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RESEARCH ARTICLE

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Effect of environmental factors on the composition of terrestrial bryophyte and lichen species in Scots pine forests on fixed sand dunes

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Abstract

Aim of the study: To investigate terrestrial bryophyte and lichen species richness and environmental factors affecting the composition of species.

Area of the study: Four Boreal zone fixed dunes were selected in the coastal area of the Baltic Sea in southwest Estonia.

Material and methods: Non-metric multidimensional scaling was performed to analyse distribution patterns and environmental factors like canopy cover, photosynthetically active radiation, soil organic horizon thickness and decomposition rates, soil volumetric water content, soil pH and electrical conductivity and soil nutrients correlated with bryophyte and lichen species composition.

Main results: Thirty bryophytes and 22 lichens were found on 232 sample plots, the most frequent species were *Pleurozium schreberi* (Willd. ex Brid.) Mitt., *Hylocomium splendens* (Hedw.) Schimp., *Dicranum polysetum* Sw. ex anon., *Cladonia arbuscula* (Wallr.) Flot. and *Cladonia furcata* (Huds.) Schrad. The lichen species richness was highest on the slopes of the dunes and decreased towards the bottoms and tops; bryophyte species richness was higher on the bottoms and decreased towards the tops of the dunes.

Research highlights: The composition of bryophytes and lichens is significantly influenced by the aspect and the location on the dune, light conditions, soil pH, soil salinity (measured as electrical conductivity) and volumetric water content, thickness of moderately decomposed organic horizon and vascular plant species cover.

Additional keywords: Inland dunes; terrestrial bryophyte and lichen communities; environmental factors; topography.

Authors´ contributions: Original idea and study design: MT. Data collection: MT and KO. Data analysis: TT and MT. Manuscript preparation and revisions: MT, KO and TT.

Supplementary material: (Table S1) and (Figure S1) accompany the paper on FS's website.

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Introduction

During the last century in Europe, mainly due to urbanization and other human-related factors, a reduction of about 70% of the dune systems has been estimated (Mc Lachlan & Brown, 2006). Vegetated dunes are complicated and fragile ecosystems which have a very high ecological and conservative value (Lemauviel *et al.*, 2003; Van der Maarel, 2003). Lichens and bryophytes have principal functional importance on boreal zone inland dune forests (Ahti & Oksanen, 1990); bryophytes dominate the forest floor vegetation and play an important role in the water and carbon budgets and improve microenvironment (Bond-Lamberty & Gower, 2007; Márialigeti *et al.*, 2016) while lichens colonize open sand surfaces and create suitable conditions for vascular plants (Ketner-Oostra & Sykora, 2000). Maintenance of biodiversity is an integral part of sustainable forest management which is a desirable goal for most forest-related initiatives and legislative bodies. Assessment of biological diversity is essential for understanding forest ecology and measuring sustainable forest management binds conservation and enhancement of biological diversity (MCPFE Liaison Unit Vienna, 2002; Canullo *et al.*, 2013). According to Pharo *et al.* (1999) the bryophytes and lichens have different patterns of diversity compared to vascular plant species and therefore management practices and conservation actions should take into account the specialty.

Multiple studies have been conducted to clarify lichen and bryophyte distribution and richness and to give insight into the different factors that influence their growth in forests. These factors include substrate availability (Pharo *et al.*, 1999; Ingerpuu, 2002), litter composition and quality (Hill, 1979; Magnusson, 1982;), soil nutrients (especially magnesium) and acidity (pH) (Oechel & Van Cleve, 1986; Pausas, 1994; Jun & Rozé, 2005; Kösta & Tilk, 2008; Košuthovà *et al.*, 2015; Jüriado *et al.*, 2016), light conditions and soil moisture (Ketner-Oostra & Sykora, 2000; Márialigeti *et al.*, 2016) and the cover of vascular plant species (Löbel *et al.*, 2006). Also, studies have pointed out stress and disturbance as important factors affecting cryptogam communities (Forey *et al.*, 2008; Cogoni *et al.*, 2011; Ciccarelli, 2015).

Topographical factors, especially the height and slope aspect, have been modestly discussed when bryophytes and lichens are concerned, whereas for the vascular plant species richness and composition the slope effect has been considered as an important factor (Jenny, 1941; Sewerniak, 2016; Sewerniak *et al.*, 2017; Tilk *et al.*, 2017). In northern hemisphere north-facing slopes receive six times less solar radiation compared to south-facing slopes and therefore microclimatic conditions on the slopes vary greatly (Auslander *et al.*, 2003; Mandre *et al.*, 2008; Sewerniak *et al.*, 2017; Sewerniak & Jankowski, 2017). Therefore, a respective variation in the species richness and composition of the understory vegetation can be expected as well (Solon *et al.*, 2007; Sewerniak & Jankowski, 2017). Previous studies have provided data for the zonation of the vascular plant species composition along the dune profile (Zoladeski, 1991; Sewerniak & Jankowski, 2017; Tilk *et al.*, 2017); however, precise information is insufficient for lichens and bryophytes. Besides, thorough knowledge of the abundance of lichens and bryophytes, as well as on topographical and environmental factors that affect their patterns in forests on fixed dunes, is still lacking.

This paper is continuation of earlier works of Tilk *et al.* (2011; 2017), where the vascular plant species richness and environmental factors were investigated. The main aim of this paper is to describe the variability of the bryophyte and lichen layer on *Pinus sylvestris* dominated fixed dunes and to give a new insight into specific environmental and topographical factors that influence bryophyte and lichen communities and species distribution. The specific objectives of the study were (1) to determine if bryophyte and lichen species richness varies along the topographical gradient on dunes; (2) to study whether zoning of the bryophyte and lichen species composition along the dune profile is possible; (3) to analyse the variability of bryophyte and lichen species in dune forests based on ecological indicator values (Düll, 1991; Wirth, 2010); and (4) to analyse the influence of environmental and topographical factors on the composition of the bryophyte–lichen layer.

Material and Methods

Study area

The investigated dune system is situated in Southwest Estonia, in the coastal area of the Baltic Sea (Fig. 1). The dunes are located on the Uulu-Võiste landscape protection area and on the Luitemaa nature reserve where, the following priority habitats according

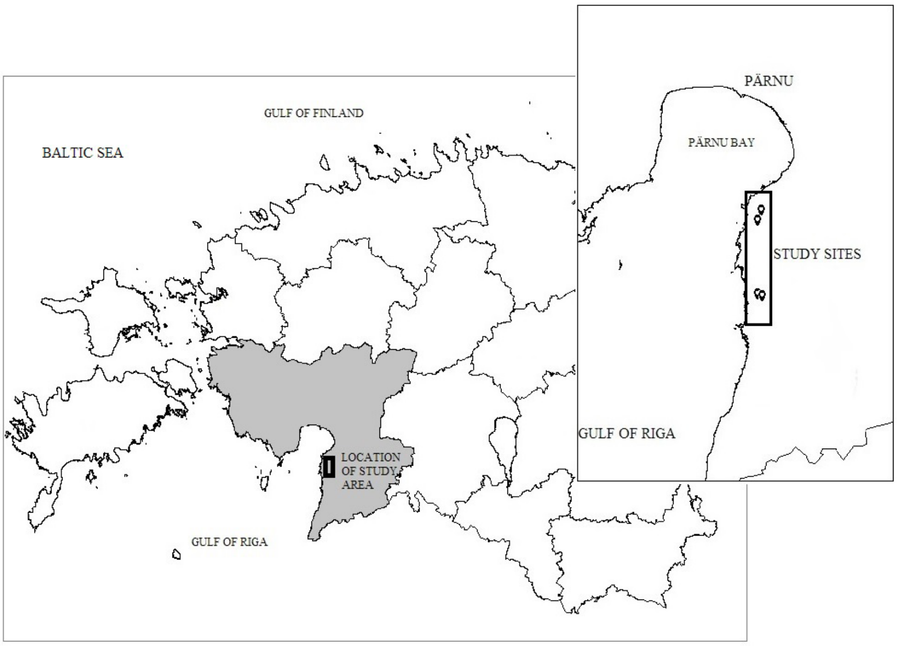

Figure 1. Location of study area and study sites in Estonia.

to Council Directive 92/43/EEC (1992), are protected: wooded dunes of the Atlantic, Continental and Boreal region (type 2180), Western Taïga (type 9010), Fennoscandian deciduous swamp woods (type 9080), fixed coastal dunes with herbaceous vegetation (grey dunes) (type 2130) and humid dune slacks (type 2190).

For the investigation of bryophyte and lichen flora on wooded dunes of different height, four sampling sites were selected (Table 1). Sampling sites distance to Baltic Sea (Pärnu Gulf) is ranging between 2 and 3 km.

According to information from State Forest Management Centre database the dunes belong to the *Cladonia* and *Vaccinium vitis-idaea* forest site type, where the average stand age is 195 years; the average stand canopy cover is 55%; the average height of pines is 23 m; the site quality index is IV and the density of the understorey is low.

According to the closest weather station of the Estonian Weather Service in Pärnu, the main climate characteristics during the period of our investigations in 2010 were as follows: average annual temperature 5 ºC with maximum average of 21.8 ºC in July and minimum average of -12.3 ºC in January; total average precipitation 908 mm with maximum of 122.8 mm in August and minimum of 27 mm in January.

Mean relative air humidity was 84% in the area. The length of the thermal growing period (mean temperature above 5 ºC) was 203 days (from 25.04.2010 to 14.11.2010). During the winter of 2009/2010 there was permanent snow cover recorded of 112 days (11.12.2009 — 01.04.2010) and throughout winter there was altogether 143 days with snow.

Methods

Field studies on four *Pinus sylvestris* dominated dunes were carried out in July 2010 for bryophyte and lichen species determination. On every dune, quadrats with the size of 1 m^2 formed a continuous transect over the dune, starting from the bottom in front of the dune and moving over the top to the bottom beyond with the distance of one meter between the quadrats (n = 232). Additional quadrats (n = 464) to determine species that did not occur on the basic quadrats of the transect were placed one meter to the left and one meter to the right of the basic quadrat. Data about species found on the additional quadrats were added into overall species list but were not included into the further statistical analysis.

On every quadrat, the total cover of the bryophyte and lichen layer, the total cover of vascular plants and the cover of each bryophyte and lichen species were estimated visually, using the scale 1—100%. Dominant species were determined based on Braun-Blanquet five-point cover-abundance scale: 5 — very abundant; 4 — abundant; 3 — plentiful; 2 — sparsely; 1 — single. The individuals that could not be identified in the field were collected and determined in the laboratory; species identification included using the Tallinn Botanical Garden bryophyte and lichen herbarium for comparative analysis. The nomenclature of lichens and bryophytes follows Randlane *et al.* (2016) and Ingerpuu *et al.* (1998) respectively.

On every quadrat, canopy cover was assessed visually by two evaluators as a measure of the percentage of forest floor covered by a vertical projection of the tree canopies expressed at scale 0 to 1 (Masing, 1979; Pihelgas, 1983). Below-canopy photosynthetically active radiation (PAR, μmol m^{-2}s^{-1}) was measured (n = 10 per quadrat) with light interception device AccuPAR (Model PAR-80) in 23 of July 2008 at midday full sunshine. As light is highly variable, measurements were performed simultaneously during a very short time period (from 11:00 to 13:00) at all sites.

Absolute heights (meters above sea level, m.a.s.l) and aspects of the quadrats on the dune slopes (N; S; E; W) were determined using Garmin GPSMap 76CSx device and relative heights were calculated using the first quadrat on the bottom of the dune as a zero. An inclinometer was used to assess the incline of slopes and quadrats were classified into five groups according to angle value: 1 (1 — 10 degrees); 2 (11 — 20 degrees); 3 (21 — 30 degrees); 4 (31 — 40 degrees) and 5 (41 — 50 degrees).

Table 1. Study sites, number and direction of quadrats.

Site No.	Coordinates	Absolute height of the dune (m.a.s.l)	Relative height of the dune (m)	No. of quadrats on the dune	Direction of the transect
Site 1	58º8´20”N 24º30´27”E	28	16	58	S->N
Site 2	58º8´23“N 24º30´36“E	33	21	108	W->E
Site 3	58º14´28“N 24º31´21“E	12	6	32	S->N
Site 4	58º13´51“N 24º30´47“E	10	6	34	W->E

Soil organic horizon (O-horizon) thickness and its decomposition rates: 1 — poorly decomposed (O_i) sub-horizon; 2 — medium decomposed (O_e) sub-horizon and 3 — well decomposed (O_a) sub-horizon, were assessed.

Volumetric water content (VWC, %) in the soil was determined in every quadrat with Field Scout™ TDR 300 at a depth of 20 cm (n = 3). The data were collected in May, July and September 2008 and there was no rain recorded at least 3 days before measurements. Soil samples of every quadrat were collected in July 2010 from a depth of 20 cm from ground level (for measuring soil pH and electrical conductivity). Soil pH and electrical conductivity were measured from a soil-distilled water mixture (1:2.5 or for samples with high organic matter 1:5) with Eutech Instruments PC300 pH/conductivity meter.

Soil samples from mineral topsoil for analysing nitrogen (N), phosphorous (P), potassium (K), calcium (Ca) and magnesium (Mg) content were collected from a depth of 20 cm (n = 15 per site) on the bottoms, slopes and tops of the dunes. The results are presented as N: P; N: K and Ca: Mg ratios and absolute values are presented in an article by Tilk *et al.* 2017. The concentrations of N, P, K, Ca and Mg in the mineral topsoil samples (n = 60) were determined in the Laboratory of Plant Biochemistry of the Estonian University of Life Sciences. The soil samples were analysed for their extractable concentration of P (ammonium lactate; by FiaStar5000 (Flow Injection Analyser)), K (ammonium lactate; Flame Photometric Method), Ca (ammonium acetate: Flame Photometric Method), Mg (ammonium acetate; by FiaStar5000 (Flow Injection Analyser)) and for total concentration of N (Copper Catalyst Kjeldahl Method).

Data analysis

Bryophytes and lichens were grouped based on the ecological indicator values of species according to Düll (1991) and Wirth (2010).

For statistical analysis, quadrats were grouped according to location based on the relative height and the angle of the quadrat as follows: bottom (n = 52 quadrats), slope (n = 142 quadrats) and top (n = 38 quadrats). Correlation analysis was performed with Microsoft Excel 2010 to determine relations between canopy cover and some topographical variables with the precondition of checked data normality. To clarify significant differences between groups one-way ANOVA of multiple groups followed by post-hoc Tukey HSD test using Tukey-Kramer formula for unequal observations was performed (Vasavada, 2016).

A linear mixed model using free statistical software R Version 3.2.3 (R Core Team, 2015) function "lmer" in package lme4 (Bates *et al.*, 2015) (with a site as a random factor) was applied to clarify the effect of location on environmental factors and cryptogams characteristics. If a statistically significant effect of location was observed, a Tukey HSD test was applied to compare the group means. A level of significance of α = 0.05 was used to reject the null hypothesis after statistical tests.

The effect of grouping factors on bryophyte and lichen data was tested using Multiple Response Permutation Procedure (MRPP) (Mielke *et al.*, 1976). To correct the p-values for multiple comparisons in MRPP, Bonferroni correction was applied. Indicator species analysis (ISA) was conducted to specify indicator species for different zones (Dufrene & Legendre, 1997). The statistical significance of indicator values was proven using Monte Carlo simulation. MRPP and ISA were performed with PC-ORD Version 6 (McCune & Mefford, 2011).

To analyse species distribution patterns and environmental variables correlated with bryophyte and lichen species composition, non-metric multidimensional scaling (NMDS) with free statistical software R Version 3.2.3 (R Core Team, 2015) in the community ecology package Vegan (Oksanen *et al.*, 2016) was performed. NMDS was run using the function "metaMDS" (default settings) and Bray-Curtis dissimilarities. For fitting environmental vectors and factors onto ordination, function "envfit" was used (Oksanen, 2015).

The analyses of species composition (MRPP and NMDS) were performed twice: 1) based on the abundance data of bryophytes and lichens; 2) based on the abundance data of bryophytes. Separate analysis based on lichen data was not performed, as lichens were present on only 22% of the studied quadrats.

Results

Environmental factors

Soils are Haplic Podzols with A-horizon on the bottoms and Haplic Podzol on the slopes and on tops of the dune. Average values for light conditions and soil characteristics are presented in Table 2. Canopy cover showed a negative correlation (r = -0.67) with the aspect of the quadrat, being higher on the northern and eastern quadrats and lower on southern and western quadrats. Canopy cover was significantly higher on the slopes (Table 2), while PAR showed no significant differences between locations on dunes. In addition, significant differences were found for soil volumetric water content (VWC), pH_{H2O} and electrical conductivity

Table 2. Average values (±SE) for photosynthetically active radiation (PAR, µmol $m^{-2}s^{-1}$), canopy cover, soil volumetric water content (VWC, %), pH, electrical conductivity (EC, µS cm^{-1}), average ratios of N:P, N:K and Ca:Mg and thicknesses of soil organic horizons with different decomposition rates (O_i — poorly decomposed; O_e — medium decomposed and O_a — well decomposed, cm) from different locations on the dunes according to linear mixed model. Letters denote significant differences between locations according to Tukey HSD test. Average values of soil and light characteristics from different locations on the dunes for each study site are presented in Tilk *et al*. 2017: table 4.

	Location on dune		
	Bottom	**Slope**	**Top**
PAR	420.4±64.2^a	440.4±54.5^a	431.1±70.0^a
Canopy cover	0.4±0.07^a	0.6±0.07^b	0.4±0.08^a
VWC	12.8±1.6^c	8.6±1.6^b	6.2±1.7^a
pH	4.2±0.1^a	4.4±0.1^b	4.4±0.1^b
EC	185.0±21.0^b	140.6±19.8^a	131.2±21.7^a
N:P	147.2±28.6^a	141.9±28.6^a	136.2±34.1^a
N:K	41.2±3.7^a	39.0±3.7^a	39.9±5.2^a
Ca:Mg	3.9±1.0^a	6.0±1.0^b	5.1±1.2^{ab}
O_i	2.8±0.4^a	2.6±0.4^a	2.7±0.5^a
O_e	5.3±0.9^a	4.5±0.9^a	5.7±1.1^a
O_a	1.0±0.7^a	0.9±0.7^a	0.0±0.8^a

between different locations (Table 2). Average soil VWC was highest on the bottoms of the dunes, being on average 48% higher compared to the top of the dunes. Average soil VWC on the north facing quadrats was significantly higher compared to the south, east and west facing quadrats ($p < 0.01$), while differences between soil volumetric water contents on the southern, western and eastern quadrats were not significant ($p > 0.05$).

Bottoms of the dunes also obtained higher electrical conductivity and lower soil pH values. The average values for N: P and N: K ratios were similar in all of the observed locations; only the Ca: Mg ratio showed statistically significant differences between bottoms and slopes (Table 2). Soil organic horizon averaged 9.1 cm on the bottom, 8 cm on the slope and 8.4 cm on the top of the dunes. The poorly decomposed organic layer made up 30.8% of the bottoms, 32.5% of the slopes and 32.1% of the tops of the dunes; the medium decomposed organic layer formed 58.2% of the bottoms, 56.3% of the slopes and 67.9% of the tops and the well decomposed organic horizon formed 11% of the bottoms, 11.3% of the slopes and was missing from the tops of the dunes.

Species richness and composition changes along topographical and environmental gradients

Altogether, 52 species of bryophytes and lichens were distinguished on the quadrats (30 species of bryophytes and 22 species of lichens). Bryophytes were present on all 232 quadrats while lichens were recorded on 50 quadrats. Six bryophyte species were common to all four dunes while 17 species were recorded only on one dune. The most frequent bryophyte species were *Pleurozium schreberi* (present on 90% of the quadrats), *Hylocomium splendens* (64%) and *Dicranum polysetum* (51%). None of the lichen species was recorded on all dunes; the most frequent lichen species, *Cladonia arbuscula* (present on 6% of the quadrats), was found on three dunes. Fourteen lichen species were recorded on only one dune. There were four species found on the additional quadrats: lichen *Cladonia cornuta* (L.) Hoffm. and bryophytes *Cephaloziella hampeana* (Nees) Schiffn., *Ptilidium pulcherrimum* (Weber) Vain. and *Scleropodium purum* (Hedw.) Limpr. *P. schreberi* dominated on 128 quadrats, *H. splendens* on 76 and *D. polysetum* on 11 quadrats. *Cladonia rangiferina* (L.) F.H. Wigg. (on four quadrats) was the only dominated lichen species more than once.

Average lichen species richness was the highest on the slopes of the dunes and decreased towards the bottoms and tops (Table 3). Bryophyte species richness was significantly higher on the bottoms of the dunes, decreasing towards the tops of the dunes. The cover of the bryophyte and lichen layer was remarkably higher on the tops, contrary to the cover of vascular plants, which was the highest on the bottoms of the dunes (Table 3).

Table 3. Average species richness for lichens (S_{Lichen}), bryophytes ($S_{Bryophyte}$), total cover of lichen and bryophyte layer ($Cover_{LichBryo}$) and total cover of vascular plant species layer ($Cover_{Vascular}$) (±SE) on different locations according to the linear mixed model. Letters denote significant differences between locations according to Tukey HSD test.

Location	S_{Lichen}	$S_{Bryophyte}$	$Cover_{LichBryo}$	$Cover_{Vascular}$
Bottom	0.1±0.1^a	3.0±0.2^b	82.9±5.0^{ab}	63.2±4.7^b
Slope	0.5±0.1^b	2.6±0.1^a	80.3±4.6^a	39.1±4.0^a
Top	0.1±0.2^a	2.5±0.2^a	91.6±5.3^b	43.6±5.1^a

According to the ecological indicator values (Düll, 1991), the highest number of bryophyte species were light-demanding species (with light value 8, 26% of all bryophyte species), while there were some (6% of bryophyte species) shade-tolerant species (Fig. S1 A [supplementary]). The moisture preference of bryophyte species was variable as the most frequent values of moisture index varied between 4 and 7, referring to the preference of moderately dry to moist habitats. Based on pH indices assigned to bryophyte species, the majority of species preferred acidic substrate; two species were with broad pH tolerance (Fig. S1 A [suppl.]).

Light index (according to Wirth, 2010) was not available for 36% of lichen species, however, according to available indices, lichens were mainly light-demanding species (the most frequent values of the light index were 7 and 8) (Fig. S1 B [suppl.]). Based on moisture and substrate pH indices, the highest number of lichen species was species with broad amplitude; however, it must be considered that moisture and substrate pH indices were unavailable for 8 lichen species in each case (Fig. S1 B [suppl.]).

According to the MRPP test based on zones on dunes, bryophyte and lichen communities were significantly different on the bottoms *versus* tops (p-value = 0.015) and slopes *versus* tops (p-value = 0.012) while bottoms and slopes showed no statistically significant differences (p-value = 0.535) (Table 4). When only bryophyte communities were concerned, slopes and tops were similar (p-value = 0.263), while bottoms *versus* slopes (p-value = 0.001) and bottoms *versus* tops (p-value = 0.002) showed statistically significant differences. The distribution of bryophyte and lichen species in different locations on the dunes is shown in Table S1 ([suppl.]). Indicator species analysis based on bryophyte and lichen species data pointed out characteristic species for zones on dunes: *Brachythecium erythrorrhizon, Brachythecium oedipodium* and *Hylocomium splendens* for the bottoms, *Ceratodon purpureus, Cladonia rangiferina* and *Cladonia stygia* for the slopes of the dunes and *Pleurozium schreberi* for the tops.

Table 4. The results of multiple response permutation procedure (MRPP) tests for the comparison of bryophyte and lichen species (p-value$_{bryolich}$) and bryophyte species (p-value$_{bryo}$) composition on different zones on dunes.

Test pair	Bottom *vs.* Slope	Bottom *vs.* Top	Slope *vs.* Top
p-value$_{bryolich}$	0.535	0.015	0.012
p-value$_{bryo}$	0.001	0.002	0.263

Bold values are significant after the Bonferroni correction.

Environmental factors affecting bryophyte and lichen species composition

NMDS analysis (Table 5) suggested that the most significant environmental factors (level of significance $p \leq 0.001$) affecting epigeic bryophytes and lichens were site-specific factors such as aspect and height of the quadrat, but also vascular plant cover, PAR, soil VWC, pH, electrical conductivity and thickness of O_e sub-horizon (Fig. 2). When only bryophyte communities were concerned, NMDS analysis pointed to the aspect, vascular plant cover, PAR, canopy cover, thickness of O_e sub-horizon and soil VWC, pH, and electrical conductivity as the most significant factors (Table 5).

Discussion

Coastal sand dunes are one of the most threatened ecosystems in the world because of human activities and plant invasion (Cogoni *et al.*, 2011; Vaz *et al.*, 2014). Changes in traditional land use and invasions of non-native species affect the composition and structure of native vegetation and may lead to loss of biodiversity (Latorre *et al.*, 2013; Rivis *et al.*, 2016). Most of the Estonian coastal vegetation consists of semi-natural plant communities with moderate human management (Rivis *et al.*, 2016). Lichens and bryophytes are considered to be pioneer species on open dune areas; they form habitats for other plants, collect humus and wither the substrate. They also play an important role in protecting the surface of the dunes from water and wind erosion (Cogoni *et al.*, 2011) as well as provide stability, nutrients and moisture to the soil (Fernández & Barradas, 1997). Therefore, the significance of lichens and bryophytes on dunes should not be underestimated. In northern and boreal temperate zones, lichen-rich assemblages are restricted to edaphically specific stressful environments with nutrient insufficiency (Košuthovà *et al.*, 2015).

In Estonia 594 species of bryophytes (according to Vellak *et al.*, 2015) and 1176 species of lichens (according to Randlane *et al.*, 2016) have been identified. In this study, a total of 30 species of epigeic bryophytes and 22 species of epigeic lichens were distinguished on the quadrats. In forests of the northern hemisphere, epigeic bryophyte communities are primarily dominated by a few common species with very broad ranges of tolerance such as *P. schreberi* (Frego, 2007). As regards this point, the dune forest in our study area is not an exception and *P. schreberi* was observed in 90% and *H. splendens* in 64% of the quadrats respectively. The species composition on Rannametsa dunes seems to have been quite stable over three decades as the most

Table 5. Relationships between species composition (NMDS ordination, Fig. 2) and environmental factors on the dunes. H_{rel} — relative dune height (m); H_{abs} — absolute dune height (m.a.s.l); PAR — below-canopy photosynthetically active radiation (µmol $m^{-2}s^{-1}$); VWC_{aver} — soil volumetric water content (%); AvpH — average pH_{H2O}; EC — average electrical conductivity (µS cm^{-1}); Cancov — canopy cover; O_i — poorly decomposed soil organic horizon thickness (cm); O_e — medium decomposed soil organic horizon thickness (cm); O_a — well decomposed soil organic horizon thickness (cm); A — humic horizon thickness (cm); N — nitrogen content (%); P — phosphorus content (mg kg^{-1}); K — potassium content (mg kg^{-1}); Ca — calcium content (mg kg^{-1}); Vasccov — vascular plant species coverage (%); Loc — location on dune; Asp — aspect of the quadrat (N; S; E; W). sc significance codes: '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'n.s.' not significant.

Variable	Bryophyes and lichens			Variable	Bryophytes		
	R^2	*p*-value	sc		R^2	*p*-value	sc
Asp	0.1846	0.001	***	Asp	0.182	0.001	***
Vasccov	0.1715	0.001	***	Vasccov	0.1805	0.001	***
PAR	0.1616	0.001	***	PAR	0.146	0.001	***
O_e	0.1191	0.001	***	VWC_{aver}	0.1082	0.001	***
Site	0.1102	0.001	***	O_e	0.0939	0.001	***
VWC_{aver}	0.0971	0.001	***	AvCond	0.0934	0.001	***
AvCond	0.0891	0.001	***	AvpH	0.0821	0.001	***
AvpH	0.0837	0.001	***	Site	0.0703	0.002	**
H_{abs}	0.0626	0.001	***	Cancov	0.0592	0.001	***
H_{rel}	0.0445	0.004	**	H_{rel}	0.0489	0.005	**
Cancov	0.036	0.018	*	H_{abs}	0.0453	0.002	**
O_a	0.0343	0.025	*	K	0.0381	0.012	*
A	0.0298	0.033	*	Mg	0.0314	0.033	*
Loc	0.0297	0.012	*	A	0.0304	0.028	*
K	0.0295	0.033	*	P	0.028	0.044	*
P	0.0243	0.066	.	N	0.0272	0.058	.
Mg	0.0242	0.06	.	Loc	0.025	0.036	*
N	0.0229	0.063	.	Ca	0.0107	0.269	n.s.
O_i	0.0116	0.259	n.s.	O_a	0.0061	0.491	n.s.
Ca	0.007	0.434	n.s.	O_i	0.0009	0.898	n.s.
EA	0.0017	0.83	n.s.	EA	0.0003	0.97	n.s.

common species in our study were also mentioned by Örd (1972), who pointed out different *Cladonia* species and *Cetraria islandica* (L.) Ach. as the most common species in the same dune area. Two lichen species are according to the IUCN Red List near threatened (NT) and vulnerable (VU) in Estonia: *Cladonia portentosa* (Dufour) Coem. (NT) and *Cladonia scabriuscula* (Delise) Nyl. (VU).

Soil and vegetation units of the coastal landscape in Estonia strongly depend on the topography, geological structure and water regime (Rivis *et al.*, 2016). Haplic Podzols, characteristic of Estonian coastal areas, are nutrient-poor soils. The most important plant growth-limiting elements in the terrestrial ecosystems are nitrogen and phosphorus (Güsewell, 2004). The high value of the N: P ratio indicates P limitation in the observed dune sands. Our results showed that the N: P and N: K ratios did not differ between the different locations. Only the Ca: Mg ratio was significantly different between locations, varying from 3.9 to 6.0. Dune soils on the bottoms of the dunes showed lower pH values which can be explained by accumulation of soil organic material (debris of coniferous trees, shrubs, accumulation of acid humus) (Sewerniak & Jankowski, 2017; Sewerniak *et al.*, 2017). Nutrient limitation and nutrient availability affect the competition between different species and the species composition of plant communities (Chapin *et al.*, 1986; Koerselman & Meuleman, 1996).

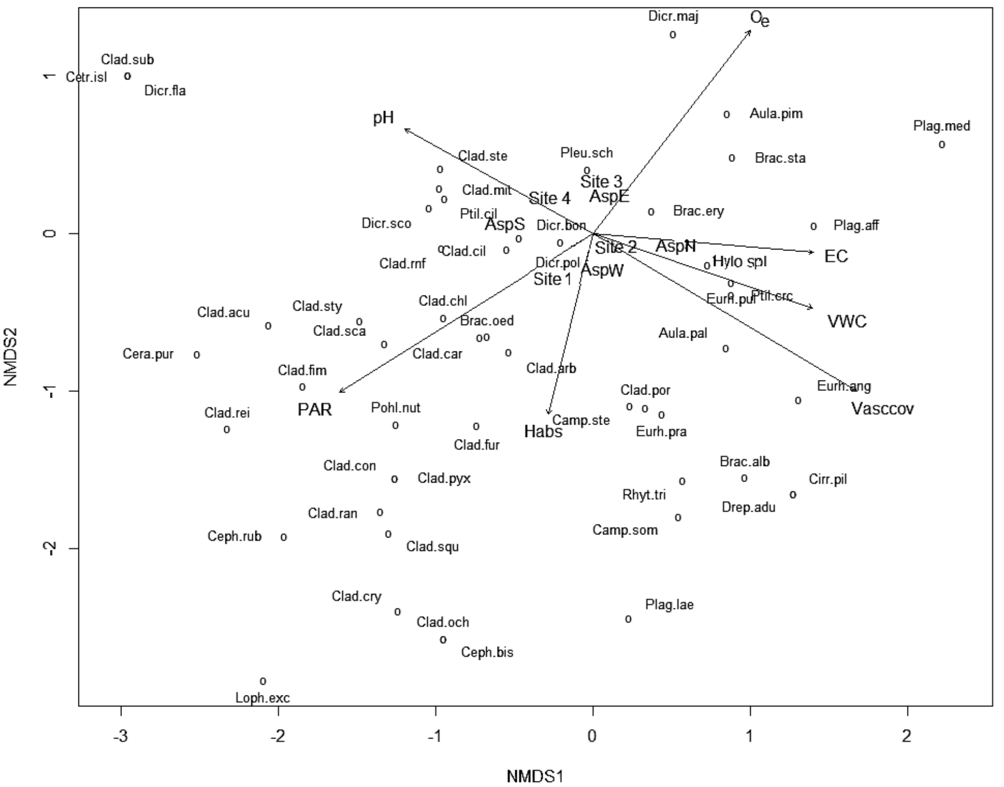

Figure 2. NMDS ordination (stress type 1), based on the abundance data of bryophytes and lichens. The arrows indicate environmental factors that were the most significantly ($p \leq 0.001$) related to the ordination (see also Table 5). Environmental factors: Habs = absolute height (m.a.s.l); Asp = aspect of the quadrat (S; N; E; W); EC = average conductivity (µS cm^{-1}); pH = average soil pH; VWC = average soil water content (%); PAR = photosynthetically active radiation (µmol $m^{-2}s^{-1}$); O_e = average thickness of moderate decomposed organic horizon layer (cm); Vasccov = cover of vascular plants. List of lichen and bryophyte species: Aula. pal = *Aulacomnium palustre*; Aula. pim = *Aulacomnium palustre var. imbricatum*; Brac. alb = *Brachythecium albicans*; Brac. ery = *Brachythecium erythrorrhizon*; Brac. oed = *Brachythecium oedipodium*; Brac. sta = *Brachythecium starkei*; Camp. som = *Campylium sommerfeltii*; Camp. ste = *Campylium stellatum*; Ceph. bis = *Cephalozia bicuspidata*; Ceph. rub = *Cephaloziella rubella*; Cera. pur = *Ceratodon purpureus*; Cetr. isl = *Cetraria islandica*; Cirr. pil = *Cirriphyllum piliferum*; Clad. arb = *Cladonia arbuscula*; Clad. cil = *Cladonia ciliata*; Clad. mit = *Cladonia mitis*; Clad. por = *Cladonia portentosa*; Clad. ran = *Cladonia rangiferina*; Clad. ste = *Cladonia stellaris*; Clad. sty = *Cladonia stygia*; Clad. acu = *Cladonia acuminata*; Clad. car = *Cladonia cariosa*; Clad. chl = *Cladonia chlorophaea*; Clad. con = *Cladonia coniocraea*; Clad. cry = *Cladonia cryptochlorophaea*; Clad. fim = *Cladonia fimbriata*; Clad. fur = *Cladonia furcata*; Clad. och = *Cladonia ochrochlora*; Clad. pyx = *Cladonia pyxidata*; Clad. rnf = *Cladonia rangiformis*; Clad. rei = *Cladonia rei*; Clad. sca = *Cladonia scabriuscula*; Clad. squ = *Cladonia squamosa*; Clad. sub = *Cladonia subulata*; Dicr. bon = *Dicranum bonjeanii*; Dicr. fla = *Dicranum flagellare*; Dicr. maj = *Dicranum majus*; Dicr. pol = *Dicranum polysetum*; Dicr. sco = *Dicranum scoparium*; Drep. adu = *Drepanocladus aduncus*; Eurh. ang = *Eurhynchium angustirete*; Eurh. pra = *Eurhynchium praelongum*; Eurh. pul = *Eurhynchium pulchellum*; Hylo. spl = *Hylocomium splendens*; Loph. exc = *Lophozia excisa*; Plag. aff = *Plagiomnium affine*; Plag. med = *Plagiomnium medium*; Plag. lae = *Plagiothecium laetum*; Pleu. sch = *Pleurozium schreberi*; Pohl. nut = *Pohlia nutans*; Ptil. cil = *Ptilidium ciliare*; Ptil. crc = *Ptilium crista-castrensis*; Rhyt. tri = *Rhytidiadelphus triquetrus*.

According to ordination analysis, bryophyte and lichen species composition on fixed *P. sylvestris* dominated dunes was most significantly determined by aspect, vascular plant species cover, amount of photosynthetically active radiation, thickness of the O_e sub-horizon and soil volumetric water content, acidity and electrical conductivity. As observed by Sewerniak *et al.* (2017), on dune areas topography plays an important role in soil development, thereby affecting the variability and distribution of vegetation. Our results confirmed this statement as far as epigeic bryophytes and lichens were concerned. As to an earlier finding by Sewerniak (2016), the height and slope aspect play an important role in determining the light and moisture regime on dune forests, our results confirmed the importance of the slope aspect in modifying the soil moisture regime on sites with different cardinal directions.

Zonal variation of ground vegetation is considered typical for dunes, although it has been described mostly for vascular plant species (Lane *et al.*, 2008; Tilk *et al.*, 2017). The study on Rannametsa dunes showed that the species richness of bryophytes and lichens varied along the dune profile. According to our results, bryophytes preferred lower and moister bottoms of the dunes where their species richness was the highest. In addition, the species composition of bryophytes on the bottoms differed significantly from the species composition of the slopes and tops, according to the results of MRPP tests. This can be explained by more humid soils on the bottoms of the dunes. Higher moisture availability on dunes raises plant-specific diversity and the number of plant groups increases (Latorre *et al.*, 2013). Soil moisture is important to moss species composition (Proctor, 2008), and fine-scale differences in soil moisture probably have a major effect on the bryophyte community (Grytnes *et al.*, 2006). Analysis of indicator species also pointed out *Brachythecium erythrorrhizon* and *B. oedipodium* (species preferring moist habitats according to Düll (1991)) as indicator species for dune bottoms.

At the same time, the lichen species richness was the highest on the slopes of the dunes where patches without vascular plants occurred and bryophyte species were not dominated. In stable and stress-free areas, slow-growing lichens are usually crowded out by vascular plants and by the more vigorous bryophytes because of lichens inability to cope with shading by shrubs or tree canopies, accumulation of humus and leaf litter or substrate instability (Hale, 1974). According to our results, the composition of bryophyte and lichen species was affected by the cover of vascular plant species; similar results were registered by Pharo *et al.* (1999), who found that the cover of vascular plants explains significant variations in fern, bryophyte and lichen species richness.

The light radiation are another key factor determining the diversity and composition of terrestrial lichens (Palmquist, 2000; Márialigeti *et al.*, 2016) because lichens require sufficient light for photosynthesis and growth, while mosses are able to efficiently take advantage of the low irradiances in the shade of the tree canopies (Kolari *et al.*, 2006). Terrestrial lichens are probably limited by light availability rather than soil moisture (Palmquist, 2000). Based on our results, certain lichens (species of *Cladonia*) seem to prefer open dune areas, where PAR is high and soil moisture is low. The proportion of light-demanding species was high among lichen species (the most frequent values of light indices 6—8). Bryophyte species showed more variable light preferences (the values of light indices varied between 3 and 9) and both shade-demanding and full-light requiring bryophyte species were represented on dunes.

Acidity preference of bryophyte species was also variable, ranging on a scale from acid to weakly acid/weakly neutral. Although bryophytes receive nutrients mainly from precipitation (including leachates from tree canopies and plant leaves) (Oechel & Van Cleve, 1986), the nutrient properties and pH of the substrate can also be important and affect bryophyte and lichen species composition (Pausas, 1994). Ketner-Oostra & Sykora (2000) found that when carbon content and acidity increase, the vegetation will change from lichen-poor to moss-rich communities. The number of moss species is more limited by soil moisture than by soil nutrients and a positive relationship for the pH was found by Pausas (1994). Based on NMDS ordination it can be concluded that lichen and bryophyte species composition was dependent on the soil pH, although a previous work compiled in the dune area in south-west Estonia (Kösta & Tilk, 2008) found no influence of the soil pH on the distribution of bryophyte and lichen species.

In addition, a previous study (Sun *et al.*, 2013) indicates that bryophyte distribution depends on the depth of litter. Our results agree with this statement, as the bryophyte and lichen species composition was affected by the thickness of the moderately decomposed organic layer. Magnusson (1982) found that certain lichens (species of *Cladonia*) colonise coastal dune areas in southern Sweden where litter has accumulated. Considering future research, we suggest that lichens and bryophytes should be separately analysed because of their different responses to environmental factors.

Conclusions

Altogether 30 species of bryophytes and 22 species of lichens were found on the study area. The average lichen species richness was the highest on the slopes of the dunes, while the highest average bryophyte species richness occurred on the bottoms of the dunes. The highest number of lichen species was identified as light-demanding while the light preference of bryophyte species was more variable. The distribution of bryophyte and lichen species between zones showed significant differences, and therefore it can be concluded that zonation of bryophyte and lichen species can be found on dunes just as it has been described for vascular plant species. In conclusion, it can be said that factors affecting the bryophyte and lichen species composition are related to the dune slope effect, which causes differentiation of soils and therefore a complex of different microhabitats populated by different species. According to our results, some of the most important factors are the aspect of the dune, vascular plant species cover, light conditions, a thickness of the medium decomposed soil organic horizon and soil pH, electrical conductivity and volumetric water content.

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