Environmental and Experimental Biology (2010) 8: 49–58 *Original Paper*

Bryophyte community composition on an island of Lake Cieceres, Latvia: dependence on forest stand and substrate properties

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Abstract

The aim of this study was to describe bryophyte communities on three substrate types (living tree stem, decaying log, forest floor) in natural deciduous tree forest stands in a small-scale heterogeneous habitat. In total, six liverwort and 42 moss species were recorded. Bryophyte community composition and species richness were strongly related to forest stand properties (forest age, soil moisture, and tree species) and substrate pH value. Most of the recorded woodland key habitat indicator species occurred on living tree stems in *Quercus robur* and *Tilia cordata* forest stands. The highest bryophyte species richness was observed on decaying trees in the successional stage from epiphytic to epigeous species communities. As the forest floor layer was not suitable for epigeous bryophytes on Ozolu Island, many of these species occurred on decaying logs.

Key words: bryophyte, canonical correspondence analysis, community composition, forest, island, species richness, substrate.
Abbreviations: CCA, Canonical Correspondence Analysis; DBH, diameter at breast height.

Introduction

Bryophytes inhabit various substrates in woodlands such as the forest floor layer, decaying trees, tree base, and tree branches. They are important for forests as colonists of bare soil, moisture absorbers and retainers, contributors to the overall energy flow and nutrient cycling and as habitat for invertebrates and other microorganisms (Porley, Hodgetts 2005).

It is known that phorophyte species, tree bark chemistry and structure, and growing height and exposure on tree stems are important factors for epiphytic bryophytes (Barkman 1958; Stringer, Stringer 1974; Szövényi et al. 2004; Mežaka et al. 2008). Decay stage, diameter of log and habitat humidity are factors determining epixylic bryophyte species richness (Humphrey et al. 2002; Ódor, Van Hees 2004; Āboliņa 2008). Variability of microniches, moisture, pH, and litter cover can explain epigeous bryoflora composition (Ingerpuu et al. 1998; Vellak et al. 2003; Márialigeti et al. 2009). In most cases, these studies have examined large regions or have been conducted in homogenous habitats. Islands present an interesting study area for investigation of bryophyte communities since they are characterized by small scale heterogeneous habitats.

In total eight lakes are protected in Latvia, because of the high biological diversity in their islands, mainly in natural forests (Republic of Latvia 1993). Islands may therefore offer an opportunity to study habitats which have escaped human impact for a long period of time. The natural deciduous forests on Ozolu Island in Lake Cieceres have been protected almost hundred years (Laiviņš 1976) and were described as primeval forests a long time ago (Anonymous 1938). Vascular and fern species on Ozolu Island have been described by Lancmanis in 1922, Jansons in 1936, Laiviņš from 1973 to 1975, and by Tabaka in 1975 (Laiviņš 1976). Cryptogamic species were surveyed by Mežaka (2009) in *Quercus robur* forest stands on the island. Nevertheless, quantitative studies of bryophyte communities within all forest types on Ozolu Island are lacking.

The objectives of the present study were to characterise epiphytic, epixylic and epigeous bryophyte species communities in natural forests on Ozolu Island in relation to forest stand properties (forest age, species in tree layer, moisture level) and substrate traits (phorophyte species and diameter, log dimensions, soil pH etc.).

Materials and methods

Study area

The study was conducted on Ozolu Island (56°39' E; 22°34' N, maximum elevation 6.5 m), which is the only island in Lake Cieceres (Fig. 1). Mean annual temperature and annual rainfall are about 5.75 °C and 600 – 700 mm, respectively (Strautnieks 1998). The island is 14 ha in size and entirely covered by forest, dominated by *Populus tremula*, *Quercus*

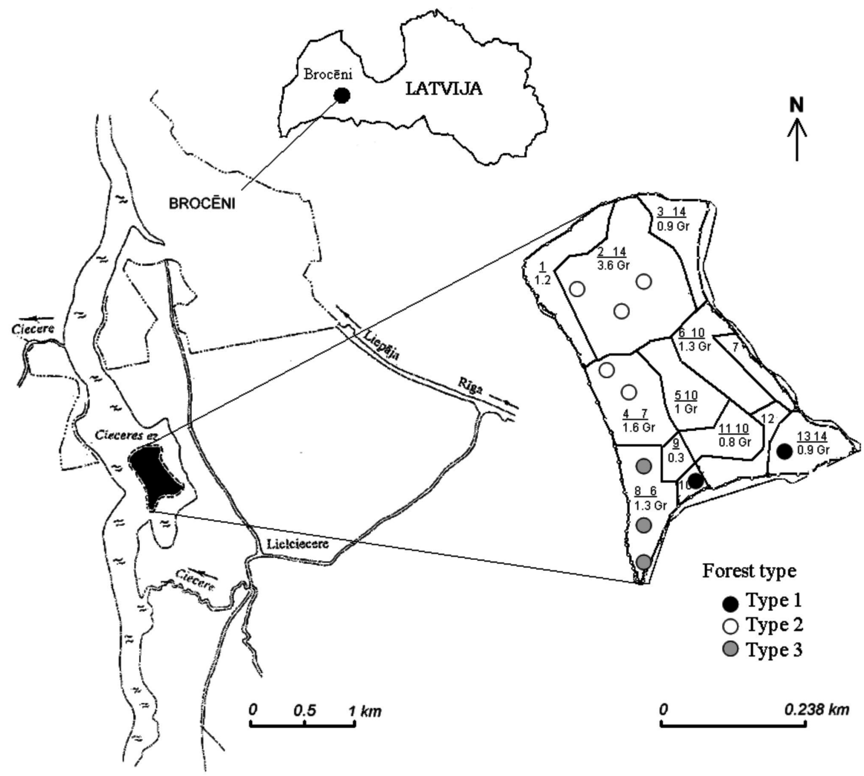

Fig. 1. The study area in Lake Cieceres (left) (Cabinet of Ministers of Latvia 1999). Dots represent sample sites on Ozolu Island (right) (Latvian State Forest Agency 2010, http://www.vmd.gov.lv/). Black circles, dry forest stands with *Quercus robur* and *Tilia cordata* (Type 1); white circles, moist forest stands with *Tilia cordata, Quercus robur, Picea abies* and *Fraxinus excelsior* (Type 2); grey circles, moist forest stands with *Alnus incana, Fraxinus excelsior, Betula pendula* and *Picea abies* (Type 3).

robur and *Tilia cordata* (Laiviņš 1976).

The Ozolu Island Nature Reserve has been under protection since 1923 (Laiviņš 1976) and is now a NATURA 2000 site (EU 1992).

Sampling design

Bryophytes on Ozolu Island were collected from 2008 to 2009. Forest stands were classified in three types along a moisture gradient and depending on dominant tree species, in accordance with vegetation communities described on Ozolu Island by Laiviņš (1976): type 1, dry forest stands with *Quercus robur* and *Tilia cordata*; type 2, moist forest stands near the coastline of Ozolu Island with *Tilia cordata, Quercus robur, Picea abies* and *Fraxinus excelsior*; type 3, moist forest stands with *Alnus incana, Fraxinus excelsior, Betula pendula* and *Picea abies*. Characteristics of the forest types are given in Table 1. Ten sampling plots were located randomly across the entire island (Fig. 1). Two sampling plots were located in forest type 1, five in forest type 2, and three in forest type 3. Each sampling plot was 20 × 20 m in size. Bryophytes were collected from the forest floor layer, coarse woody debris (CWD) and living tree stems within each plot. Epiphytic bryophytes were collected up to a 2-m height on 85 individual trees of ten tree species, mostly from *Tilia cordata* (21 trees), *Fraxinus excelsior* (18 trees), *Quercus robur* (14 trees), *Picea abies* (11 trees), and *Betula pendula* (10 trees). Epixylic bryophytes on the whole visible part of 45 decaying trees were recorded. Epigeic bryophytes were recorded in 47 1 × 1 m forest floor quadrats. Bryophyte species that could not be identified in the field were collected for identification in the laboratory. Taxonomic references used were Smith (1996) for liverworts and Āboliņa (2001)

Table 1. Characteristics of sampling sites (n = 10). Means and standard deviation are given for all sites, and separately for sampling sites from the three studied forest types. Forest type 1 includes two sampling sites, forest type 2 includes five sampling sites, and forest type 3 includes three sampling sites

Variables	All sites	Type 1	Type 2	Type 3
Forest age (years)	99 ± 32	116 ± 21	99 ± 45	66 ± 0
Diameter of trunks and logs (m)	0.244 ± 0.10	0.395 ± 0.05	0.227 ± 0.07	0.172 ± 0.04
Soil pH	4.81 ± 0.91	5.85 ± 0.04	4.76 ± 0.98	4.18 ± 0.33

Table 2. Mean parameters and standard deviation for studied living tree species. Only species with more than ten trees are shown

Tree species	Stem diameter (m)	Bark pH	Number of bryophyte species per tree
Betula pendula (n = 10)	0.325 ± 0.17	4.59 ± 0.58	6.50 ± 2.37
Fraxinus excelsior (n = 18)	0.211 ± 0.08	5.50 ± 0.27	9.89 ± 4.43
Picea abies (n = 11)	0.272 ± 0.16	4.01 ± 0.23	4.91 ± 1.87
Quercus robur (n = 14)	0.455 ± 0.28	4.59 ± 0.54	9.79 ± 2.89
Tilia cordata (n = 21)	0.250 ± 0.15	5.20 ± 0.38	9.29 ± 4.69

and Ignatov, Ignatova (2003; 2004) for mosses.

Several parameters were measured for each substrate type. Tree species, diameter at breast height (DBH), bark pH, and height of continuous bryophyte cover on all sides (N, W, S, and E) of tree stems were recorded. Characteristics of the five most represented living tree species are given in Table 2. Length, diameter, and bark pH were estimated for every decayed log. Distance to the nearest tree, tree species, and soil pH were estimated for every forest floor plot.

Percentage cover of all bryophyte species was estimated visually using a modified Braun-Blanquet five-point cover scale: 0 to 5 %, 6 to 25 %, 26 to 50 %, 51 to 75 %, and 76 to 100 %.

Bark and soil pH

The pH of living and decaying tree bark and soil samples was determined in the laboratory in accordance with a standardized method (Programme Centre EDC 1989). Soil samples were first dried at 100 °C for 5 h. Dry samples of soil and bark (0.5 g each) were put into flasks and shaken in 20 mL 1 M KCl for 1 h. The pH value of the solution was determined with a GPH 014 pH meter (Greisinger Electronic).

Data analysis

Bryophyte species specificity to a substrate was determined using Indicator Species Analysis. Canonical Correspondence Analysis (CCA) was used to examine the relationship between environmental parameters and bryophyte species composition. The Monte Carlo test (n = 9998) was used to determine if the first canonical axis of each ordination was significantly related to environmental variables. As the bryophytes were collected on three different substrates, ordinations were performed separately for the epiphytic, epixylic and epigeous species. All calculations were performed with PC-ORD using the Windows Version 5.0 program package (McCune, Mefford 1999). Spearman's rank correlations were calculated between environmental variables and total cover and species richness (number of species) of bryophytes for all studied forest types using the R programme package 2.8.1. version (R Development Core Team 2008).

Continuous variables used in the analysis included age of forest stand (Latvian State Forest Agency 2010, http://www.vmd.gov.lv/), tree stem diameter, tree bark pH, height of continuous bryophyte cover on tree stem on N, E, S and W sides; decayed log pH, length and diameter of logs, soil pH, distance from nearest tree to forest floor layer sample plot, average diameter of stem of living trees and logs. Categorical variables used in the analysis included three forest type classes and five substrate pH value classes (1, 3.50 to 3.99; 2, 4.00 to 4.49; 3, 4.50 to 4.99; 4, 5.00 to 5.49; 5, 5.50 to 6.00).

Results

Species richness

Altogether, 177 micro plots were described from three substrates (living tree stem, decaying log and forest floor layer), in which 48 bryophyte species were recorded (Table 3). Among these, six were liverwort and 42 were moss species. The data set included 85 stems of living trees (29 epiphytic bryophyte species), 44 decaying logs (32 epixylic bryophyte species), and 47 forest floor quadrats (19 epigeous bryophyte species). Among the ten most frequently recorded species (found in more than 20 micro plots), two were liverworts (*Radula complanata* and *Metzgeria furcata*) and eight were mosses (*Hypnum cupressiforme, Homalia trichomanoides, Leucodon sciuroides, Brachythecium rutabulum, Orthotrichum affine, Leskea polycarpa, Eurhynchium hians* and *Amblystegium serpens*). Thirteen bryophyte species were present in only one sample plot, including one liverwort (*Plagiochila asplenioides*) and twelve mosses (e.g., *Antitrichia curtipendula, Ditrichum flexicaule, Orthotrichum lyellii, Ulota crispa*).

The average number of species per micro plot (species richness) was highest on living tree stems (3.81, SD = 2.11), followed by CWD (3.56, SD = 2.15) and forest floor layer (1.89, SD = 0.96). The bryophyte species richness on all studied substrates was highest in forest type 1, followed by forest type 2 and forest type 3 (Fig. 2). The highest total number of species occurred on CWD (33), followed by living tree stems (29) and the forest floor layer (19) (Fig. 3). Of the recorded species 15% were included in various protected and indicator or signal species lists (Table 3).

Substrate and forest type specificity

In total, 60% of the species observed did not show any clear substrate preference. However, 19 bryophyte species had specificity to a substrate, suggest by Indicator Species Analysis (Table 4). Among the indicator species, only two (*Metzgeria furcata* and *Homalia trichomanoides*) were

Table 3. List of the taxa (six liverwort and 42 moss species) identified in this study with abbreviations used in tables and figures. Signal, bryophyte species included in various lists of protected and indicator species; RL, red listed species in Latvia (Āboliņa 1994); SP, specially protected species (Cabinet of Ministers of Latvia 2000); WKH, woodland key habitat species (Ek et al. 2002)

Groups	Species	Abbreviations	Signal
Liverworts	*Frullania dilatata* (L.) Dum.	Fruldila	
	Lophocolea bidentata (L.) Dum.	Lophbide	
	Lophocolea heterophylla (Schrad.) Dum.	Lophhete	
	Metzgeria furcata (L.) Dum.	Metzfurc	RL, WKH
	Plagiochila asplenioides (L. emend. Tayl.)	Plagaspl	
	Radula complanata (L.) Dum.	Raducomp	
Mosses	*Amblystegium serpens* (Hedw.) B., S.et G.	Amblserp	
	Amblystegium varium (Hedw.) Lindb.	Amblvari	
	Anomodon attenuatus (Hedw.) Hüb.	Anomatte	WKH
	Antitrichia curtipendula (Hedw.) Brid.	Anticurt	RL, SP, WKH
	Atrichum undulatum (Hedw.) P. Beauv.	Atriundu	
	Brachythecium oedipodium (Mitt.) Jaeg.	Bracoedi	
	Brachythecium populeum (Hedw.) B., S. et G.	Bracpopu	
	Brachythecium rutabulum (Hedw.) B., S. et G.	Bracruta	
	Brachythecium salebrosum (Web. Et Mohr) B., S. et G.	Bracsale	
	Bryum subelegans Kindb.	Bryusube	
	Climacium dendroides (Hedw.) Web. et Mohr.	Climdend	
	Dicranum montanum Hedw.	Dicrmont	
	Dicranum scoparium Hedw.	Dicrscop	
	Ditrichum flexicaule (Schwaegr.) Hampe.	Ditrflex	
	Eurhynchium angustirete (Broth.) T. Kop	Eurhangu	
	Eurhynchium hians (Hedw.) Sande Lac.	Eurhhian	
	Eurhynchium striatum (Hedw.) Schimp.	Eurhstri	
	Fissidens taxifolius Hedw.	Fisstaxi	
	Herzogiella seligeri (Brid.) Iwats.	Herzseli	
	Homalothecium sericeum (Hedw.) B., S. et G.	Homaseri	
	Homalia trichomanoides (Hedw.) B., S. et G.	Homatric	WKH
	Hylocomium splendens (Hedw.) B., S. et G.	Hylosple	
	Hypnum cupressiforme Hedw.	Hypncupr	
	Isothecium alopecuroides (Dubois) Isov.	Isotalop	WKH
	Leskea polycarpa Hedw.	Leskpoly	
	Leucodon sciuroides (Hedw.) Schwaegr.	Leucsciu	
	Mnium hornum Hedw.	Mniuhorn	
	Orthotrichum affine Brid.	Orthaffi	
	Orthotrichum lyellii Hook. et Tayl.	Orthlyel	RL, SP
	Orthotrichum pumilum Sw.	Orthpumi	
	Plagiomnium affine (Bland.) T. Kop.	Plagaffi	
	Plagiomnium cuspidatum (Hedw.) T. Kop.	Plagcusp	
	Plagiomnium undulatum (Hedw.) T. Kop.	Plagundu	
	Plagiothecium denticulatum (Hedw.) B., S. et G.	Plagdent	
	Platygyrium repens (Brid.) B., S. et G.	Platrepe	
	Pseudobryum cinclidioides (Hüb.) T. Kop.	Pseucinc	
	Pylaisia polyantha (Hedw.) Schimp.	Pylapoly	
	Rhytidiadelphus triquetrus (Hedw.) Warnst.	Rhyttriq	
	Sanionia uncinata (Hedw.) Loeske.	Saniunci	
	Schistidium apocarpum (Hedw.) B. et S.	Schiapoc	
	Tetraphis pellucida Hedw.	Tetrpell	
	Ulota crispa (Hedw.) Brid.	Ulotcris	WKH

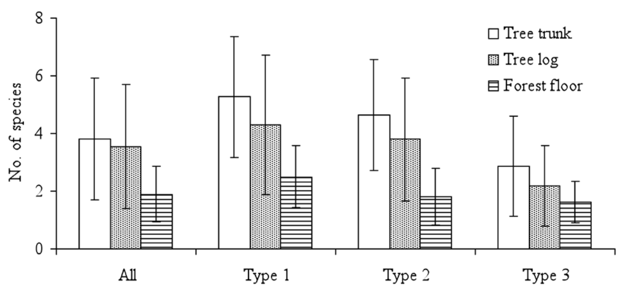

Fig. 2. Average number of bryophyte species in studied forest types on all substrates.

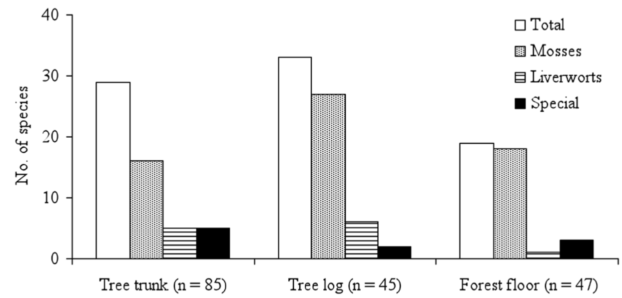

Fig. 3. Total number of liverwort, moss and signal (explanation in Table 3) species recorded on three substrates on Ozolu Island.

special species (Table 3). These were found only on living trees along with other typical epiphytes (*Homalothecium sericeum, Leskea polycarpa, Leucodon sciuroides, Orthotrichum affine* and *Radula complanata*). Only one indicator species of CWD, *Hypnum cupressiforme*, was a typical epixylic bryophyte. All five indicator species of forest floor layer (*Eurhynchium hians, E. striatum, Fissidens taxifolius, Plagiomnium undu-latum* and *Pseudobryum cinclidioides*) were found mostly on this substrate.

Only 13 bryophyte species (27% from all species) showed significant forest type specificity (Table 4). Most of these were related to forest type 1 (six species) and forest type 2 (five species). Only two species (*Leskea polycarpa* and *Orthotrichum affine*) were indicators of forest type 3.

Environmental varibles and canonical correspondence analysis

The overall effect of the environmental variables on the composition and abundance of the bryophyte vegetation was not significant (Table 5). However substrate pH, age of forest stand and diameter of living trees and CWD in sampling sites were important environmental factors explaining total bryophyte species richness and cover (Table 5). Also, Spearman's rank correlations with environmental variables, was calculated separately for each studied substrate (Table 5), showed a positive correlation between all seven variables and epiphytic bryophyte species richness and cover. Only stand age showed a positive correlation with epigeous bryophyte species richness and cover. None of the four environmental variables was correlated with epixylic bryophyte species richness and cover.

The results of canonical correspondence analysis performed separately for all three substrate types studied are shown in Fig. 4 to 6. In the ordinations the three forest types were well segregated by species composition likely, due to differences between the types in moisture, dominant tree species (Fig. 4) and forest floor layer (Fig. 6). Differences in species composition on CWD appeared to be explained best by substrate pH (Fig. 5). Of the epiphytic bryophyte species (Fig. 4) *Isothecium alopecuroides* and *Anomodon attenuatus* occurred most often on lime, which has basic bark pH and is more common in older and dryer forest stands. *Frullania dilatata* and *Homalia trichomanoides* were strongly associated with moist forest stands where the existing tree species had basic bark and a intermediate DBH, mostly *Fraxinus excelsior*. *Orthotrichum affine* and *Leskea polycarpa* were found most often on tree species with acidic bark pH, like *Betula pendula* and *Picea abies*, which were common in younger and moister forest stands.

Epixylic bryophyte species composition was strongly related to pH of CWD (Fig. 5). Species on the right side of the ordination (e.g. *Dicranum scoparium* and *Eurhynchium angustirete*) occurred most often on CWD with a low pH value (3.50 to 3.99), and these species are also found in

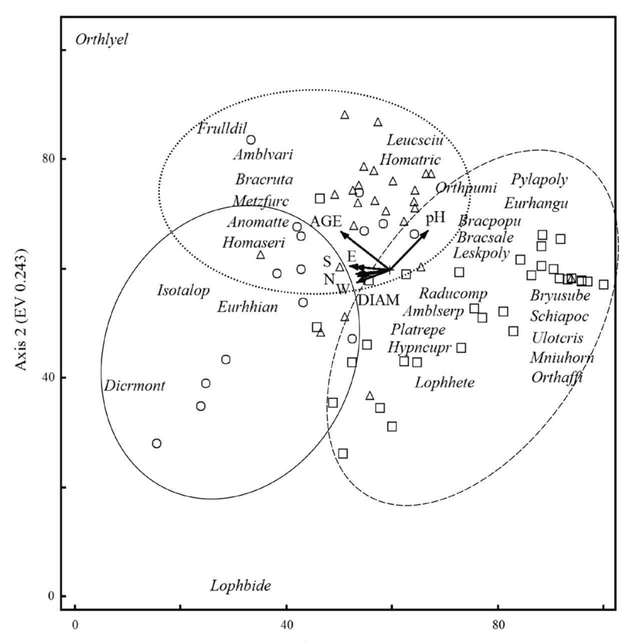

Fig. 4. CCA ordination of the 85 living tree trunks and 29 bryophyte species; axes 1 and 2. Species abbreviations as in Table 3. Symbols represent forest type classes: circles, dry forest stands with *Quercus* and *Tilia* (Type 1); triangles, average moist forest stands with *Tilia*, *Quercus*, *Picea* and *Fraxinus* (Type 2); squares, moist forest stands with *Alnus, Fraxinus, Betula* and *Picea* (Type 3). Environmental variables are marked as arrows and uppercase text labels. AGE, age decade of forest stand; pH, pH value of tree bark; DIAM, tree stem diameter; N, E, S, W, height of continuous bryophyte cover on stem in north, east, south and west side accordingly.

Table 4. Specificity of bryophyte species for substrate and forest type identified by Indicator Species Analysis. Only species showing significant differences (P < 0.05) (Monte Carlo test) are shown. Species abbreviations as in Table 3

Substrate type	Species	Relative abundance	Relative frequency	Monte Carlo test
Tree stem	Homaseri	100	7	0.0400
	Homatric	88	48	0.0002
	Leskpoly	84	32	0.0002
	Leucsciu	52	31	0.0426
	Metzfurc	65	36	0.0006
	Orthaffi	63	31	0.0034
	Raducomp	86	58	0.0002
Decaying log	Bracruta	64	40	0.0002
	Bracsale	86	11	0.0046
	Dicrscop	100	7	0.0156
	Hypncupr	55	91	0.0002
	Lophbide	90	7	0.0264
	Lophhete	97	27	0.0002
	Plagaffi	88	11	0.0054
Forest floor	Eurhhian	79	34	0.0002
	Eurhstri	88	23	0.0002
	Fisstaxi	100	26	0.0002
	Plagundu	88	9	0.0222
	Pseucinc	100	6	0.0344
Forest type 1	Amblvari	100	6	0.0360
	Dicrmont	100	6	0.0370
	Dicrscop	100	9	0.0060
	Frulldil	94	14	0.0010
	Isotalop	100	17	0.0002
	Metzfurc	52	34	0.0288
Forest type 2	Bracruta	53	34	0.0118
	Bracsale	100	10	0.0052
	Homatric	67	41	0.0010
	Leucsciu	53	31	0.0442
	Lophhete	66	14	0.0374
Forest type 3	Leskpoly	57	27	0.0258
	Orthaffi	69	35	0.0006

the forest floor layer. Species on the left side of the CCA ordination (e.g. *Radula complanata* and *Frullania dilatata*) occurred on CWD with a high pH value (5.50 to 6.00) and are common as epiphytes on Ozolu Island.

The epigeous bryophyte community composition (Fig. 6) was mostly determined by forest type and soil pH. The first axis was related to a pH gradient along which species formed two distinct groups (Table 5; Fig. 6). *Mnium hornum* and *Eurhynchium striatum* occurred more often on acidic moist soil, while *Plagiothecium denticulatum* and *Pseudobryum cinclidioides* were found mostly on basic dry soil in older forest stands with a sparse tree layer and dominance of large diameter trees like *Quercus robur. Fissidens taxifolius* and *Atrichum undulatum* were most common on moderately moist soil in dense forest stands with *Picea abies* and *Tilia cordata*.

Discussion

Species richness and composition in relation to substrate properties and environmental variables

A dense herb layer (Ingerpuu et al. 1998) and litter cover (Márialigeti et al. 2009), which is characteristic for rich deciduous forests, might explain the observed lower forest floor layer bryophyte species richness and cover, in the comparison to the other substrates. Bryophytes are weak competitors, and as colonists mostly occur only in temporarily available small microhabitats like the soil plates of wind-thrown trees and old burrows made by forest animals (Porley, Hodgetts 2005; Tinya et al. 2009). Size of dominant trees (Márialigeti et al. 2009) and distance to nearest tree (Rambo, Muir 1998; Vellak et al. 2003; Tinya et al. 2009) showed no strong correlation with total

Table 5. Intra-set correlation coefficients of forwardly selected environmental variables with the three significant axes produced by CCA and calculated separately for epiphytic, epixylic and epigeous bryophytes. A Monte Carlo test (P) (n = 9998) was used to test the significance of the environmental variables. Spearman's rank correlation coefficients (r_S) calculated between environmental variables and the cover and species richness in total and separately for each substrate type. *, P < 0.05; **, P < 0.01

Substrate type	Environmental variables	Correlation coefficients			p	r_S	
		Axis 1	Axis 2	Axis 3		Cover	Richness
Total (n = 175)	Eigenvalues	0.263	0.145	0.080	0.0002		
	Species-environment correlations	0.687	0.604	0.462	0.0046		
	Substrate pH					0.174*	0.299**
	Forest age decade					0.292**	0.185*
	Diameter of trunks and logs					0.294**	0.314**
Tree stem (n = 85)	Eigenvalues	0.288	0.243	0.169	0.0015		
	Species-environment correlations	0.781	0.764	0.811	0.0987		
	Height of continuous bryophyte cover in:						
	north side	–0.453	–0.189	0.210		0.554**	0.455**
	west side	–0.466	–0.058	0.108		0.511**	0.380**
	south side	–0.543	0.064	–0.030		0.576**	0.418**
	east side	–0.467	0.056	–0.809		0.493**	0.397**
	Stem DBH	–0.440	–0.085	0.333		0.339**	0.313**
	Bark pH	0.527	0.610	–0.258		0.293**	0.398**
	Stand age	–0.666	0.596	0.361		0.541**	0.398**
Decaying log (n = 44)	Eigenvalues	0.297	0.185	0.158	0.0416		
	Species-environment correlations	0.817	0.781	0.716	0.1527		
	Length of log	0.188	0.317	0.677		0.161	0.236
	Diameter of log	0.428	0.537	0.712		0.182	0.184
	Log pH	–0.854	0.512	0.064		0.014	0.174
	Stand age	–0.281	–0.542	0.675		0.107	–0.036
Forest floor (n = 47)	Eigenvalues	0.468	0.296	0.178	0.0073		
	Species-environment correlations	0.747	0.705	0.517	0.1081		
	Distance from nearest tree	–0.185	–0.578	–0.684		0.164	–0.085
	Diameter of living trees and logs	0.177	–0.929	0.255		0.076	0.123
	Soil pH	0.648	–0.540	–0.025		0.004	0.119
	Forest age decade	0.397	–0.400	0.562		0.319*	0.459**

bryophyte species richness and cover on the forest floor. Epigeous bryophyte species richness tends to increase with age of forest stand, due to presence of microsites and large trees which are potential substrates (Rambo, Muir 1998; Márialigeti et al. 2009). Suitable habitat on the forest floor layer is not readily available for epigeous bryophytes on Ozolu Island, and many of these species occur on CWD. The environmental conditions on CWD in moist areas like riparian areas are probably suitable for mosses typically found on soil (Āboliņa 2008).

As bryophyte species succession from epiphytic to epigeous species communities is common on CWD, recently fallen trees initially support epiphytic bryophyte communities with *Homalia trichomanoides, Orthotrichum affine, Frullania dilatata* and *Radula complanata* (Mills, Macdonald 2005; Heylen, Hermy 2008), which are replaced by epixylic species, such as *Hypnum cupressiforme, Herzogiella seligeri* and *Tetraphis pellucida* (Ingerpuu et al. 1998; Āboliņa 2008). Epigeous species like *Dicranum scoparium* and *Plagiochila asplenioides* dominate the community on CWD in the last decay stage (Āboliņa 2008). That might explain why the highest total species richness was found on CWD. Indicator Species Analysis identified characteristic species of the bryophyte species succession on CWD (Table 5). Only one indicator species of decaying logs (*Hypnum cupressiforme*) is an obligate epixylic bryophyte. Other species, such as *Brachythecium rutabulum, B. salebrosum, Dicranum scoparium*, and *Lophocolea heterophylla*, are generalists and can be found not only on CWD, but also on soil, rocks, and tree bases. Furthermore, *Lophocolea bidentata* and *Plagiomnium affine* are typical forest ground dwellers (Söderström 1993; Ingerpuu et al. 1998; Āboliņa 2008).

In contrast to other studies (Humphrey et al. 2002), log diameter and length showed no significant correlation with epixylic bryophyte species richness and percentage cover in

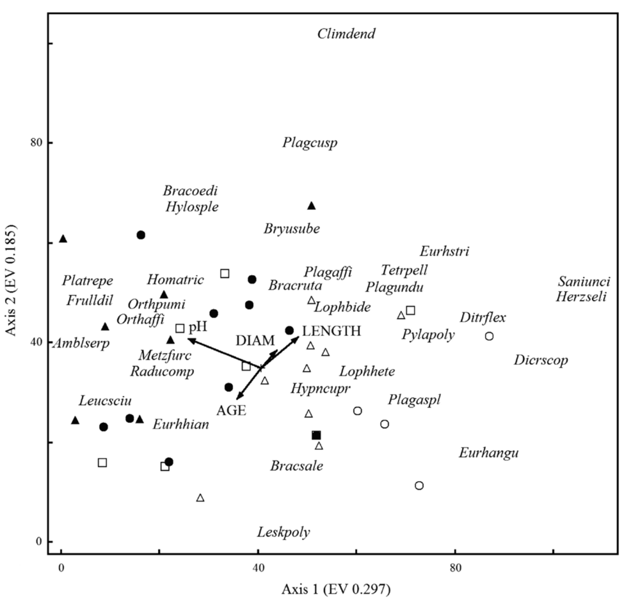

Fig. 5. CCA ordination of the 44 decaying tree logs and 32 bryophyte species (one sample plot was removed); axes 1 and 2. Species abbreviations as in Table 3. Symbols represent decayed log pH classes: open circle, 3.50 to 3.99; open triangle, 4.00 to 4.49; square, 4.50 to 4.99; closed circle, 5.00 to 5.49; closed triangle, 5.50 to 6.00. Environmental variables are marked as arrows and uppercase text labels. pH, value of decaying tree pH; LENGTH, length of decaying tree log; DIAM, diameter of decaying tree log; AGE, age decade of forest stand.

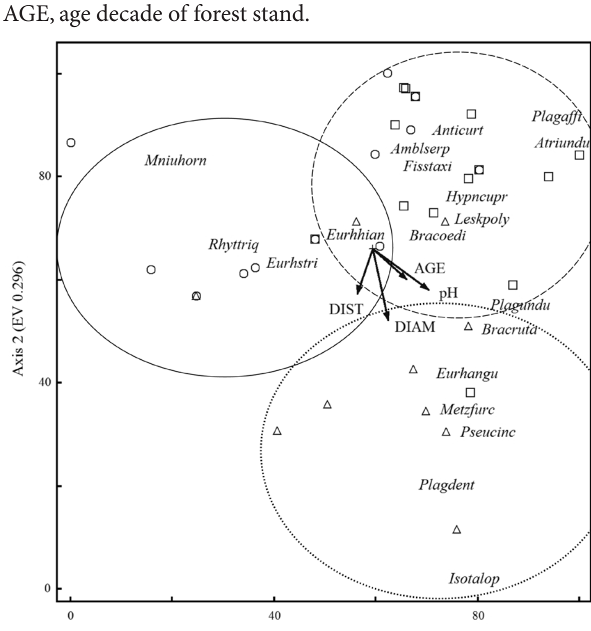

Fig. 6. CCA ordination of the 47 forest floor layer sample plots and 19 bryophyte species; axes 1 and 2. Species abbreviations as in Table 3. Symbols represent forest type classes: triangles, dry forest stands with *Quercus* and *Tilia* (Type 1); squares, moderate moist forest stands with *Tilia, Quercus, Picea* and *Fraxinus* (Type 2); circles, moist forest stands with *Alnus, Fraxinus, Betula* and *Picea* (Type 3). Environmental variables are marked as arrows and uppercase text labels. pH, soil pH; AGE, age decade of forest stand; DIAM, average diameter of living tree stems and logs studied in sample site; DIST, distance from nearest tree.

Ozolu Island. Some authors have found only a weak effect of tree age on species composition (Turner, Pharo 2005). Unfortunately, parameters like decay stage and tree species were not determined in this study, but it is well known that they play an important role in occurrence of epixylic bryophyte species (Humphrey et al. 2002; Heilmann-Clausen et al. 2005; Āboliņa 2008; Madžule, Brūmelis 2008; Mežaka et al. 2009). It is also been shown that pH is correlated with decay stage (Madžule, Brūmelis 2008).

Epiphytic bryophyte species composition and richness highly depend on forest stand properties, as well as on dominant tree species in the tree layer. Tree species were clearly separated in two groups depending on bryophyte species richness on stem. According to the literature (Barkman, 1958; Stringer, Stringer 1974; Berg et al. 2002; Mežaka et al. 2008; Mežaka 2009) broadleaved tree species with basic bark and a large stem diameter (*Quercus robur* and *Tilia cordata*) support the highest epiphytic bryophyte species and woodland key habitat indicator species richness. In our study, tree species with acid bark and a small stem diameter (*Picea abies* and *Betula pendula*) supported the lowest number of bryophyte species. It is important to stress that the youngest forest stands on Ozolu Island supported the lowest bryophyte species richness, as described previously (Fritz 2009).

Differences in bryophyte species composition in relation to forest type

Vascular and fern species composition on Ozolu Island shows great differences in relation to dominant tree species and forest stand conditions (Laiviņš 1976). The results of the present study suggest that tree age, dominant tree species, soil moisture and pH were important factors explaining bryophyte species composition.

As expected, most of the bryophyte species on the studied substrates were observed in the oldest forest stands with large broadleaved tree species dominated in the tree layer and had a high pH value. Large living trees and CWD provide a suitable substrate for bryophytes because of rougher bark structure (Barkman 1958) and longer length of time for development of large bryophyte cover (Humphrey et al. 2002). The light transmittance to the forest floor is higher in older forest stands (Rambo, Muir 1998), which positively influences forest floor bryophyte cover (Tinya et al. 2009). Forest stands with high soil pH also contain some microsites with low pH, thereby increasing total species richness in a particular sampling site (Hylander, Dynesius 2006). Thus species richness might best be explained by diversity of suitable microhabitats.

Pioneer tree species like *Alnus incana, Fraxinus excelsior* and *Betula pendula* and dense understory vegetation with reed Phragmites australis occurred in the coastal forest stands with high moisture conditions (Laiviņš 1976). Increased edge effect (Gignac, Dale 1995), smooth bark, low bark pH and young age of trees (Fritz et al. 2009), low soil pH and dense forest floor layer (Vellak et al. 2003) in these forest stands supported occurrence of common forest pioneer species, like epigeous bryophytes *Eurhynchium striatum* and *Rhytidiadelphus triquetrus* and epiphytes *Leskea polycarpa, Orthotrichum affine* and *Radula complanata* which were rare or uncommon in forest stands in the interior of Ozolu Island.

Conclusions

Forest heterogeneity plays an important role in determining bryophyte species richness and diversity. Dry and old forest stands with broadleaved tree species like *Quercus robur* and *Tilia cordata* and high soil pH provide variable microhabitats for rare and protected bryophyte species. Young forest stands with a dense shrub layer and dominance of narrowleaved tree species like *Fraxinus excelsior* and *Betula pendula* on moist and acid soils are important for pioneer bryophyte species. Light-loving pioneer bryophytes are more common at the forest edge near the island coast. Tree age, soil moisture, tree species and substrate pH were the most significant environmental variables explaining bryophyte species variation on Ozolu Island. Living tree and decaying logs supported the highest bryophyte species richness. Epigeous bryophyte species had the lowest richness and cover and mostly occurred on coarse woody debris, stressing the importance of fallen down trees and branches in mesic dry habitats. The results of the present study emphasize the importance of nature protection of small scale habitats like lake islands.

Acknowledgements

The present study was supported financially by European Social Fund project "Support for Doctoral Studies at the University of Latvia" Nr. ESS2009/77. I am grateful to my family for assisting in the field work. Guest hotel 'Zvejnieki 2000' helped with arriving to island. Valuable comments on the manuscript have been provided by Anna Mežaka, Ģederts Ieviņš and Guntis Brūmelis. Guntis Tabors helped in the laboratory measuring bark and soil pH.

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Received 31 August 2010; received in revised form 23 September 2010; accepted 4 October 2010