main objective of the present thesis was to contribute to the knowledge about the response of pine forest ecosystems (**I**), epiphytic communities (algae, lichens, bryophytes) on pines (**II**, **III**), and genetic diversity of populations of a common lichen-forming fungus (**IV**) to changed environmental conditions induced by a long-term alkaline dust pollution.

In summary, the aims of the current thesis were:

- To investigate the successional response of the *Vaccinium myrtillus* site type Scots pine forest communities to changed pH conditions induced by long-term cement dust pollution (**I**). This study particularly aimed to investigate (1) how much the chemical properties of soil litter horizon have been changed by over century persisted alkaline dust pollution; (2) the niche breadth along the soil pH gradient; (3) how resilient the forest community was considering the responses of core species to the changed pH conditions.
- To find out the potential bioindicators of air quality near sources of alkaline dust pollution (**I**, **II**, **III**), and, especially, to shed light on the possibilities to use *Trentepohlia umbrina* (Kützing) Bornet as an indicator of alkaline dust pollution (**II**). To our knowledge, no direct measurements of the abundance of *T. umbrina* or any other *Trentepohlia* species have been made in habitats with different level of alkaline dust pollution so far.
- To evaluate the response of two cryptogamic groups, lichens and bryophytes, including their diversity and cover, in relation to alkaline dust pollution emitted by the processes connected with limestone quarrying (**III**). To our knowledge, no direct measurements of the species richness and cover of epiphytic bryophytes on pine trees have been made so far in sites with different limestone dust pollution level.
- To estimate the effects of limestone dust pollution from unpaved roads on the genetic diversity of *Usnea subfloridana* Stirt. populations using fungus-specific microsatellite markers (**IV**). No previous study has considered the microsatellite variation of lichen-forming fungus populations under long-term air pollution, particularly under alkaline dust pollution.

2. MATERIALS AND METHODS

2.1. Study area and sample plots

The studies were carried out in Estonia (Fig. 1), northern Europe. Estonia has temperate climate; the mean annual temperature is 5°C, and the total annual precipitation is 770 mm (Estonian Weather Service 2016). The vegetation of Estonia belongs to the hemiboreal subzone of the boreal forest zone, lying in the transitional area, where southern taiga forest subzone changes into spruce-hardwood subzone (Ahti et al. 1968; Laasimer and Masing 1995).

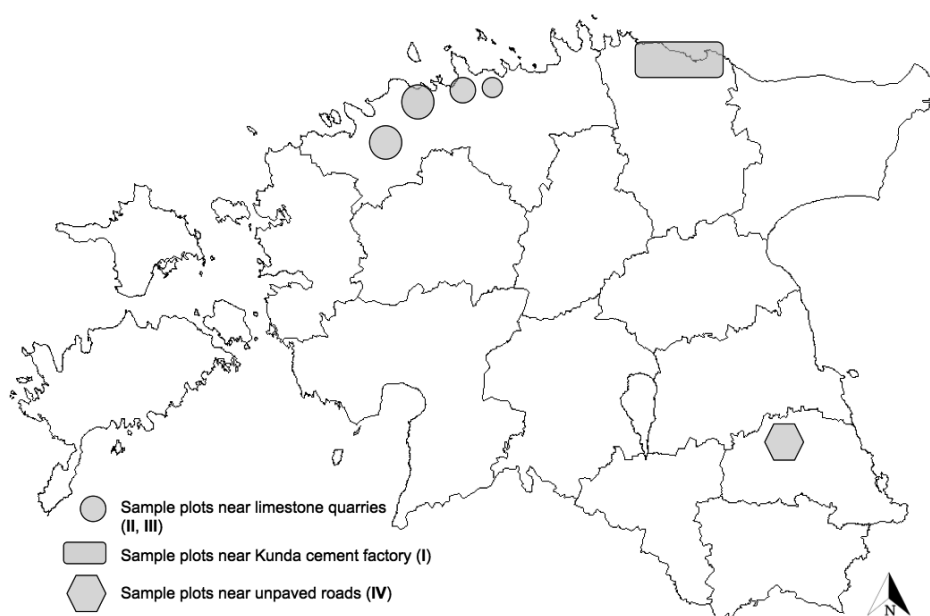


Figure 1. Study areas and location of sample plots in the vicinity of different sources of alkaline dust pollution in Estonia (papers I–IV).

The studies were carried out in the surroundings of three different sources of alkaline dust pollution; cement plant (I), limestone quarries (II, III), and limestone unpaved road (IV; Fig. 1; Table 1). The extraction and using of limestone have a long tradition in Estonia, beginning already in the 13th century (Ministry of the Environment 2011). The study I was performed in the vicinity of Kunda cement factory (Fig. 1; Fig. 2; Fig. 1 in I). The Kunda cement factory was established in 1871, and since that time has emitted alkaline dust in substantial amount into the surrounding area. The emissions of cement kiln dust have been varying greatly during the years, reaching the level of about 100 000 tons per

year in the late 1980s and early 1990s (Estonian Environment 1995). For now, after the installation of powerful dust filters in 1996, the dust emission considerably decreased – to 34 tons per year (Kunda Nordic Tsement 2016), and stayed within allowed permits (Environmental Board 2016). However, the dust pollution impact is still detectable, for example, in 2008 the Ca content in the snowmelt water exceeded the unpolluted measures by ten-fold in Mahu bog (about 4.5 km NE of Kunda cement plant; Paal et al. 2010). In papers **II** and **III**, the study sites were situated in the surroundings of four major limestone quarries in northern Estonia: Vasalemma, Harku, Vão, and Maardu (Fig. 1; Fig. 1 in **II**; Fig. 1 in **III**). The mean quantity of quarried limestone in Estonia per year is 2.6 million m³, and about half of it is extracted from the aforementioned quarries, which have been functioning during last 50–60 years (Geoguide Baltoscandia 2012). The unpaved road, which is the source of dust pollution in paper **IV**, has been marked as a road on the map at least from the end of 19th century (earlier maps are not available), however, serious pollution started ca. 60 years ago, in 1960s when motors vehicles, including agricultural machines, became widely used.

The study sites were located in *Pinus sylvestris*-dominated boreal forests (**I–IV**) and forested parks (**II**, **III**). The studies were conducted in forests belonging to the *Vaccinium myrtillus* site type (**I**, **IV**), the *Oxalis-Vaccinium myrtillus* site type (**IV**), and the *Vaccinium vitis-idaea* site type (**IV**). Those forest site types are also widely distributed in other Baltic states (Kairiükštis 1966; Buš 1997), in Fennoscandia (Dierßen 1996), and in northwest Russia (Fedorchuk et al. 2005). In undisturbed conditions, soil from those forest site types is naturally acidic; pH_{KCL} of the litter and humus horizon ranges between 2.5 and 5.5 (Paal 1999; Lõhmus 2004). The study sites were selected using the maps of Estonian State Forest Management Centre (**I**), Estonian Forest Public Registry (**I–IV**), and the soil maps of the Estonian Land Board (**I**). The sample plots were located at different distances from the pollution sources (Kunda cement plant in **I** and the nearest limestone quarry in **II** and **III**), representing thus the pollution gradient (Fig. 1; Fig. 2; Fig. 1 in **II**; Fig. 1 in **III**). Furthermore, the sample plots were situated in more than 100 m from the nearest paved or gravel road for minimizing the potential impact of traffic pollution (**I**, **II**, **III**). In **IV**, where genetic diversity of *Usnea subfloridana* populations was studied, eight sample plots were investigated: four of them were within polluted forest stands, which were located close to unpaved roads, and four within undisturbed forest stands, which were situated more than 180 meters from the source of dust pollution, as reference data (Table 1 in paper **IV**). Lichen populations were delimited according to the boundaries of forest sites having different average age of the lichen phorophyte (Forest Public Registry 2012).

Table 1. Short overview of study objects, sources of pollution, total number of studied species/samples, total number of sample plots, and applied statistical and molecular analyses

Papers	Study objects	Source of pollution	Total number of studied species/ samples	Total number of sample plots	Statistical analyses	Molecular analyses
I	Vascular plants, epigeic bryophytes	Cement factory	86 species (including 25 bryophytes)	20	PCA, ANOVA, Tukey post hoc test, MRPP, ISA, GRM, GLZ	–
II	Epiphytic green alga on Scots pine	Limestone quarries	1 species (<i>Trentepohlia umbrina</i>)	32	Spearman's rank correlation analysis, logistic regression, Kruskal-Wallis test	–
III	Epiphytic bryophytes and lichens on Scots pine	Limestone quarries	34 bryophytes, 84 lichens	32	Spearman's rank correlation analysis, Kruskal-Wallis test, ANOVA, Tukey post hoc test, GLZ	–
IV	Lichenized fungi on Norway spruce	Limestone unpaved road	1 species (<i>Usnea subfloridana</i>), 274 specimens	8	GLZ, AMOVA, Wilcoxon signed-rank test, allele frequency distribution test	Fungus-specific micro-satellites (9 loci)

2.2. Field methods and data collection

Fieldworks were carried out between summer 2008 and summer 2014. To estimate the vegetation changes under long-term cement pollution, twenty 65–90 years old pine stands were selected, and a circular sample plot of 0.1 ha was set in the centre of the each pine stand (I). We characterised the tree layer by crown closure, tree basal area, average height, and age of trees (I). The basal area was measured for each tree species as an average of three to five measurements (I). The density of shrub layer species was the average stem count on five randomly placed 2 m radius subplots (I). Cover of vascular plant species in the herb layer and moss layer was registered in 12 randomly located 1 m × 1 m sample squares in a radius of 10 m within the centre plot (I). Species outside sample squares were also recorded and included in the analyses as cover 0.01% (I). The composite sample of the soil litter horizon was collected from three randomly selected pits around plot centre within a radius of 10 m (I). The pH_{H2O}, Ca, Mg, N, P, K, and ash content of soil samples were estimated in laboratory (see methods in paper I). In papers II and III five random Scots pine (*Pinus sylvestris* L., hereafter ‘pine’) trees were examined in a 25-m radius circle of 32 sample plots; only trees with more than 50 cm circumference were included. The line cover method was used to estimate the cover of *Trentepohlia umbrina* (II), lichens (III), and bryophytes (III) on pine trunks. A measuring tape was attached round each sample tree trunk at the height of 120 cm; all the millimetres, where any species was crossing the lower edge of the tape, were recorded. Sample tree circumference was measured for later calculating of the cover of *T. umbrina* (II), the cover of lichens (III), and the cover of bryophytes (III). Additionally, the occurrence of all epiphytic lichen and bryophyte species was registered on trunk of every sample tree from 0.5 to 2 m above ground (III). In paper IV, shrubby *Usnea* thalli were randomly collected from Norway spruces (*Picea abies* (L.) Karst., hereafter ‘spruce’) in forest stands with different average age (between 70–114 years) of spruces from eight sample plots. The specimens (three specimens per tree on average) were sampled up to six meters from the ground using tree pruner. If there were less than three thalli, only one or two specimens were sampled while in other cases more than three (but not more than five) specimens were collected per tree to balance sampling.

2.3. Bark pH measurement

The pine bark pH was measured *in situ* at breast height (DBH of at least 90 cm) on three stems in three repeats at each sample plot in study I. In studies II, III, and IV, two bark pieces were collected at the height of 120 cm from the ground from every studied pine tree (II, III), and from five random spruces from polluted and unpolluted forest stands (IV). In studies II and III, one piece of pine bark was gathered from the side of the quarry and another from the opposite side of tree. In paper IV, in polluted forest sites one piece of bark was

taken from the northern side (N), which was adjacent to unpaved road, and second piece from the opposite, southern, side (S) of tree. In unpolluted forest sites (IV), bark pieces were analogously collected, keeping the same cardinal direction. Then bark pH of collected bark pieces was measured in laboratory (II, III, IV). The flathead pH meter Consort C532 was used for all bark pH measurements (I–IV). To allow rapid solution of hydrogen ions, 0.5 mL of 0.1 M KCl was dripped on the bark 1 min before the measurement following Schmidt et al. (2001). The mean bark pH of every tree was expressed as an arithmetic mean of two (II, III, IV) or three (I) measurements of bark pH values (all calculations of mean pH were based on mean hydrogen ion concentrations and then transformed back into pH value).

2.4. Species identification

The species that were difficult to identify in the field were collected for later determination (I, III). Additionally, in study II, at least one sample was taken for examination and confirming the identification under a light microscope from every sample plot, where epiphytic green alga *Trentepohlia umbrina* occurred. Thin layer chromatography (TLC) with solvent A (Orange et al. 2001) was performed for those lichen specimens that were difficult to identify by morphology or by chemical spots (III), and for confirming the identification of *Usnea subfloridana* (IV). In paper I, the bryophyte nomenclature follows Hill et al. (2006) and the nomenclature of vascular plants follows Tutin et al. (1964–1980), in paper III, the bryophyte nomenclature follows Vellak et al. (2015), and in papers III and IV, the lichen nomenclature follows Randlane et al. (2013).

2.5. Molecular analyses

In study IV, the total DNA of *Usnea subfloridana* specimens was isolated using PowerPlant® Pro DNA Isolation Kit (MO BIO Laboratories, Inc., USA) according to the manufacturer's protocol. Nine unlinked fungus-specific microsatellite loci (Tõrra et al. 2014) were analyzed and amplified in three different multiplex PCR following the protocol described in Tõrra et al. (2014) except the reverse primer sequences, which had erroneously been presented as direct sequences from the genome. Therefore, we used the modified set of the reverse primer sequences (Table 2 in paper IV). Additionally, the final primer concentration of Us01 (multiplex I) was increased to 0.05 μ M to get PCR amplification (see Tõrra et al. 2014 for other primer concentrations). Fragment lengths of PCR products were determined on a 3730xl DNA Analyzer (Applied Biosystems, Zurich, Switzerland). The electropherograms were analyzed using GENEMAPPER ver. 5 (Applied Biosystems) using LIZ-500 (all multiplexes) as size standard.

2.6. Statistical analyses

The collected data (e.g., bark pH values, soil chemical characteristics, abundance and occurrence of species) were averaged per sample plot (I–IV), and statistical analyses were performed on the plot level (Table 1; I–IV).

In paper I, the principal component analysis (PCA) with Varimax rotation was applied on variables describing the alkaline pollution; litter horizon pH, logCa, logK, logMg, and logAsh content were included. The first principal component was defined as the compound pollution factor (CF). The variation in soil chemistry and forest structure measures between pollution zones were estimated with a one-way ANOVA; Tukey post hoc test was used to test the significant difference between the pollution zones (I). The multiple response permutation procedure (MRPP) was used to estimate the difference on species composition between pollution zones (Bonferroni correction was applied for p-values). Indicator species analysis (ISA; Dufrêne and Legendre 1997) was applied to find out indicator species for each pollution zone (I). The statistical significance of the indicator values was estimated with a Monte Carlo permutation test. The indicator value pattern between pollution zones was used to outline niche width for species having indicator value >15 in at least one pollution zone (I). Species were classified into six groups: acidophilous, acidoneutrophilous, neutrophilous, neutrophilous-calcicolous, and calcicolous. Species with high indicator values through three zones or at least in the unpolluted and heavily polluted zones were classified as generalists.

The two-way step-wise general regression model (GRM) analysis was applied to estimate plant species reaction to the alkaline pollution. Some species had sharply asymmetric abundance distribution (i.e., observation included of too many zeros), and the assumption of the normal error distribution could not be applied (I). Therefore, the generalized linear model (GLZ) with binominal distribution and ‘logit’ link function analysis was carried out on presence-absence data of these species (I). The GRM analysis was also applied to test the effect of litter chemical properties on species richness and on the variables of tree layer structure (I). Spearman’s rank correlation analysis was used to find the relationships between the cover of *Trentepohlia umbrina* and distance from the quarry (II), between the cover of bryophytes and the cover of lichens (III), between the number of bryophytes and the number of lichens (III), between the mean tree circumference and the cover of lichens and bryophytes (III), between the mean tree circumference and the number of lichens and bryophytes (III), and between the mean tree circumference and the cover of *Trentepohlia umbrina* (II). Logistic regression was used for describing the occurrence probability of *T. umbrina* in relation to bark pH (II). Kruskal-Wallis test was applied for checking the differences in the cover of *T. umbrina* (II), and in the cover and species richness of bryophytes and lichens between the quarries (III, separately for lichens and bryophytes). One-way analysis of variance (ANOVA, type III) was used for estimating the effects of distance from the nearest quarry (distance groups 0–500, 501–1000, 1001–2000, >2000 m) on the cover of

bryophytes and lichens, on the bryophyte richness, and on pH value of pine bark (III). Two-way ANOVA (type III) was applied for checking the effects of distance on the lichen richness; the type of quarry was taken as additional categorical independent variable (III). Additionally, Tukey post hoc test was used to test the significant statistical differences between the distance groups (III). GLZ analysis with binominal distribution and ‘logit’ link function was used to describe the relationships between the presence of species and bark pH (taken as a continuous independent variable); species that were recorded in only one sample plot were excluded from this analysis, and species that were recorded on genus level were also excluded (III). PCA, ISA, and MRPP were performed in PC-ORD 5 (McCune and Mefford 1999). The Kruskal-Wallis test, ANOVA, Tukey test, t-test, Spearman’s rank correlation analyses, logistic regression, GRM, and GLZ analyses were performed in STATISTICA 7 (Statsoft 2004).

In paper IV, the total number of alleles, the mean number of alleles, the maximum and the minimum number of alleles, the number of private alleles (P), heterozygosity, i.e., genetic diversity (H), allelic richness (A), and Shannon's information index (I) for eight *Usnea subfloridana* populations were estimated in the GenAlEx ver 6.5 software (Peakall and Smouse 2012) and the Microsatellite Analyzer (MSA) software (Dieringer and Schlötterer 2003). The number of multilocus genotypes (G), the percentage of multilocus genotypes, and the minimum number of colonisation events (C) per population were calculated in the R software (R Core Team 2012) using the script written by Werth et al. (2006). GLZ analysis with normal distribution and “identity” link function was applied to find an effect of dust pollution on the G, M, C, A, I, H, and P of *U. subfloridana* populations. To estimate genetic differentiation among populations from polluted and unpolluted habitats, hierarchical analyses of molecular variance (AMOVA) with 999 permutations was performed using the GenAlEx ver 6.5 software (Peakall and Smouse 2012). T-test was used for detecting the differences between polluted and unpolluted forest stands (according to bark pH value of spruces). To measure bottlenecks of population (to undergone the significant reductions in size or bottleneck effect), the Wilcoxon signed-rank test and the allele frequency distribution test (mode-shift test) were performed using the software BOTTLENECK (Piry et al. 1999).

3. RESULTS

3.1. Environmental variables and pollution zones

Three pollution zones around cement plant in Kunda were distinguished using primarily the pine bark pH, and refined considering CF scores: (1) unpolluted (bark pH \leq 3; CF \leq -0.5); (2) moderately polluted (bark pH=3–4; CF -0.5–0.2); (3) heavily polluted (bark pH $>$ 4; CF $>$ 0.2) zone (Fig. 2; I). The pH of the forest litter horizon around the cement plant gradually decreased with increasing distance from cement plant from 7.1–7.4 to 3.6–4.5 at 30 km distance (Table 1 in paper I). The content of K, Ca, and Mg of soil samples followed a similar gradient (I). The absolute pH values on pines in the vicinity of limestone quarries varied between 2.9 and 6.6, and the mean values per sample plot between 3.2 and 6.3 (II, III). The bark pH depended significantly on the distance from quarries ($F(3, 28)=19.5$; $p<0.000001$; Fig. 2 in paper III) and also gradually decreased with increasing distance from the quarries (II, III). The bark pH gradually decreased with increasing distance from the limestone quarries, being ca. 3.5 at the distance of 1001–2000 m from the quarry, and reaching the mean minimum value, ca. 3.4, further than 2000 m from the quarry (Fig. 2 in paper III). The mean bark pH of spruces per forest site varied between 3.5 and 6.6 (Table 1 in paper IV) and significantly differed between polluted and unpolluted forest stands ($t=14.6$; $df=6$; $p<0.00001$; IV).

The closure of tree stands and shrub layer density were highest in the moderately polluted zone and lowest in the unpolluted zone in vicinity of Kunda cement plant (I). The average height of the tree layer and the basal area of pines and spruces were rather similar between zones (Table 1 in paper I).

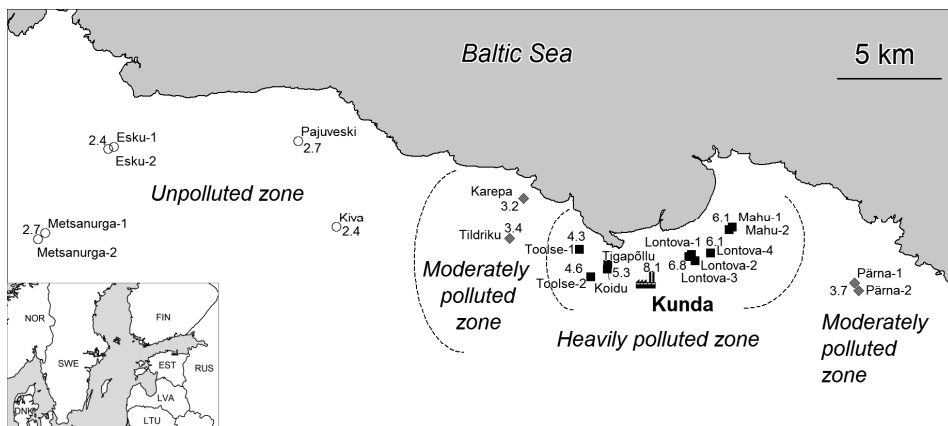


Figure 2. The grading of study area around the Kunda cement plant by three pollution zone: (1) unpolluted zone, marked with open (white) symbols; (2) moderately polluted zone, marked with partly filled (grey) symbols; (3) heavily polluted zone, marked with filled (black) symbols.

3.2. Species richness and cover

Altogether, we recorded 86 species (including 25 epigeic bryophytes; Table 1; Appendix S1 in paper I) in the study concerning boreal forest communities in the vicinity of Kunda cement plant (I), and 34 epiphytic bryophytes and 84 lichens on pines near limestone quarries (Table 1; Tables 1 and 2 in paper III). Comparing the three pollution zones near Kunda cement plant, the pooled species richness was lowest in unpolluted forests (average = 31, SD = 3 species in 0.1-ha sample plot), it increased considerably in the moderately polluted zone (44 ± 14) and was almost two times higher in the heavily polluted zone (63 ± 7 ; I). The variation in species number (SD) was highest in the moderately polluted zone (I). The MRPP test showed that the species composition of ground vegetation (herb and moss layer) in the heavily polluted zone was significantly different from that in unpolluted and moderately polluted zones ($P=0.001$; $P=0.006$), but species compositions in unpolluted and moderately polluted zones did not differ ($P=0.254$).

The cover of bryophytes per tree varied between zero and 12%, and mean value per sample plot between zero and 4% near limestone quarries (III). The species richness of bryophytes per tree ranged between zero and 8 bryophyte species, and between zero and 11 species per sample plot (III). The cover of lichens per tree varied between zero and 75%, and mean value per sample plot between 3 and 60% near limestone quarries (III). The species richness of lichens per tree ranged between zero and 18 species, and between 8 and 31 species per sample plot (III). The results of Kruskal-Wallis test did not indicate significant differences in the species richness and the cover of epiphytic bryophytes between the four quarries ($H(3,32)=3.8$, $p=0.28$; $H(3,32)=1.0$, $p=0.80$; III), in the cover of *Trentepohlia umbrina* between the four quarries ($H(3,32)=1.54$; $p=0.67$; II), and in the cover of epiphytic lichens between the four quarries ($H(3,32)=0.9$, $p=0.84$; III). However, this test revealed a significant difference in species richness of lichens between the four quarries ($H(3,32)=12.1$, $p=0.01$; III).

3.2.1. Factors influencing species richness and cover

Results of analyses revealed that species richness and cover were correlated with pollution intensity, but various species groups differently responded to pollution impact. According to the GRM analyses, the number of species in the herb and moss layers of boreal forest communities near Kunda cement plant was positively correlated with pollution intensity (I). Herb layer richness was well described by the model consisting of three environmental variables (adj $R^2 = 91.0\%$). The herb layer richness increased most clearly along the pH gradient (standardized slope estimate $b=0.707$, $p=0.0001$; Fig. 3 in paper I); moreover, it increased together with the P content ($b=0.360$, $p=0.0002$), whereas N content of the litter horizon had a significant negative relationship to the species richness ($b=0.281$, $p=0.0055$ in paper I). Species richness of epigeic bryophytes

was dependent on pollution gradient via Ca content ($b=0.643$, $P=0.0022$; adj $R^2=38.1\%$; Fig. 3 in paper I).

The GRM analyses also revealed that abundance of frequent plant species depended mainly on the litter horizon pH (Table 2 in paper I). The significant impact of the litter horizon N content was observed only for a restricted number of species; the P content affected only the abundance of *Alnus incana* and moss species *Cirriphyllum piliferum*. The increase of litter horizon pH was positively associated with the abundance of several shrub layer species (*Corylus avellana*, *Ribes alpinum*, and *Sorbus aucuparia*) and *Quercus robur* saplings. The increased pH of the litter horizon had different impacts on the herb and moss layer species: abundance of species that were natural to boreal pine forests (e.g., *Calluna vulgaris*, *Vaccinium myrtillus*, and *V. vitis-idaea*, and bryophytes *Hylocomium splendens*, *Pleurozium schreberi*, and *Ptilium crista-castrensis*) decreased, while abundance of nemoral species (e.g., *Mycelis muralis*, *Vicia sepium*, *V. sylvatica*, and bryophytes *Cirriphyllum piliferum* and *Rhytidia-delphus triquetrus*) increased (I).

According to the results of one-way ANOVA, the species richness of epiphytic bryophyte per sample plot depended significantly on the distance from quarry ($F(3,28)=9.9$; $p=0.0001$): the species richness of bryophytes was higher near quarries and decreased gradually at increasing distances from quarries (Fig. 3; III). The bryophyte cover also depended significantly on the distance from quarries ($F(3,28)=21.7$; $p<0.00001$; Fig. 3; III). The cover of epiphytic lichens per sample plot depended significantly on the distance from the quarry ($F(3,28)=10.0$, $p<0.001$) being lower near limestone quarries and increasing gradually with increasing distances from quarries (Fig. 3; III). The results of two-way ANOVA showed that the distance from the quarry had effect on the number of epiphytic lichens ($F(3,25)=4.3$, $p=0.01$): species richness was lowest near quarries, increased gradually till 2000 m from quarries, and started to decrease further than 2000 m from quarries (Fig. 3; III). According to two-way ANOVA, the type of quarry had an effect on the number of lichens ($F(3,25)=6.9$, $p=0.01$). The results of Spearman's correlation demonstrated no significant effect of mean tree circumference per plot on the number and the cover of bryophytes ($N=32$: $R_s=-0.1$, $p=0.46$; $R_s=-0.03$, $p=0.89$ in III), on the number and the cover of lichens ($N=32$: $R_s=-0.3$, $p=0.07$; $R_s=-0.3$ $p=0.13$ in III), and on the cover of *Trentepohlia umbrina* on pines ($N=32$: $R_s=-0.06$; $p=0.75$ in II).

The cover of *T. umbrina* was strongly correlated with pine bark pH (Fig. 2 in paper II). The results of logistic regression analysis revealed that the occurrence probability of *T. umbrina* reached 50% at pH 3.4 and 90% at pH 3.9–4.0 (II).

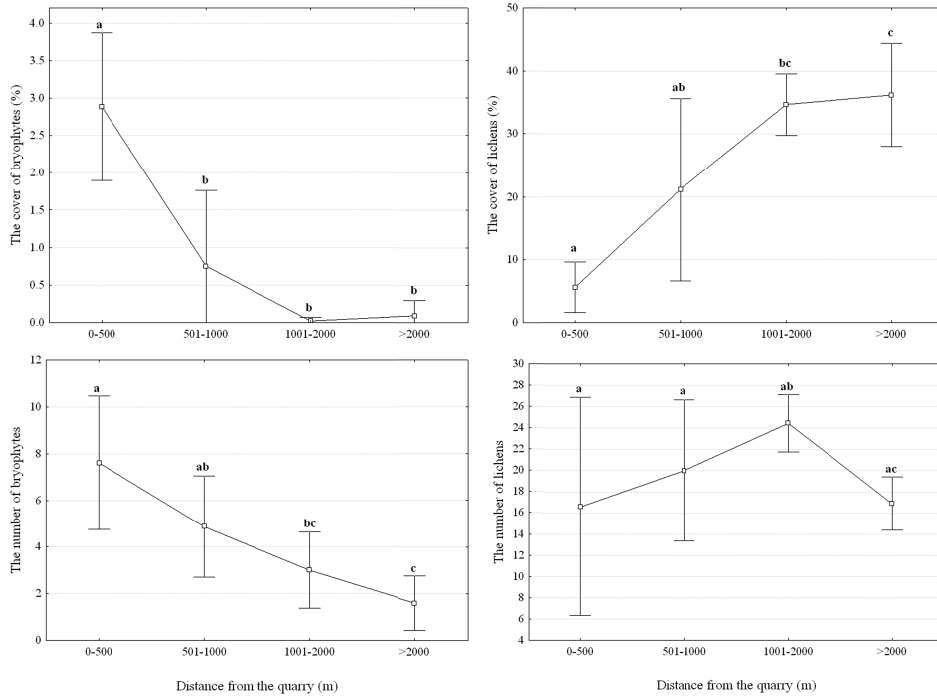


Figure 3. The mean percentage of bryophyte and lichen cover (± 0.95 confidence interval) and the mean number of bryophyte and lichen species (± 0.95 confidence interval) on Scots pines per sample plot at different distances from the quarries; the significant differences between the groups are marked with letters *a-c* according to Tukey' HSD test.

3.3. Bioindicators of dust pollution

According to results of ISA, 12 species (among them two orchids – *Neottia ovata* and *Neottia nidus-avis*) appeared to be significant indicators for the heavily polluted zone, and six species – for the moderately polluted zone around Kunda cement factory (Appendix S1 in paper I).

Spearman's correlation analyses confirmed a significantly higher cover of *Trentepohlia umbrina* in the vicinity of limestone quarries (Fig 2 in paper II). The cover of this species decreased steeply at the distance of 800–900 m from the quarry; further than 1000 m from the quarry the maximum cover value of *T. umbrina* was already less than 4%, and further than 2000 m less than 1% (Fig. 2 in paper II).

The GLZ analysis revealed that six epiphytic bryophyte species (*Orthotrichum pallens*, *O. speciosum*, *Pylaisia polyantha*, *Radula complanata*, *Schistidium apocarpum*, and *Syntrichia calcicola*) preferred a higher bark pH of pines in the vicinity of limestone quarries (Table 1 in paper III). No bryophyte species were significantly associated with lower bark pH (III). Thirteen lichen species

favoured a higher bark pH of pines in the vicinity of limestone quarries, and 21 lichen species preferred a lower bark pH of Scots pines (Table 2 in paper III).

3.4. Niche width along the soil pH gradient (I)

We categorized the species using their indicator value patterns between pollution zones near Kunda cement plant (Appendix S1 in paper I); 17 species were defined to acidic soils, 48 species were associated with calcareous soils, and 13 species were related to neutral soils (Fig. 4). Eight species (having frequency $\geq 10\%$) were common species with no preference pH, and were considered as pH generalists. The species reactions measured with the parametric model (GRM and GLZ; Tables 2 and 3 in paper I) were in good agreement with the non-parametric niche definitions based on the indicator species analysis (Appendix S1 in paper I), particularly for the species at the extreme ends of pH/Ca gradients. The exceptions were two generalists (*Vaccinium vitis-idaea* and *Hylocomium splendens*), but as shown by GLM, their abundance decreased along the pollution gradient linearly, and indicator values also indicated this. We revealed that niche width classes, which were generated using species indicator value patterns were acceptable, because parametric models did not allow evaluation of species with lower frequencies or species with a neutrophilous niche. The number of narrow and wide niche species increased from the acidophilous-neutrophilous niche class in both directions according to species counts in each niche class, but particularly toward calcicolous species (Fig. 4).

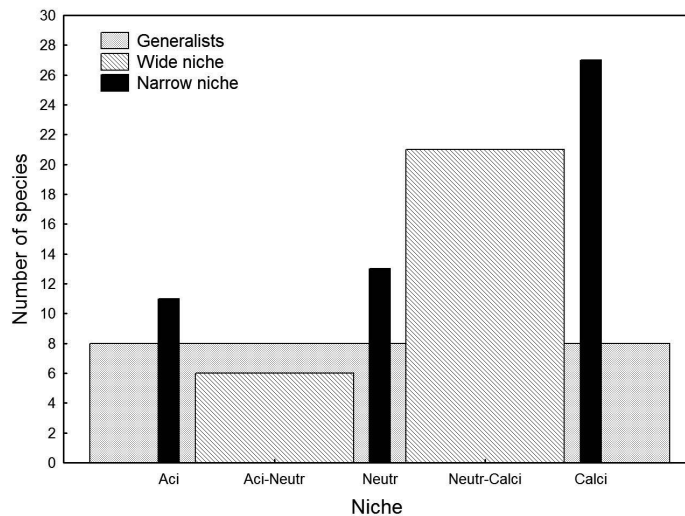


Figure 4. Number of common species (frequency $\geq 10\%$) in pH-based niche classes: Aci, acidophilous; Aci-Neutr, acidophilous-neutrophilous; Neutr, neutrophilous; Neutr-Calci, neutrophilous-calcicolous; Calci, calcicolous. pH generalist species are shown as background bar. The combined summary of these species by pollution zone describes the major pattern of species richness along the pH gradient.

3.5. Genetic diversity of *Usnea subfloridana* populations (IV)

In total, 274 specimens of *Usnea subfloridana* were analysed and genotyped using nine microsatellite fungus-specific markers. We found 72 alleles at studied loci that provided 168 different genotypes across eight populations of lichen-forming fungus. All microsatellite loci were highly polymorphic. Detailed genetic estimates and number of alleles per each marker and population are given in Tables 1 and 3 in paper IV.

The GLZ demonstrated that the presence of dust pollution and number of collected samples or sample size (sqrt N) revealed significant impact on allelic richness (A); this measure was higher in unpolluted forest sites than in polluted forest sites (Table 2). The presence of dust pollution showed the same significant effect on the Shannon's information index (I) and genetic diversity (H) per population, but sqrt N revealed significant influence only on I (Table 2). GLZ also demonstrated that the number of multilocus genotypes (G) and the number of private alleles (P) were significantly contingent on the sample size (sqrt N), but did not differ between polluted and unpolluted forest sites (Table 2). There was no statistically significant relationship between C and the presence of dust pollution (data not shown). There was also no significant interaction between clonal diversity (M) and dust pollution, and M did not correlate with sqrt N (Table 2). The average age of spruces in forest sites (sqrt AGE) did not show significant effect on any measures of genetic diversity of *U. subfloridana* populations in all CLZ analyses (Table 2, results of analyses shown partially).

Hierarchical analyses of molecular variance (AMOVA) revealed no genetic differentiation between studied *U. subfloridana* populations from polluted and unpolluted forest sites (1% differentiation; $\Phi_{RT}=0.01$; $P=0.06$). The proportion of alleles showed a 'shifted mode' distribution in population 4 and 5 (Table 5 in paper IV). The results of Wilcoxon signed-rank test under all tree mutation models per population are given in Table 5, in paper IV.

Table 2. Results of generalized linear model (GLZ) for the allelic richness (A), the Shannon's information index (I), the genetic diversity (heterozygosity) (H), the number of multilocus genotypes (G), the clonal diversity (M), and the number of private alleles (P) in examined *Usnea subfloridana* populations. df, degrees of freedom; F, Wald-type F-statistic; p, significance level; sqrt Age, the square root of average age of spruces in each forest site; sqrt N, the square root of number of collected thalli in each population; Pollution, the presence of dust pollution. Bold-faced values represent significant effect

Effect	A			I			H		
	df	F	p	df	F	p	df	F	p
sqrt Age	1	1.60	0.21	1	1.26	0.26	1	0.32	0.57
sqrt N	1	16.86	<0.001	1	18.41	<0.001	1	1.89	0.17
Pollution	1	10.03	0.002	1	12.30	<0.001	1	4.17	0.04
Effect	G			M			P		
	df	F	p	df	F	p	df	F	p
sqrt Age	1	0.18	0.67	1	0.21	0.64	1	0.09	0.76
sqrt N	1	247.6	<0.001	1	1.75	0.19	1	10.68	0.001
Pollution	1	0.10	0.75	1	0.06	0.81	1	1.30	0.25

4. DISCUSSION

4.1. Environmental variables under alkaline dust pollution

Effect of long-term alkaline dust pollution from various pollution sources (viz., cement plant, limestone quarries, and unpaved road) on different organism groups was studied in boreal forest ecosystems. According to our results, the long-term dust pollution had a remarkable neutralizing effect on natural substrates in pine forest ecosystems; both, the pH value of litter horizon (Table 1 in paper **I**) and pine bark (**I**, **II**, **III**) significantly decreased along an increasing distance from the sources of dust pollution. Additionally, the pH value of spruce bark had also increased (up to 5.9–6.6) in polluted habitats that were adjacent to limestone unpaved road, and significantly differed between polluted and unpolluted forest stands (**IV**).

Similarly, several studies have showed the noticeable decrease of soil and bark acidity (e.g., Gilbert 1976; Farmer 1993; Cutillas-Barreiro et al. 2016), and increase of Ca, Mg, and K content (Mandre 1995; Haapala et al. 1996a) in the vicinity of sources of alkaline air pollution. We also found that Ca, Mg, and K content of soil litter horizon followed the similar decreasing tendency along the dust pollution gradient (**I**). The Ca content of soil litter horizon was ten times higher near Kunda cement plant than in unpolluted areas. Previous studies from the early 1990s in the vicinity of Kunda factory had detected a 15-fold increase in Ca content from the unpolluted to the heavily polluted zone (Annuka and Mandre 1995). Comparing our results with previous 20-yr-old monitoring (Annuka and Mandre 1995), we can observe that the soil litter is recovering after the drastic reduction of alkaline emissions from the cement plant, but the over a century accumulated dust and its impact are still evident and persisted nowadays. Amarell (2000) also noticed the delayed recovery of soil in the pine forests of Central Germany. The observed delay in soil recovery may be explained by the saturation of pollution impacts, where increasing Ca content does not increase the pH above a certain level (Fig. 2 in paper **I**), and consequently, after the reduction of pollution, the Ca level in soil can decrease over a long time before pH will reduce. The natural self-restoration of soils and pine forest ecosystems at whole is possible but it will last for decades. There have been no controlled studies that consider the restoration of pine ecosystems after long-term alkaline cement dust accumulation. Therefore, further continuing observations are required to evidence when total recovery processes will occur.

4.2. Bioindication of alkaline dust pollution

Bioindicators are biological species, biological processes or communities, which are used to evaluate the quality of environmental conditions (Holt & Miller 2010). Comparing with monitoring stations and directly measured physical parameters, the using of bioindicators has several advantages as they allow assessing the cumulative impacts of chemical pollutant, habitat changes over time, and could provide the monitoring data about environment that is not covered with direct measurements (Conti and Ceccheti 2001; Sujetovienė 2015). The good bioindicators should have some features, for instance, they should be well-studied, common in studied geographical region, and have measurable indicator ability (Holt & Miller 2010).

The present study confirms some previously known, and suggests a few new bioindicators of dust pollution among algae, lichens, bryophytes, and vascular plants. The results of paper **II** confirm that green alga *Trentepohlia umbrina*, if growing on pines, could be used as an ecological indicator of alkaline dust pollution. Our results revealed that the abundance of *T. umbrina* on pine trunks was clearly higher near the limestone quarries, its maximum cover values reaching ca. 30% (mean of five trees studied per sample plot). We suggest that $\geq 10\%$ cover of *T. umbrina* on pines indicates considerable dust pollution (Fig. 2 in paper **II**). These results are in agreement with those obtained by Haapala et al. (1996b), who also observed high abundance of *T. umbrina* on pine trunks in dust-polluted areas in Leningrad Oblast, Russia. Such reddish powdery cover of *Trentepohlia* on pine bark is easily recognizable at field (Appendix A in paper **II**); however, further separating between the species without microscopical examination might be challenging.

The cover and species richness of epiphytic bryophytes also responded to limestone dust pollution (**III**). The cover of bryophytes had the highest mean values (2.9 %) up to 500 m from limestone quarries; further from the quarries, the cover of bryophytes decreased significantly, being 0.02 % at the distance range between 1001 and 2000 m and 0.1 % further than 2000 m (Fig. 3). The number of bryophyte species on pines was significantly higher near the limestone quarries and decreased steadily along an increasing distance from the source of limestone dust pollution (Fig. 3). In the same way, we detected the inflated species richness of epigeic mosses and vascular plants in *Vaccinium myrtillus* site type pine forests in vicinity of Kunda cement plant (**I**). The number of species in the herb and moss layer was positively correlated with pollution intensity, but expressed via different indicators, pH of litter horizon for vascular plants and litter logCa content for bryophytes, which were more significant predictors than combined pollution factors (Fig. 3 in paper **I**). However, the pollution intensity has a different impact on abundance of vascular plants and epigeic mosses. For example, the increase of litter horizon pH was positively correlated with abundance of several shrub layer species (Table 2 in paper **II**) and negatively correlated with abundance of species that were natural to boreal pine forests (Table in paper **II**).

Lichen cover responded to dust pollution in a different way compared with alga *Trentepohlia umbrina* (II) and epiphytic bryophytes (III); correlation analysis confirmed the negative association between the bryophyte cover and lichen cover, while the maximum cover of bryophytes was considerably lower than lichen cover (viz., 12 and 75% per tree, correspondingly, in paper III). The lichen cover on pines increased considerably with the increasing distance from quarries up to 3340 m; the lichen cover was ca. 35% at the distance range between 1001 and 2000 m and further than 2000 m continued to increase slightly (Fig. 3). The number of lichen species was lowest near the source of pollution, increased at the distance of 1001–2000 m, and then started to decrease, being almost at the same level as in the closest vicinity near quarries (Fig. 3). In general, we revealed the shift of natural communities along a pollution gradient (I, III). These results are in agreement with the previous findings concerning the effect of alkaline dust pollution, for instance, on lichens, where the number of species was altered due to the change of bark pH from acidic to subneutral, and increased bark pH favoured the occurrence of basiphytic and neutrophytic species and even saxicolous species on the originally acid-barked trees (Gilbert 1976; Loppi and Pirintsos 2000; Marmor et al. 2010). The monitoring of cryptogamic communities (Rola and Osyczka 2014) and communities of vascular plants could be useful in bioindication studies. At the same time, the community structure could be an even better predictor of environmental conditions than occurrence or absence of a specific species (van Haluwyn and van Herk 2002). Therefore, we suggest that increased bryophyte diversity and cover on pines due to invasion of species typical for nutrient-rich communities (III), diversification effect (to some extent) of lichens (III), the appearance of typical species for mesotrophic and meso-eutrophic habitats and increased abundance of shrub species in vegetation of *Vaccinium myrtillus* site type forests (I), as well as replacement of acidophilous/acido-tolerant species by neutrophilous and calciphilous (I, III) could provide useful and promising tool for detecting environmental changes and, particularly, monitoring the dust pollution and its extent in dust-impacted areas. However, the relation between species richness and dust pollution may not be universal and simply linear in all cases (Marmor and Randlane 2007). Therefore, such findings need to be interpreted with caution, taking into account the initial environmental conditions and variation among different taxonomic groups and ecosystems.

We also found that the occurrence of six epiphytic bryophytes was strongly correlated with the pH of their substrate: *Orthotrichum pallens*, *O. speciosum*, *Pylaisia polyantha*, *Radula complanata*, *Schistidium apocarpum*, and *S. calcicola* preferred a higher bark pH of pines (Table 1 in paper III). Some of them have been already proposed as indicator species of polluted areas with different dust pollution level: *P. polyantha* and *R. complanata* as indicators for moderate dust-polluted zones, and *S. calcicola* for heavy dust-polluted zones (Paal and Degtjarenko 2015). Here, we proposed that *O. pallens*, *O. speciosum*, and *S. apocarpum*, if growing on pines, can be regarded as new additional indicators of

alkaline dust pollution (III). Conifers, especially pines, are commonly colonized by few epiphytic mosses in natural conditions (Király and Ódor 2010) due to the fact that Scots pines have an extremely acidic and oligotrophic bark, which is a rare habitat for bryophytes (Barkman 1958). Therefore, the occurrence of epiphytic calcicolous bryophytes on pines could serve as a very good indicator of dust pollution in dust-impacted areas. Our results in paper I also revealed that some epigeic bryophyte species can be indicators of alkaline dust pollution in pine forests (Appendix S1 in paper I), however many of them were in low abundance in the pollution areas and so they should be pooled for analyses and used as an indicator species complex.

Several lichens were also correlated with the pine bark pH according to our results (III). Thirteen lichens (e.g., *Lecania cyrtella*, *Lecania naegelii*, *Lecanora hagenii* etc.) favoured a higher bark pH of Scots pine (Table 2 in paper III). Several of them were previously known as alkaline dust indicators if growing on pines (Marmor and Randlane 2007; Smith et al. 2009). *Alyxoria varia*, *Caloplaca cerinelloides*, *Lecania cyrtella*, and *Lecidella elaeochroma* have been repeatedly recorded in areas impacted by dust pollution that was released from limestone quarries (Loppi and Pirintsos 2000; Smith et al. 2009; Paoli et al. 2014). Hence, the presence of these species on Scots pines can be considered as a further indication of alkaline dust pollution. In addition, changes and loss of genetic diversity observed in *Usnea subfloridana* populations (IV) could be used as an additional sign to highlight environmental disturbances induced by alkaline air pollution.

4.3. The impact of alkaline dust pollution on natural communities in boreal ecosystems

Local long-term dust pollution has led to destruction of natural communities in pine forests, including epiphytic communities on pines. We outlined the process of ‘nemoralization’ in the vegetation of the studied *Myrtillus* site type pine forests (I). The ‘nemoralization’ of this habitat was expressed as step-by-step replacement of acidophilous/acidotolerant species by several neutrophilous and then by calcicolous species. In the heavily polluted zone near Kunda cement factory, numerous herb layer species and bryophytes typical of unpolluted *Myrtillus*-type forests were absent (I). The most indicating was the loss of dwarf-shrub species (*Vaccinium myrtillus* and *Calluna vulgaris*), a specific plant growth form of oligotrophic habitats (I). However, the species-poor undergrowth and ground vegetation of unpolluted *Vaccinium* site type forests was diversified by invasion with non-typical species for local communities along the cement pollution gradient (I). The characteristic arrival species, including several orchid species, were typical for mesotrophic and meso-eutrophic habitats and for boreo-nemoral woodlands. These arrival species are generally common in calcareous habitats with nutrient-rich soils, but as in the

present study the addition of nutrients was not noticed (cement dust did not contain much N and P). Therefore, we outlined that pH was the most limiting factor for these species (I).

Similarly, dust pollution and its alkalization effect for pine bark provoked the shift of cryptogamic communities along a pollution gradient (III). The structure of cryptogamic communities clearly responded to changing habitat conditions along the pollution gradient. For instance, the increased bark pH of pines promoted increased diversity of epiphytic bryophytes, including the occurrence of tolerant bryophyte species, which withstand or even favour alkalinity of substrates, and typically occur on limestone outcrops (e.g., *Anomodon longifolius*, *Ditrichum flexicaule*, *Fissidens dubius*, and *Pseudoleskeella catenulata*), concrete substrates (e.g., *Amblystegium serpens*, *Brachythecium salebrosum*, and *Syntrichia calcicola*) or on nutrient-rich bark (e.g., *Orthotrichum diaphanum* and *Leskea polycarpa*) (Ingerpuu and Vellak 1998; Ignatov and Ignatova 2004; Atherton et al. 2010). The increased bark pH from acidic to subneutral also favoured lichens that commonly occur on basic nutrient-rich bark of deciduous trees (e.g., *Lecania cyrtella*, *Lecania naegelii*, and *Lecanora hagenii*) (Smith et al. 2009).

Besides species-specific reactions, dust pollution caused the ‘diversification effect’ of vascular plant (I) and bryophyte (I, III) communities and increased the total species richness (including several protected and rare species). The air pollution is considered as environmental stress to vegetation and other biota, and it commonly leads to the decrease of overall biodiversity and impoverishment of natural communities (Zvereva et al. 2008). However, the increase of species richness can occur in low-diversity oligotrophic habitats in the response to stress (Odum 1984). Indeed, the alkaline dust pollution through increasing the soil and bark pH and nutrient input (e.g., Ca, Mg, and K) has a positive effect (to certain extent) on species richness in studied pine forests or on pine barks near the source of alkaline dust pollution. The rise of vascular species richness (e.g., Ksenofontova and Zobel 1987; Annuka 1995; Stravinskiene 2011) and increased diversity of epiphytic bryophytes (Kannukene 1995; Paal and Degtjarenko 2015) induced by alkalization of environment has been noted in several previous studies; other studies, however, have indicated the negative impact and the loss of species richness among vascular plants (Stravinskiene et al. 2004; Sujetovienė 2008), epigeic bryophytes (Meininger and Spatt 1988; Auerbach et al. 1997), *Sphagnum* mosses among others, in naturally acidic ombrotrophic bogs (Paal et al. 2010; Vellak et al. 2014). This difference might be explained by the immigration time, initial natural conditions, pollution load, and variation in regional species pool size or availability of alternative species in the region, accumulated in communities with different environmental conditions. Indeed, in the neighbourhood of studied pine forest communities in Kunda (I), there were boreo-nemoral and limestone escarpment forests, which are characterized by high richness of vascular plant species and bryophytes, among them several red-listed species (Paal 2001; Ingerpuu et al. 2003).

Therefore, those adjacent forests may also contribute to availability of alternative species in Kunda region (I).

We also revealed that species responded with different sensitivity to the changes in the environment, revealing their different ecological niche width along the pH gradient (Fig. 4). The niche width of species along the pollution gradient ranged among species and only a few species acted as pH generalists. The pH specificity of species, and the species niche widths along the dust pollution gradient, demonstrated that the species pool of calcicolous species was several times larger than species pool of acidophilous species, which was presumed according to large-scale analyses (Pärtel 2002; Ewald 2003). We also proposed that species filtering success is regulated, as suggested by Tilman (1988), by a critical level at the one end of the niche width along the limiting gradient (Lawesson 2003; Lõhmus and Kull 2011). In general, the study in paper I supported the classical individualistic approach of community assembly (Gleason 1926; Tilman 1988). According to that theory, species arriving in the community are filtered from the available species pool (Zobel 1997) not by their environmental average tolerance, but by niche thresholds or niche location and width along the limiting factor gradients. The species ecological niche space boundaries could be useful and could be kept in long-term database for future floristic studies.

Moreover, we found that alkaline dust pollution revealed a ‘parapositive’ effect on species diversity. We recorded several locally rare species [(e.g., bryophytes *Leskea polycarpa*, *Orthotrichum diaphanum*, and *Pseudoleskeella catenulata*, red-listed in Estonia as NT (Vellak et al. 2015), and e.g., lichens *Agonimia tristicula*, *Strangospora pinicola*, and *Caloplaca ulcerosa* (red-listed in Estonia as VU; Randlane et al. 2008)], two woodland key habitat bryophyte indicators (*Anomodon longifolius* and *Ulota crispa*), and two woodland key habitat lichen indicators (*Alyxoria varia* and *Pseudoschismatomma rufescens*) on pines at the closest distance from the pollution source (Estonian Acts of Law 2016). In the areas heavily polluted by cement dust, several orchids species having conservation value in Estonia were also recorded. The altered environment, e.g., increased bark pH of Scots pines or soil, dust cover and other changed environmental conditions, such as drier microclimatic conditions (Loppi and Pirintsos 2000), in dust-polluted areas could eventually shape a particular and alternative habitat for species, contributing to diversification of communities and the distribution of locally rare species. Although some rare species can even benefit from these environmental changes induced by pollution, the alkaline dust pollution has heavily disturbed the natural communities (I, III) and affected the genetic diversity of lichen populations (IV) in the vicinity of pollution sources. Those artificial communities containing rare or protected taxa are temporary phenomena, depending strongly on the continuation of pollution (Gilbert 1976). Consequently, those disturbed areas have a scientific importance as long-term ecological experiments but they do not contribute permanently to the local species richness.

4.4. The effects of dust pollution on genetic diversity of *Usnea subfloridana* populations (IV)

Little is known about impacts of environmental pollution on the genetic pattern of cryptogams. For example, extensive urban pollution lowered the genetic diversity of the epiphytic bryophyte *Leptodon smithii* (Spagnuolo et al. 2007); moreover, gene diversity was correlated with airborne trace element content in moss tissue (Spagnuolo et al. 2009). No studies have been performed concerning the genetic variation of populations of lichenized fungi in air polluted conditions; however, lower genetic diversity of the photobionts of the lichenized fungus *Parmotrema tinctorum* was demonstrated in the urban area compared to that in suburbs and mountainsides (Ohmura et al. 2006).

We compared the variables of genetic diversity of eight *Usnea subfloridana* populations, a common lichen-forming fungus, from different habitats (polluted vs unpolluted) and defined that several variables of genetic variation were significantly different in *U. subfloridana* populations. Populations that developed under road dust pollution revealed significantly lower values of the allelic richness (A), Shannon's information index (I), and genetic diversity (H) than populations in unpolluted forest sites (Table 2). Previous studies have demonstrated that habitat quality was a crucial factor shaping the genetic variation of lichenized fungi populations (Werth et al. 2006; Jürriado et al. 2011; Ojalora et al. 2011). At the same time, long-term dust pollution can change drastically local environmental conditions in the vicinity of the source of dust pollution (**I**, **II**, **III**), and influence the natural composition of epiphytic lichen communities and alter the species richness of lichens (Marmor et al. 2010; Paoli et al. 2014; **III**). The habitats located near the dusty roads suffer from similar changes (Marmor and Randlane 2007; Madl et al. 2010). Results of this study also indicated the increased mean bark pH value (5.9–6.6) of spruces growing in polluted habitats, while natural pH value of spruce bark is about 3.3–3.8 in unpolluted sites of Estonia (Marmor et al. 2010; 3.5–3.6 in our sites without dust pollution). Furthermore, *Usnea* species are usually sensitive to alkaline dust pollution (Martin and Nilson 1992) and generally prefer a lower bark pH (Marmor and Randlane 2007). Additionally, alkaline dust pollution contributes to drier microclimatic conditions (Loppi and Pirintsos 2000), and thus decreases the habitat quality for *Usnea* species even more. Hence, we suggest that reduced habitat quality increased *Usnea* mortality, which could cause a decline in population size (not directly measured in this study). Therefore, studied *Usnea* populations in polluted habitats may have experienced a continuing bottleneck reducing the allelic richness (A) of *Usnea* populations in polluted habitats but not yet other examined measures of genetic variation (e.g., M or P) in this study. The measure of A is usually more sensitive to the impact of bottleneck and is reduced by bottlenecks faster than other commonly reported variables of genetic variation (Leberg 2002; Kalinowski 2004). The observed measures of I and H support our results (Table 2), although, those measures were not

corrected for sample size as A. The bottleneck analysis showed a strong evidence of the bottleneck only in one lichen population from polluted habitat in this study (Table 5 in paper **IV**). Still, it has been recently demonstrated that microsatellite-based bottleneck tests often either failed to recognize bottleneck in populations known to have experienced reductions or detected bottlenecks in putatively stable populations (Peery et al. 2012). For example, the significant heterozygosity excess was also detected under infinite alleles mutation model (IAM) in stable populations (Luikart and Cornuet 1998). Taking into account the insufficiency of microsatellite-based bottleneck tests, we hypothesize that probable population bottleneck (although detected only in one population from polluted habitat), which is caused by considerable changes of local environment due to the presence of alkaline dust pollution, may have reduced the genetic variation of studied *U. subfloridana* populations.

The observed changes in genetic diversity in *U. subfloridana* populations that were exposed to dust pollution may theoretically have also experienced the negative edge effect of habitat, which could disrupt spore dispersal and exchange of individuals or genes among populations, resulting in genetic drift, increasing the genetic differentiation between populations, and reducing the genetic variation (Frankham et al. 2010; Holderegger and Di Giulio 2010). However, exchange of individuals still exists between the populations according to AMOVA analysis that showed no genetic differentiation (1% differentiation; $\Phi_{RT}=0.01$; $P=0.06$) among the lichen populations from polluted and unpolluted habitats. Therefore, we consider population bottleneck more reasonable cause than negative edge effect for the reduced genetic variation in the studied populations of *Usnea subfloridana* in polluted habitats.

CONCLUSIONS

The current study reviewed long-term influence of alkaline dust pollution emitted from different sources (cement plant, limestone quarry, and unpaved road) on species diversity, including vascular plants, bryophytes, lichens, and alga; and, additionally, on the genetic diversity of populations of a common lichen-forming fungus in Estonia. The results of this thesis demonstrate considerable local contamination and destruction of natural communities around the sources of alkaline dust pollution, and provide different approaches of bio-indication of dust pollution.

In general, the results of this thesis can be summarized as follows.

1. Long-term dust pollution had a remarkable neutralizing effect on natural substrates in forest stands; both, the pH value of soil litter horizon and pine and spruce barks significantly decreased along an increasing distance from the sources of dust pollution. We also found that Ca, Mg, and K content of soil litter horizon followed the similar decreasing tendency along the dust pollution gradient. The resilience of soil litter horizon was observed but accumulated (over century persisted) pollution impact was still evident in the vicinity of Kunda cement plant.
2. The long-term alkaline pollution has caused destruction of natural communities and formation of novel communities in the vicinity of dust pollution sources. The alkaline pollution has induced remarkable and long-lasting successional changes in pine forest ecosystems and has caused the 'nemoralization' of the studied *Vaccinium myrtillus* site type pine forests close to Kunda cement plant. Dust pollution and its alkalizing effect on pine bark also provoked the shifts of epiphytic cryptogamic communities along a pollution gradient. The linear increase of species richness among vascular plants, epigeic and epiphytic bryophytes from unpolluted to newly formed polluted habitats was detected. The diversification took place by invasion of non-typical and pollution-tolerant species for local communities, including calcicolous species and species characteristic for nutrient-rich habitats. The increased bark pH from acidic to subneutral also favoured lichens that commonly occur on basic and nutrient-rich bark of deciduous trees or even limestone outcrops, while cover of lichens responded to dust pollution in a different way compared with cover of epiphytic bryophytes and *Trentepohlia umbrina*. We provided, for the first time, one-time inventory of the two cryptogamic groups (epiphytic bryophytes and mosses) growing on pine trees in the vicinity of limestone quarries.
3. The results of this study confirmed usability of several previously proposed bioindicators and suggested new, additional bioindicators of alkaline dust pollution among algae, lichens, bryophytes, and vascular plants. The presence of species being typical for mesotrophic and meso-eutrophic habitats (e.g., several orchid species) in vegetation of *Vaccinium myrtillus* site type forests or of cryptogams typical for basic nutrient-rich bark of

deciduous trees on originally acid-barked phorophytes could be used as bio-indication of dust pollution. We also outlined that total community changes, species richness and abundance of selected species groups could be also useful and helpful indicators of alkaline dust pollution in biomonitoring studies around sources of similar pollution.

4. Our results revealed ‘parapositive’ impact of alkaline dust pollution on natural communities, suggesting that pollution might, besides disturbing natural communities, temporarily also contribute to the distribution of rare and protected species. Despite the fact that some rare and protected species can even benefit from these drastic environmental changes induced by alkaline dust pollution, the dust pollution has heavily destroyed the natural communities in the vicinity of pollution sources. Such polluted areas with disturbed communities had a high scientific importance as long-term ecological experiments, but they are temporary phenomena, depending strongly on the continuance of pollution and are certainly not suggested as a tool for supporting rare taxa.
5. We revealed that species grouping along the alkaline dust pollution gradient indicates the existence of different ecological association in terms of ecological niche use, and establishment of a new community is defined by the tolerance level of each species. This result also supports the classical individualistic approach of community assembly. We also conclude that for future floristic studies to predict community changes and species co-existence, the species ecological niche space boundaries should be evaluated and kept in long-term data sets.
6. We recorded for the first time that long-term alkaline dust pollution released from unpaved roads had a negative impact on the genetic variation of *Usnea subfloridana* populations, a common species of lichen-forming fungi. We suggest that studied *Usnea* populations in polluted habitats may have experienced a continuing bottleneck reducing the allelic richness (A) of populations, but not yet other examined measures of genetic variation (e.g., M or P) in this study. The loss of genetic diversity and changes in genetic structure of populations of common lichen-forming fungi may serve as a warning to the vulnerability of lichen-forming fungi populations to environmental disturbances caused by air pollution.

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SUMMARY IN ESTONIAN

Aluselise tolmusaaste mõju taimede ja samblike mitmekesisusele: kooslustest geneetilise mitmekesisuseni

Keskkonnareostus (sh õhusaaste) ohustab märkimisväärselt üldist looduslikku mitmekesisust, avaldades mõju erinevatel bioloogilistel tasemetel – alates rakulisest ja koelisest tasemest kuni ökosüsteemide tasemeni. Näiteks õhusaastest tingitud keskkonnatingimuste muutused muudavad ka koosluste liigilist koosseisu, struktuuri ja funktsiooni, põhjustades tundlike liikide kadu või, vastupidi, saastet taluvate liikide sissetungi. On täheldatud, et keskkonnareostus võib mõjutada ka organismide geneetilist mitmekesisust erinevates liigirühmades. Selleks, et leevendada õhusaastest tekitatud kahju bioloogilisele mitmekesisusele, on vajalik hinnata ja jälgida õhusaaste mõjusid, välja selgitada selle mõju ulatus ja otsida uusi võimalikke bioindikaatoreid täiendamaks õhuseirejaamade andmeid.

Paljude õhusaasteainete (nt SO_2 , CO , C_6H_6) emissioon on Euroopas oluliselt vähenenud, kuid tahkete osakeste (*particulate matter*, PM) või tolmu emissioon on endiselt terav probleem, kuna paljudes EL riikides ületatakse jätkuvalt EL-s lubatud PM saasteainete piirkontsentratsioone. Atmosfääriõhku saastavad tahked osakesed või tolmusaaste on kompleksne segu väikestest õhus heljuvatest osakestest, mis on erineva suurusega (ca. 0,1–10 μm), päritoluga (looduslik vs tööstuslik) ja keemilise koostisega. Käesolev töö on keskendunud jämedatele tolmuosakestele, mis vabanevad keskkonda lubjakivi kaevandamise käigus, tsemenditööstusest ja kruusateedelt. Tekkiv tolm sisaldab suures koguses CaCO_3 , MgO ja K_2O ning saasteainete vesilahus on tugevalt aluseline. Aluseline tolmusaaste on Eestis alati olnud oluline keskkonnaprobleem, kuna paljude aastate vältel moodustasid Eesti tööstusettevõtete poolt õhku paisatud saastest suure osa just tahked aluselised heitmed, mille mõjul tekkinud märkimisväärsed keskkonnamuutused Põhja-Eesti piirkonnas täheldati juba möödunud sajandi teisel poolel. Aluseline tolmusaaste võib liike otseselt mõjutada, põhjustades muutusi füsioloogilistes ja biokeemilistes protsessides, kuid võib mõju avaldada ka kasvukeskkonna (muld, puukoor, sademed) kaudu. Lisaks võib tolmusaaste kahjustada inimeste tervist, põhjustades hingamisteede ja südame-veresoonkonna haigusi ning suurendades suremuse riski.

Käesoleva töö peamine eesmärk oli uurida eri päritoluga pikaajalise aluselise tolmusaaste toimet boreaalsetele metsakooslustele (I), epifüütsetele sambliku-, sambla- ja vetikakooslustele mändidel (II, III) ning samblikku moodustava seeneliigi populatsioonide geneetilisele mitmekesisusele (IV). Töö detailsemateks eesmärkideks oli (1) välja selgitada tsemenditolmu pikaajaline mõju mustika (*Vaccinium myrtillus*) kasvukohatüübi metsakooslustele Kunda tsemenditehasest väljalastava õhusaaste mõjualas; (2) otsida uusi potentsiaalseid tolmusaaste indikaatoreid (I, II, III) ning hinnata rohevetika *Trentepohlia*

umbrina kasutamisevõimalusi tolmuksaaste indikaatorina (II); (3) uurida, kuidas lubjakivikarjäärade töötlemisprotsessis tekkiv tolmuksaaste muudab epifüütsete sammalde ja samblike liigilist koosseisu ja liigirikkust mändidel (III); (4) selgitada välja, kas ja kuidas muutub ühe tavalise, laialt levinud samblikku moodustava seeneliigi, vars-habesambliku (*Usnea subfloridana*) populatsioonide geneetiline varieerivus pikaajalise kruusateedelt lähtuva tolmuksaaste mõjul.

Kunda tsemenditehase ümbruses uuriti 20 ringkujulist prooviala suurusega 0,1 ha, kus iseloomustati puurinnet, puistu liituvust, puurinde järelkasvu, põõsarinnet ja alustaimestikku (sh maapinnal kasvavaid samblaid); lisaks koguti kolmest juhuslikust punktist mulla kõduhorisondi proove ning määrati nende pH, tuhasus, N-, P-, Ca-, K- ja Mg-sisaldus (I). Lubjakivikarjäärade mõjupiirkonnas mõõdeti 32-l proovialal samblike, sammalde ja rohevetika *Trentepohlia umbrina* katvus mändidel kasutades mõõdulindi meetodit, samas registreeriti kõikide männil kasvavate sammalde ja samblike esinemine 0,5 kuni kahe meetri kõrgusel ning koguti männikoort pH määramiseks (II, III). Vars-habesambliku populatsioonide geneetilise mitmekesisuse uurimuseks valiti kaheksa kuusel kasvavat populatsiooni, millest neli populatsiooni asusid kruusateede vahetus naabruses ning neli – saastamata/häirimata piirkonnas (IV). Ka selles uuringus näidati tolmuksaaste olemasolu sambliku kasvupinna, kuuse puukoore pH määramise kaudu. Vars-habesamblikku moodustava seene populatsioonide geneetilise varieeruvuse molekulaarseks uurimiseks kasutati üheksat seene-spetsiifilist polümorfset mikrosatelliitmarkerit (IV).

Käesolevas töös registreeriti kokku 86 liiki taimi (sh 25 maapinnal kasvavat sammalt) Kunda tsemenditehase mõjualas asuvates mustika kasvukohatüübi metsakooslustes (I) ning 34 epifüütset samblaliiki ja 84 samblikku lubjakivikarjäärade ümbruskonnas kasvavatel mändidel (III).

Töö tulemused kinnitavad, et pikaajaline tolmuksaaste on avaldanud neutraliseerivat mõju mulla keemilistele omadustele ning männi ja kuuse koorele; mulla ja puukoore pH on oluliselt tõusnud tolmuksaaste mõju piirkondades ja väheneb tolmuksaaste allikate kaugenedes (I–IV). Sarnaselt võib täheldada mulla kõduhorisondi Ca, Mg ja K sisalduse langustendentsi piki tolmu reostusgradienti (I). Saadud tulemuste põhjal võib järeldada, et Kunda tsemenditehase ümbruskonnas mulla seisund taastub pärast üle sajandi kestnud aluselist tolmuksaastet, kuid osade keemiliste elementide sisaldus mullas ja mulla pH on looduslikust foonist jätkuvalt mitmeid kordi kõrgem (I).

Pikaajaline aluseline tolmuksaaste on hävitanud looduslike kooslusi ning põhjustanud uudsete koosluste tekkimist tolmureostuse mõjupiirkondades. Saastatud ala mullastiku omaduste muutused on avaldanud olulist mõju taimestikule Kunda tsemenditehase ümbruses, põhjustades happelembeste/happetaluvate liikide järk-järgulist asendumist neutrofiilsete ja seejärel kaltsiifilsete liikidega (I). Sellega koos on toimunud koosluste mitmekesistumine ehk soontaimede, epigeiidsete ja epifüütsete sammalde liigirikkuse tõus tolmuksaaste mõjualadel (I, III). Aluselise tolmuksaaste mõjul täheldasime ka epifüütsete koosluste nihkeid mändidel (III). Männi puukoore vähenenud happelisus soodustas mändidel tavaliselt mittekasvavate, kõrgemat pH taset eelistavate liikide esinemist

(III). Epifüütsete sammalde ja *Trentepohlia umbrina* katvus mändidel oli kõrgem ning vähenes tolmusaaste allikate kaugenedes, samas kui samblike üldkatvus muutus teisiti – suurenes tolmusaaste allikate kaugenedes (II, III).

Käesoleva töö tulemused kinnitasid mõnede eelnevalt teadaolevate bioindikaatorite kasutatavust. Samas pakkusime välja mitmed uued tolmusaaste indikaatorliigid: näiteks samblikud *Alyxoria varia* (härma-kiiriksamblük) ja *Lecidella elaeochroma* (piir-kärnsamblik), rohevetikas *Trentepohlia umbrina*, samblad *Orthotrichum pallens* (kahkjäs tutik), *Orthotrichum speciosum* (tüvetutik) ja *Schistidium apocarpum* (harilik lõhistanukas) mändidel või *Neottia ovata* (suur käopõll) mustika kasvukohatüübi metsakooslustes (I–III). Väidame, et liigilise koosseisu, liigirikkuse ja katvuse muutused mõnedes organismirühmades võivad olla abiks tolmusaaste inditseerimisel.

Töös registreeriti esimest korda aluselise tolmusaaste negatiivne mõju samblikku moodustava seeneliigi, vars-habesambliku (*Usnea subfloridana*) populatsioonide geneetilisele mitmekesisusele (IV). Kruusateede vahetus läheduses kasvavate vars-habesambliku populatsioonides ilmneb pudelikaela efekt, mille tulemusel on vähenenud alleelide mitmekesisus, kuid mitte veel teised uuritud geneetilise varieeruvuse näitajad (IV). Populatsioonide geneetilise varieeruvuse kadu osutab vastupidavuse vähenemisele tolmusaastest põhjustatud keskkonnahäiringute suhtes (IV).

Veel ilmnes, et aluseline tolmusaaste mõjub looduslikele kooslustele “parapositiivselt” aidates looduslike koosluste häirimise kõrval kaasa haruldaste ja kaitstavate liikide levikule (I, III). Sellised häiritud kooslustega saastatud piirkonnad on kui kõrge teadusliku väärtusega pikaajalised ökoloogilised katsealad, samas on tegemist ajutise nähtusega, mis sõltub suurel määral saastuse kestvusest ning see ei ole haruldaste liikide leviku soodustamise soovitatav praktika.

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PUBLICATIONS

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Current position: University of Tartu, Institute of Ecology and Earth Sciences,
Department of Botany, Junior Research Fellow
University of Tartu, Institute of Ecology and Earth
Sciences, Department of Botany, PhD student

Education:
2012– University of Tartu, PhD candidate in Botany and Ecology
2008–2010 University of Tartu, MSc in Environmental Technology
2005–2008 University of Tartu, BSc in Ecology and Biodiversity
Conservation
1993–2005 Ahtme Gymnasium

Language skills: Estonian, English, Russian

Professional employment:
2015– University of Tartu, Institute of Ecology and Earth
Sciences, Department of Botany, Junior Research Fellow
2014 Estonian Fund for Nature, Translator
2011–2012 Estonian Agricultural Board, Main Specialist of Land
Reclamation

Research interests:
boreal forest ecosystems in response to long-term dust pollution, bioindication,
epiphytic cryptogamic communities, population genetics of lichenized fungi

Publications:

Degtjarenko, P., Marmor, L., Tõrra, T., Lerch, M., Saag, A., Randlane, T. &
Scheidegger, C. (2016) Impact of alkaline dust pollution on genetic variation
of *Usnea subfloridana* populations. *Fungal Biology* **120**: 1165–1174.
Degtjarenko, P., Marmor, L. & Randlane, T. (2016) Changes in bryophyte and
lichen communities on Scots pines along an alkaline dust pollution gradient.
Environmental Science and Pollution Research **23**: 17413–17425.

- Paal, J. & **Degtjarenko, P.** (2015) Impact of alkaline cement-dust pollution on boreal *Pinus sylvestris* forest communities: a study at the bryophyte synusia level. *Annales Botanici Fennici* **52**: 120–134.
- Marmor, L. & **Degtjarenko, P.** (2014) *Trentepohlia umbrina* on Scots pine as a bioindicator of alkaline dust pollution. *Ecological Indicators* **45**: 717–720.
- Paal, J., **Degtjarenko, P.**, Suija, A. & Liira, J. (2013) Vegetation responses to long-term alkaline cement dust pollution in *Pinus sylvestris*-dominated boreal forests – niche breadth along the soil pH gradient. *Applied Vegetation Science* **16**: 248–259.

Conference presentations:

- Degtjarenko, P.**, Marmor, L., Tõrra, T., Lerch, M., Saag, A., Randlane, T. & Scheidegger, C. “The genetic diversity of a widespread epiphytic lichen *Usnea subfloridana* (Parmeliaceae, Ascomycota) in response to alkaline dust pollution”. Oral presentation in the 8th International Association for Lichenology Symposium 2016, 1–5 August, Helsinki, Finland.
- Degtjarenko, P.**, Mandel, T., Tõrra, T., Marmor, L., Saag, A. & Randlane, T. “The habitat traits drive genetic diversity of a widespread epiphytic lichen *Usnea subfloridana* in hemiboreal forests”. Poster presentation in the 8th International Association for Lichenology Symposium 2016, 1–5 August, Helsinki, Finland.
- Degtjarenko, P.**, Marmor, L. & Randlane, T. “Changes in lichen and bryophyte communities on Scots pines along an alkaline dust pollution gradient”. Poster presentation in the 8th International Association for Lichenology Symposium 2016, 1–5 August, Helsinki, Finland.
- Degtjarenko, P.**, Marmor, L., Tõrra, T., Lerch, M., Saag, A., Randlane, T., & Scheidegger, C. “Assessing the impact of alkaline dust pollution on the genetic variation of lichen *Usnea subfloridana* (lichenized Ascomycota, Parmeliaceae)”. Oral presentation in the XX Cryptogamic Botany Symposium 2015, 22–25 July, Porto, Portugal.
- Degtjarenko, P.** & Marmor, L. “*Trentepohlia umbrina* on Scots pine as a bioindicator of alkaline dust pollution”. Poster presentation in the XX Cryptogamic Botany Symposium 2015, 22–25 July, Porto, Portugal.
- Degtjarenko, P.**, Marmor, L. & Randlane, T. “Searching for ecological indicators of alkaline dust pollution”. Oral presentation in the doctoral student conference of Botany Department of UT, 13–14 November, Jäeneda, Estonia.
- Degtjarenko, P.**, Marmor, L., Tõrra, T., Randlane, T. & Scheidegger, C. “Genetic diversity of *Usnea subfloridana* (lichenized Ascomycota) populations in conditions of moderate dust pollution”. Oral presentation in the XIX Symposium of the Baltic Mycologists and Lichenologists 2014, 22–26 September, Šķēde, Latvia.

Awards and scholarships:

- 2015, 2016 Kristjan Jaak Scholarships, Archimedes Foundation
2015 Travel grant from the Doctoral School of Ecology and Earth Sciences
2014 DoRa Activity 6 and 8 scholarships, Archimedes Foundation

Teaching experience at universities:

- 2015/2016 University of Tartu, LOOM.01.038 Field Course of Taxonomy of Fungi
University of Tartu, LOOM.01.107 Practical Mycology and Lichenology
Euroacademy (Tallinn), EM1070 Forest Monitoring
Euroacademy (Tallinn), GPRU6091 Fundamentals of Research
2014/2015 University of Tartu, LOOM.01.038 Field Course of Taxonomy of Fungi
University of Tartu, LOOM.01.107 Practical Mycology and Lichenology
2013/2014 University of Tartu, LOOM.01.038 Field Course of Taxonomy of Fungi
University of Tartu, LOOM.01.107 Practical Mycology and Lichenology
Euroacademy (Tallinn), EM1070 Forest Monitoring
Euroacademy (Tallinn), ER1050 General Biology
2012/2013 University of Tartu, LOOM.01.038 Field Course of Taxonomy of Fungi
University of Tartu, LOOM.01.107 Practical Mycology and Lichenology

Dissertations supervised:

- 2016 Tiina Mandel, Genetic variability of *Usnea subfloridana* populations in Estonia, MSc thesis (co-supervised with Tiina Randlane)
2014 Kristina Metsanurk, The effect of dust pollution on lichen diversity, BSc thesis

Participation in international courses:

- 2015 PhD course "Lichen ecology and identification", Swedish University of Agricultural Sciences, Sweden
2014 PhD course "Lichen ecology and biology", Swedish University of Agricultural Sciences, Sweden

Other activities:

- Research stay at Biodiversity and Conservation Biology unit led by Prof. Christoph Scheidegger (Swiss Federal Institute for Forest, Snow and Landscape Research WSL), January–February 2014, Switzerland.

- Lichen inventory in Karula National Park, summer-autumn 2014.
- Reviewer of National Contest of Young Scientists, organized by Estonian Research Council, 2014–2016.
- Different activities in popularization of science and lichenology, 2012–2016.

ELULOOKIRJELDUS

Nimi: Polina Degtjarenko
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Praegune töökoht: Tartu Ülikool, ökoloogia ja maateaduste instituut, botaanika osakond, nooremteadur
Tartu Ülikool, ökoloogia ja maateaduste instituut, botaanika osakond, doktorant

Haridus:
2012– Tartu Ülikool, doktoriõpe botaanika ja ökoloogia erialal
2008–2010 Tartu Ülikool, magistrikraad keskkonnatehnoloogias
2005–2008 Tartu Ülikool, bakalaureusekraad ökoloogias ning elustiku kaitses
1993–2005 Ahtme Gümnaasium

Keelteoskus: eesti, inglise, vene (emakeel)

Töökogemus:
2015– Tartu Ülikool, nooremteadur
2014 Eestimaa Looduse Fond, tõlkija
2011–2012 Põllumajandusamet, maaparanduse valdkonna peaspetsialist

Peamised uurimisvaldkonnad:

boreaalsed metsakooslused tolmusaaste mõju piirkondades, epifüütsete krüptogaamide kooslused, bioindikatsioon, samblikke moodustavate seente populatsioonigenetika

Teaduspublikatsioonide loetelu:

Degtjarenko, P., Marmor, L., Tõrra, T., Lerch, M., Saag, A., Randlane, T. ja Scheidegger, C. (2016) Impact of alkaline dust pollution on genetic variation of *Usnea subfloridana* populations. *Fungal Biology* **120**: 1165–1174.
Degtjarenko, P., Marmor, L. ja Randlane, T. (2016) Changes in bryophyte and lichen communities on Scots pines along an alkaline dust pollution gradient. *Environmental Science and Pollution Research* **23**: 17413–17425.

- Paal, J. ja **Degtjarenko, P.** (2015) Impact of alkaline cement-dust pollution on boreal *Pinus sylvestris* forest communities: a study at the bryophyte synusia level. *Annales Botanici Fennici* **52**: 120–134.
- Marmor, L. ja **Degtjarenko, P.** (2014) *Trentepohlia umbrina* on Scots pine as a bioindicator of alkaline dust pollution. *Ecological Indicators* **45**: 717–720.
- Paal, J., **Degtjarenko, P.**, Suija, A. ja Liira, J. (2013) Vegetation responses to long-term alkaline cement dust pollution in *Pinus sylvestris*-dominated boreal forests – niche breadth along the soil pH gradient. *Applied Vegetation Science* **16**: 248–259.

Konverentsiettekanded:

- Degtjarenko, P.**, Marmor, L., Tõrra, T., Lerch, M., Saag, A., Randlane, T. ja Scheidegger, C. “The genetic diversity of a widespread epiphytic lichen *Usnea subfloridana* (Parmeliaceae, Ascomycota) in response to alkaline dust pollution”. Suuline ettekanne 8. Rahvusvahelisel lihhenoloogide ühingu sümpoosionil, 1–5. august, 2016, Helsingi, Soome.
- Degtjarenko, P.**, Mandel, T., Tõrra, T., Marmor, L., Saag, A. ja Randlane, T. “The habitat traits drive genetic diversity of a widespread epyphytic lichen *Usnea subfloridana* in hemiboreal forests”. Posterettekanne 8. Rahvusvahelisel lihhenoloogide ühingu sümpoosionil, 1–5. august, 2016, Helsingi, Soome.
- Degtjarenko, P.**, Marmor, L. ja Randlane, T. “Changes in lichen and bryophyte communities on Scots pines along an alkaline dust pollution gradient”. Posterettekanne 8. Rahvusvahelisel lihhenoloogide ühingu sümpoosionil, 1–5. august, 2016, Helsingi, Soome.
- Degtjarenko, P.**, Marmor, L., Tõrra, T., Lerch, M., Saag, A., Randlane, T. ja Scheidegger, C. “Assessing the impact of alkaline dust pollution on the genetic variation of lichen *Usnea subfloridana* (lichenized Ascomycota, Parmeliaceae)”. Suuline ettekanne XX Krüptogaamilise botaanika sümpoosionil, 22–25. juuli, 2015, Porto, Portugal.
- Degtjarenko, P.** ja Marmor, L. “*Trentepohlia umbrina* on Scots pine as a bioindicator of alkaline dust pollution”. Posterettekanne XX Krüptogaamilise botaanika sümpoosionil, 22–25. juuli, 2015, Porto, Portugal.
- Degtjarenko, P.**, Marmor, L. ja Randlane, T. “Searching for ecological indicators of alkaline dust pollution”. Suuline ettekanne Botaanika osakonna doktorantide konverentsil, 13–14. november, 2014, Jäeneda, Eesti.
- Degtjarenko, P.**, Marmor, L., Tõrra, T., Randlane, T. ja Scheidegger, C. “Genetic diversity of *Usnea subfloridana* (lichenized Ascomycota) populations in conditions of moderate dust pollution”. Suuline ettekanne XIX Balti mükoloogide ja lihhenoloogide sümpoosionil, 22–26. september, 2014, Šķēde, Lāti.

Uurimistoetused ja stipendiumid:

- 2015, 2016 Kristjan Jaagu välissõidu stipendiumid, SA Archimedes, Euroopa Sotsiaalfond
- 2015 Välissõidutoetus, maateaduste ja ökoloogia doktorikool
- 2014 ESF DoRa T8 ja T6 stipendiumid, SA Archimedes, Euroopa Sotsiaalfond

Õppetöö läbiviimise kogemus kõrgkoolis:

- 2015/2016 Tartu Ülikool, LOOM.01.038 Fungistika välipraktika
Tartu Ülikool, LOOM.01.107 Mükoloogia ja lihhenoloogia praktikum
Euroakadeemia (Tallinn), EM1070 Metsaseire
Euroakadeemia (Tallinn), GPRU6091 Uurimistöö alused
- 2014/2015 Tartu Ülikool, LOOM.01.038 Fungistika välipraktika
Tartu Ülikool, LOOM.01.107 Mükoloogia ja lihhenoloogia praktikum
- 2013/2014 Tartu Ülikool, LOOM.01.038 Fungistika välipraktika
Tartu Ülikool, LOOM.01.107 Mükoloogia ja lihhenoloogia praktikum
Euroakadeemia (Tallinn), EM1070 Metsaseire
Euroakadeemia (Tallinn), ER1050 Üldine bioloogia
- 2012/2013 Tartu Ülikool, LOOM.01.038 Fungistika välipraktika
Tartu Ülikool, LOOM.01.107 Mükoloogia ja lihhenoloogia praktikum

Juhendatud väitekirjad:

- 2016 Tiina Mandel, Vars-habesambliku (*Usnea subfloridana*) populatsioonide geneetiline mitmekesisus Eestis, magistritöö (Tiina Randlese kaasjuhendamisel)
- 2014 Kristina Metsanurk, Tolmusaate mõju samblike mitmekesisusele, bakalaureusetöö

Osalemine kursustel:

- 2015 Doktorantide kursus "Samblike ökoloogia ja määramine", Uppsala Põllumajandusülikool, Rootsi
- 2014 Doktorantide kursus "Samblike ökoloogia ja bioloogia", Uppsala Põllumajandusülikool, Rootsi

Muu erialane tegevus:

- Uurimistegevus biodiversiteedi uuringute töörühmas prof. Christoph Scheideggeri juhendamisel Metsa-, Lume- ja Maastiku-uuringute Instituudis (Swiss Federal Institute for Forest, Snow and Landscape Research, WSL), Šveitsis, jaanuar-veebruar 2014.

- Samblike inventeerimine Karula Rahvuspargis, suvi-sügis 2014.
- Õpilaste teadustööde retsenseerimine Eesti Teadusagentuuri poolt korraldatud riikliku konkursi raames, 2014–2016.
- Erinevad teaduse ja lihhenoloogia populariseerimisega seotud tegevused, 2012–2016.

DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

1. **Toivo Maimets.** Studies of human oncoprotein p53. Tartu, 1991, 96 p.
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3. **Kristjan Zobel.** Epifüütsete makrosamblike väärtus õhu saastuse indikaatoritena Hamar-Dobani boreaalsetes mägimetsades. Tartu, 1992, 131 lk.
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