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Environmental controls of raised-bog vegetation in the Baltic boreo-nemoral zone

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Abstract Raised peat bogs harbor unique vegetation types in specific hydrological conditions. Environmental controls of peat bog vegetation are relatively well known for the boreal zone, while in the European boreo-nemoral zone healthy raised bogs are nowadays very rare. By contrast, Latvia, located in the transition zone between the nemoral and the boreal biomes, still has a large number of active raised bogs. The aim of the present study was to characterize the environmental controls on raised bog vegetation structure, species composition and ecology in Latvia. The study includes 17 raised bogs, where vascular plants, bryophytes and lichens were recorded in 480 sample plots and related to environmental variables (microtopography, litter cover, electric conductivity, pH, and macroelements Na, K, Ca, Mg and P in bog surface waters). The factor best explaining total species richness and composition was microtopography, which also affected most other explanatory factors. Thereby total species richness and cover were highest on hummocks. However, the importance and direction of the effects of microtopography and the other factors differed between vegetation groups. When disregarding microtopography, species composition was most strongly correlated with alkaline ions and litter cover and for bryophytes also with vascular plant cover. The present study is the first wide-scale study in Latvia relating raised bog vegetation to environmental conditions.

Keywords Microtopography · Peatbogs · *Sphagnum* · Vegetation

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Introduction

Peatlands are major contributors to global terrestrial carbon storage and harbour a unique biodiversity (e.g. Ellenberg 1988; Rydin and Jeglum 2013). In raised bogs, precipitation is the dominant source of water and nutrients (Goffinet and Shaw 2009) and oligotrophic plant communities predominate, which are relatively species-poor and structured into two layers: a vascular plant layer above a bryophyte and lichen layer below. *Sphagnum* species dominate the bryophyte layer and are the major peat formers. These ecosytem engineers create an acidic and nutrient-poor environment, allowing them and other typical bog plants to dominate over otherwise competetively superior vascular plant species (van Breemen 1995).

In boreal peatlands, depth of the water table and pH are considered the main factors shaping the variation in plant species composition (Nomals 1930; Rydin and Jeglum 2013). These factors vary with the microtopography within bogs, with the distance to the bog margins, and with regional hydrology and precipitation patterns. Also, electric conductivity (EC), which reflects the concentration of dissolved minerals and has been found to be a significant factor for the vegetation in peatland ecosystems (Whitehouse and Bayley 2005), and calcium content are usually low in the central part of peat bogs and tend to increase toward the bog margins with groundwater influence (Bragazza and Gerdol 1999). Additionally, the patterns observed in the bryophyte and lichen layer, which includes small vascular plants, may be under the control of microclimatic modifications and litter from the vascular-plant layer above (Belland and Vitt 1995).

In Latvia, mires (bogs, fens and transitional mires) cover around 4.9% of the country (Pakalne and Kalniņa 2005). Active raised bogs are the protected habitats listed in the European Union Habitats Directive's Annex I and covers around 4.1% of Latvia. Around 18% of them are under protection and are included in the Natura 2000 network of protected nature areas. Being located in the transition from the nemoral (or temperate) to the boreal zone, the vegetation in Latvia contains typical elements from both climate zones and therefore represents the hemiboreal vegetation zone. The original recognition of a hemiboreal (known now as boreo-nemoral) zone was based on forest vegetation (Ahti et al. 1968), while no information is available about the distinctiveness of the hemiboreal vegetation in raised bog ecosystems.

Most of the previous studies on raised bog vegetation in Latvia concentrated on the origin, stratigraphy, distribution and classification of the vegetation (e.g. Galeniece 1935, 1960, 1962; Bambe 1994; Pakalne and Kalniņa 2005; Pakalne 2008), while little attention has been given to environmental factors shaping bog vegetation at the microscale. On the other hand, Nomals (1930) studied bog chemistry, but without paying much attention to the vegetation. Namatēva (2010) studied bog vegetation in relation to microtopograpy and found clear patterns in plant-species composition. For example, *Calluna vulgaris*, *Eriophorum vaginatum*, *Ledum palustre* and *Chamaedaphne calyculata* were found on hummocks, while other species, such as *Rhynchospora alba* and *Andromeda polifolia*, typically occurred in hollows. Other environmental controls, such as water chemistry, were not studied in a vegetation context so far. Understanding such controls, however, is essential not only out of a scientific interest in bog ecology, but also for a better planning of conservation and restoration in raised bogs. Most of conservation acitivities in Latvia today are targeted directly at vegetation composition, while physical and chemical factors potentially affecting the outcome of conservation and restoration measures are ignored. Although much can be learnt from the better-studied environment-vegetation relationships in boreal bogs, understanding these relationships for the boreo-nemoral vegetation zone is essential for a tailored management of bogs in this transitional zone.

In the present study, we aimed at quantifying the spatial and chemical controls on raised bog vegetation, its structure, species composition and ecology in Latvia, and to compare them to the controls found to be important in the better-studied boreal peatbogs.

Material and methods

Study areas

Raised bogs are characterised by dome-shaped masses of peat being accumulated in the former beds of lakes or paludified terrain depressions. Raised bogs form a complex of hummocks, hollows and flatter areas (lawns); pools and bog lakes may also be found (Pakalne and Kalniņa 2005; Pakalne 2008).

Our study was conducted in 17 raised bog areas in different parts of Latvia (Fig. 1). Only living bogs were selected, excluding excavated or heavily drained bogs or bogs restored after such activities. Latvia lies in boreo-nemoral vegetation zone according to the Udvardy's (1975) classification scheme. The annual amount of precipitation varies among the studied areas, with a mean of 667 mm. The average temperature in January is about −5 °C and +17 °C in July (LVĢMC 2015).

Data collection

Data on vegetation and environmental variables were collected in the growing season of 2014. In each bog system, 30 sample plots (1 × 1 m) were established, except in Gulbītis purvs (five sample plots) and Orlovas purvs (25 sample plots). These 480 plots were all located in pristine ombrotrophic parts of the bogs, at different distances from the bog margin but excluding marginal areas with possible minerotrophic influence. Plots were placed along linear transects, with about 10-m distance between plots.

Occurrence and percent cover of each vascular plant, bryophyte and lichen species were evaluated in each sample plot. Total cover and cover per plant group was

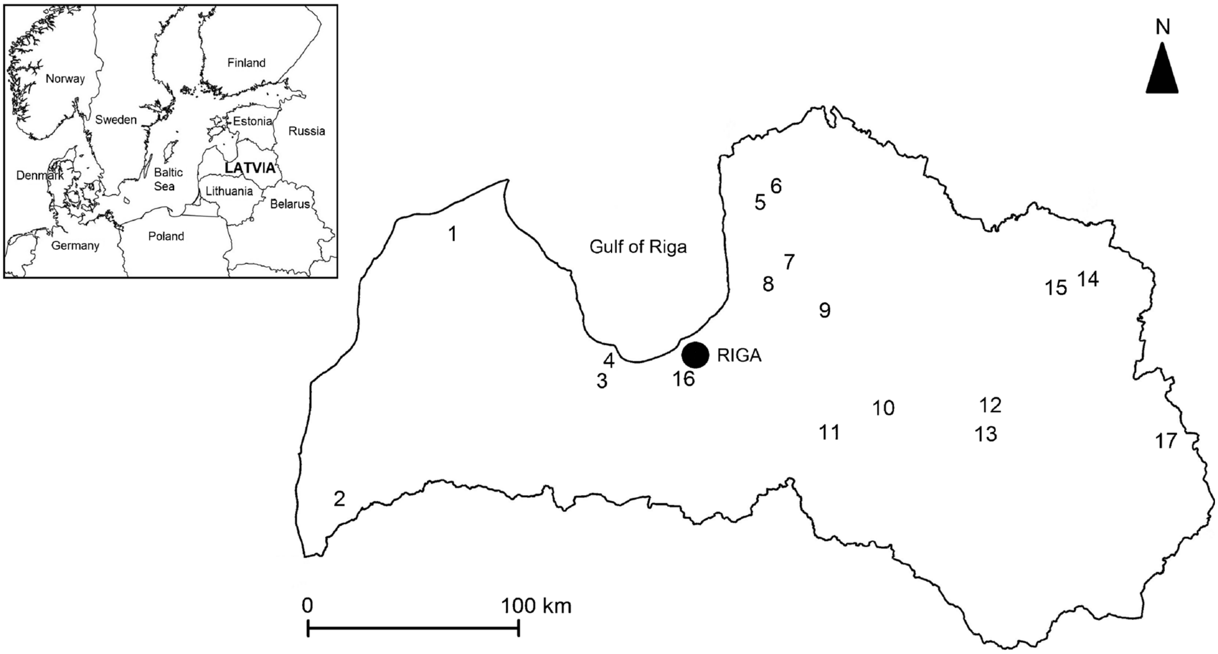


Fig. 1 Studied raised-bog areas in Latvia: 1 – Vasenieku purvs (Stiklu purvi), 2 – Tīrspurvs, 3 – Lielais Ķemeru tīrelis, 4 – Raganu purvs, 5 – Rūstužu purvs, 6 – Purezera purvs, 7 – Lielais un Pemmes purvs, 8 – Laugas purvs, 9 – Ratnieku ezers un purvs, 10 – Aizkraukles purvs, 11 – Aklais purvs, 12 – Teiču purvs, 13 – Lielais Pelečāres purvs, 14 – Orlovas purvs, 15 – Gulbītis purvs, 16 – Cenas tīrelis, 17 – Gulbju and Platpirovas purvs

calculated from the sum of the species covers. The litter cover was evaluated in 420 of the sample plots. We collected surface water or water accumulated in the water-logged moss layer in lawns and hollows, but in hummocks we dug small holes and collected water, when it filled up the hole. For very large hummocks, where the holes did not fill up with water, we collected the water in the closest distance to the hummocks. We did not collect water samples during or just after rain, but waited at least 1–2 days for stabilization of nutrient concentrations. In July there was a long drought period which might have led to a deviation of the measured values from seasonal means. As the water chemistry differed along the sampling season, we added sampling season (spring, summer, autumn) as a covariable in the analyses.

Surface water acidity and electric conductivity (EC) in each sample plot were measured in the field using a portable pH tester (HI 98127, HANNA instruments) and conductivity tester (The Original Dist, HI 98300 HANNA instruments) in surface water trapped in the moss layer. The EC was corrected for the influence of H^+ based on calculations by Sjörs (1950). Sodium (Na), potassium (K), calcium (Ca), magnesium (Mg), and phosphate (PO_4^{3-}) concentrations were determined in the laboratory by atomic absorption spectrometry (air-acetylene flame, AAnalyst 200, PerkinElmer). The concentration of phosphate in surface water was determined colourimetrically using a UV/Vis-spectrophotometer (Hach-Lange DR 5000). Phosphate concentrations were determined according to the ascorbic acid method (APHA/AWWA/WEF 2005). Due to the brown colouration of the water, nitrogen (N) could not be determined with the available spectroscopic laboratory methods.

Microtopography was evaluated in each sample plot in four classes as follows: 1 – hummock (no visible water), 2 – lawn (sites, where water appears after pressing the vegetation down), 3 – hollow with moderate water level (visible water patches appear), 4 – hollow with the highest water level (including submerged vegetation). We tried to select homogeneous sample plots, with one typical microtopography class per plot.

Lichen and bryophyte nomenclature follows Āboliņa et al. (2015) and vascular plant nomenclature follows Gavrilova and Šulcs (1999). Due to uncertainties concerning *Polytrichum strictum* occurrence in Latvian raised bogs – *P. strictum* may be identical morphologically with *P. juniperinum* growing in bogs (Abolin 1983) – we assumed that *P. juniperinum* may include *P. strictum* (Rungis et al., unpublished data) in our data.

Vegetation data of the present study are available upon request from the first author of the present article at the Global Index of Vegetation plot data base (Latvian raised bog data base) (http://www.givd.info/ID/EU-LV-003).

Data Analysis

The effects of environmental variables on the vegetation in the 480 sampled plots were analyzed with a Generalized Linear Mixed Model (GLMM, R package 'lme4', Bates et al. 2015). We analysed the richness of *Sphagnum* species as well as richness and cover of all species taken together, dwarf shrubs, graminoids (include grasses *Poaceae*, sedges *Cyperaceae*, cottongrass *Eriophorum* sp.div., and pod grass *Scheuchzeria palustris*), and trees. Lichens and bryophytes other than *Sphagnum* were not included in the modelling, because these occurred in too few sample plots. *Sphagnum* cover was not modelled, as this was near or at 100% in the great majority of the plots. For these three groups the data distribution therefore did not allow for meaningful models. Still, a clear relationship of lichen and bryophyte cover and richness with microtopography was suspected based on our field experience and was analysed using Kruskall-Wallis rank sum tests. In the GLMM, the negative binomial family was used for dealing with the overdispersion of the residuals. Site identity and sampling season were included as random effects, while all other environmental variables were treated as fixed effects. Included variables were EC, pH, microtopography, mineral content of surface water (Na, K, Ca, Mg and PO_4^{3-}, see Table 1). Litter cover was not included in the modelling, because these data were not available for all plots. No interactions were tested. Stepwise backward selection was used, deleting variables with the least significant effects until the most parsimonious models were found based on the lowest AIC value.

Species composition was related to environmental factors using a Canonical Correspondence Analysis (CCA, R packages vegan and MASS). CCAs were run separately for vascular plants and for bryophytes and lichens. Species with only one or two records were removed from the analysis as these incidental observations did not show any specific indication about the particular environmental conditions. The CCAs included data about species cover (log-transformed) in the 479 sample plots and the explanatory environmental variables (EC, pH, litter, microtopography, Na, K, Ca, Mg, PO_4^{3-}, and CSGT – cover of dwarf shrubs, graminoids and trees, the latter tested as a predictor only for lichen and bryophyte composition. Site was defined as a covariate. We ran the CCA twice, once with microtopography as a variable and once with microtopography as a covariate, to study the effect of the chemical and structural parameters without the strong dominance of microtopography. The inclusion of explanatory variables in the CCA models was aimed obtaining the model with the lowest AIC value.

Kendall's correlation test (R package PMCMR, Pohlert 2014) was used to test for correlations between variables (EC, microtopography, litter, pH, Na, Mg, K, Ca, PO_4^{3-}, CSGT), as this method is suitable for non-normally distributed data. Differences in environmental variables as well as in species richness and cover for all species together and for lichens and bryophytes other than *Sphagnum* among the microtopographical classes (Fig. 2, 3 Appendix 2) were tested using Kruskall-Wallis rank sum tests, as data were not normally distributed, followed by Dunn's post hoc tests with Bonferroni correction.

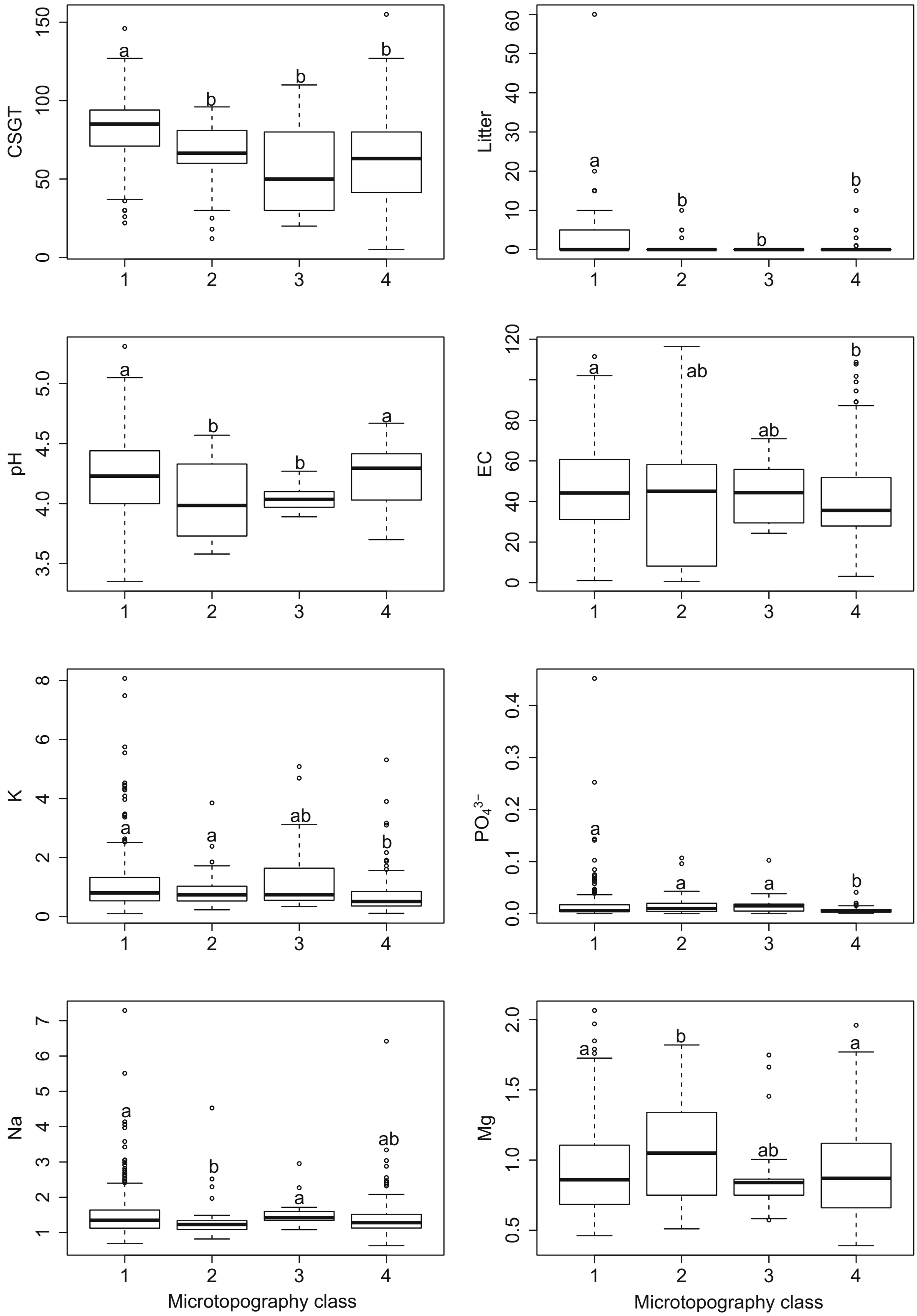
An Indicator Species Analysis (McCune and Grace 2002) was applied to species occurrence data and microtopography for identifying significant ($P < 0.05$) indicator species (with an indicator value of at least 10) for each microtopography class.

Most analyses were performed in R (version 3.2.1, R core team 2013), only the Indicator Species Analysis was performed in the PCord software (version 5, McCune and Grace 2002).

Results

In total, 19 vascular plant, 27 bryophyte and 13 lichen species were found in the studied raised bogs

Fig. 2 Boxplots of studied environmental variables in Latvian raised bogs in relation to microtopographical classes: 1 – hummock, 2 – lawn, 3 – hollow with moderate water level, 4 – hollow with high water level. Ca is not included, as no differences were found between microtopographical classes ($P > 0.05$). Significant differences are indicated with small letters. Sample plots studied (N) = 480 (Microtopography, Electric conductivity, CSGT, pH), 420 (litter), or 479 (Na, Mg, K, Ca and PO_4^{3-})


CSGT
Litter
pH
EC
K
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Na
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Microtopography class
Microtopography class

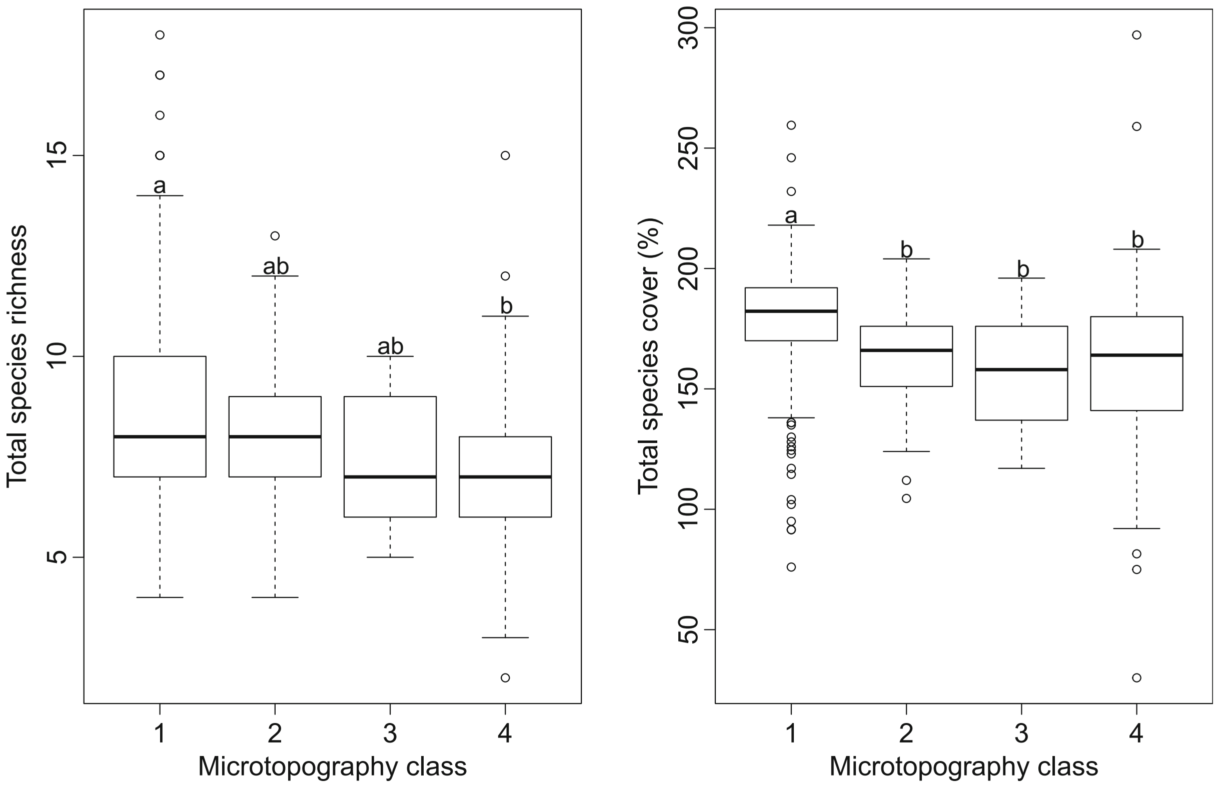


Fig. 3 Boxplots of total species richness and cover (%) in Latvian raised bogs for different microtopographical classes. 1 – hummock, 2 – lawn, 3 – hollow with moderate water level, 4 – hollow with high water level. Significant differences are indicated with small letters. Sample plots studied (*N*) = 480

Table 1 Average values and standard deviations of the chemical variables of surface water in raised bogs in Latvia

Bog name	EC, $\mu S \cdot cm^{-1}$	pH	Na^{+}, $mg \cdot l^{-1}$	Mg^{2+}, $mg \cdot l^{-1}$	K^{+}, $mg \cdot l^{-1}$	Ca^{2+}, $mg \cdot l^{-1}$	PO_4^{3-}, $mg \cdot l^{-1}$
Aizkraukles purvs	56.3 ± 10.7	4.00 ± 0.10	1.71 ± 0.75	1.07 ± 0.43	2.47 ± 2.03	4.51 ± 1.77	0.044 ± 0.005
Aklais purvs	52.8 ± 8.5	4.10 ± 0.20	1.02 ± 0.39	0.64 ± 0.06	0.87 ± 0.40	2.78 ± 1.21	0.025 ± 0.020
Cenas tīrelis	36.65 ± 13.42	4.37 ± 0.09	1.24 ± 0.23	0.82 ± 0.17	0.71 ± 0.47	3.41 ± 0.55	0.007 ± 0.001
Gulbītis	12.69 ± 2.35	3.83 ± 0.04	1.50 ± 0.61	0.60 ± 0.10	1.51 ± 0.91	2.33 ± 0.38	0.047 ± 0.020
Gulbju un Platpirovas purvs	87.66 ± 11.61	4.19 ± 0.18	1.35 ± 0.30	1.17 ± 0.18	0.93 ± 0.79	4.88 ± 0.71	0.035 ± 0.080
Lielais Ķemeru tīrelis	29.28 ± 8.80	4.07 ± 0.08	1.48 ± 0.47	0.79 ± 0.35	0.73 ± 0.38	2.91 ± 1.70	0.018 ± 0.010
Laugas purvs	59.06 ± 16.64	4.52 ± 0.11	1.23 ± 0.20	1.03 ± 0.14	1.15 ± 0.70	4.08 ± 0.51	0.004 ± 0.001
Lielais Pelečāres purvs	74.99 ± 19.79	4.48 ± 0.06	1.38 ± 0.44	1.27 ± 0.20	1.41 ± 0.82	5.09 ± 0.57	0.006 ± 0.004
Lielais un Pemmes purvs	47.40 ± 11.65	4.51 ± 0.19	1.65 ± 0.79	0.89 ± 0.16	1.47 ± 1.49	4.09 ± 0.77	0.004 ± 0.001
Orlovas purvs	7.41 ± 5.93	3.68 ± 0.08	1.44 ± 0.48	1.39 ± 0.32	1.10 ± 0.89	4.79 ± 1.04	0.023 ± 0.030
Purezera purvs	35.04 ± 5.56	4.08 ± 0.10	1.50 ± 0.37	0.80 ± 0.12	0.74 ± 0.61	4.35 ± 1.02	0.003 ± 0.001
Raganu purvs	43.99 ± 9.11	4.04 ± 0.15	1.48 ± 0.15	0.78 ± 0.15	0.61 ± 0.19	3.24 ± 0.57	0.011 ± 0.010
Ratnieku ezers un purvs	33.21 ± 11.40	4.43 ± 0.11	1.18 ± 0.21	0.65 ± 0.15	1.11 ± 1.05	2.91 ± 0.69	0.005 ± 0.001
Rūstužu purvs	18.91 ± 3.72	4.41 ± 0.13	1.23 ± 0.20	0.62 ± 0.10	0.49 ± 0.31	2.67 ± 0.50	0.003 ± 0.001
Teiču purvs	56.59 ± 8.66	4.12 ± 0.13	1.09 ± 0.25	1.31 ± 0.22	0.94 ± 0.40	3.70 ± 0.95	0.011 ± 0.008
Tīrspurvs	43.03 ± 17.00	4.34 ± 0.28	3.07 ± 1.18	0.78 ± 0.16	0.98 ± 0.79	2.84 ± 0.37	0.005 ± 0.007
Vasenieku purvs (Stiklu purvi)	32.75 ± 3.73	3.99 ± 0.04	1.55 ± 0.22	1.11 ± 0.17	0.33 ± 0.23	3.64 ± 0.96	0.004 ± 0.001

(Appendix 1). The most common vascular plant species were *Eriophorum vaginatum* (found in 384 or 80% of all sample plots) and *Oxycoccus palustris* (found in 344 or 72% of all sample plots). The most common bryophyte was *Sphagnum magellanicum* (found in 326 or 68% of all sample plots), and the most common lichen was *Cladonia stygia* (found in 22 or 5% of all sample plots).

The average values of all studied variables per bog system are given in Table 1. The average EC values varied about ten-fold among the studied bogs, with Gulbju un Platpirovas purvs showing the highest values (87.7 $\mu S \cdot cm^{-1}$), in contrast to Orlovas purvs with a value of only 7.41 $\mu S \cdot cm^{-1}$. The highest average value of Na (3.07 $mg \cdot l^{-1}$) was found in Tīrspurvs, while in all other areas Na varied between 1.1 and 1.7 $mg \cdot l^{-1}$. The values of other chemical variables did not vary much among the bogs studied. Significant correlations ($P < 0.05$) were found among most of the studied variable pairs (Table 2). The highest correlation was found between Mg and Ca ($r = 0.65$).

In spite of considerable overlap due to the wide range of bogs sampled (Fig. 2, 3), significant differences between microtopographical classes were found for vegetation cover (dwarf shrubs, graminoids and trees), total species richness and cover, EC, pH, litter, Mg, Na, K, and PO_4^{3-}, though not for Ca.

Indicator species analysis revealed several indicator species for each of the microtopographical classes (Appendix 2). For instance, typical hummock species were *Calluna vulgaris*, *Eriophorum vaginatum* and *Sphagnum fuscum* (class 1), while *Rhynchospora alba*, *Cladopodiella fluitans* and *Sphagnum tenellum* were indicators for conditions in hollows with high water level (class 4).

According to the GLMM, total species richness and cover were best explained by microtopography, with hollows showing fewer species and lower percentage cover of vegetation than hummocks (Fig. 3). However, the different organism groups differed in their controlling factors. Microtopographic moisture had a negative effect on tree species richness and cover and dwarf-shrub cover, but a positive effect on graminoid cover (Table 3). For vascular plant richness, the second most important predictor was pH, with significant negative effect on dwarf shrub richness, but positive effect on tree species richness. Tree cover showed a negative association with K and a positive association with Na. In contrast, dwarf-shrub cover was positively associated with K, as well as EC and negatively with Mg. Ca showed a positive relationship with tree richness. We did not find any significant model explaining *Sphagnum* species richness. The cover and richness of lichens and bryophytes other than *Sphagnum* were generally low, but depended on the microtopography (Appendix Fig. 5). Thereby, hummocks showed the highest lichen cover, which was significantly higher than that in hollows. Hummocks further showed highest maximum cover of bryophytes other than *Sphagnum*, although their total cover did not significantly differ from the other microtopographical classes. The mean species richness of lichens was highest in hollows (class 3 and 4, with 0.4 species), but there were only two species ever occurring in hollows, with a maximum number of one species in a

Table 2 Kendall's correlation coefficients for environmental variables in raised bogs in Latvia., EC – electric conductivity, MT – microtopography, Litter – total litter cover, Mg, K, Ca, PO_4^{3} – concentrations of the respective elements in surface water, CSGT – cover of dwarf shrubs, graminoids, trees

	EC								
pH	0.12**	pH							
MT	−0.11**	0.02	MT						
Litter	0.09*	0.21**	−0.33**	Litter					
Na	0.06	−0.04	−0.05	−0.03	Na				
Mg	0.29**	−0.08*	−0.02	0.11**	0.15**	Mg			
K	0.20**	0.07*	−0.19**	0.13**	0.12**	0.17**	K		
Ca	0.28**	−0.01	−0.03	0.18**	0.22*	0.65**	0.20**	Ca	
PO_4^{3-}	0.16**	−0.29**	−0.09*	−0.09*	−0.05	0.03	0.14**	0.02	PO_4^{3-}
CSGT	0.07*	0.06	−0.32**	0.13**	0.02	−0.02	0.05	−0.01	< 0.01

* – significance level 0.05, ** – significance level 0.01

Table 3 Most parsimonious models resulting form a GLMM analysis of species richness and cover in relation to environmental variables for different plant groups in Latvian raised bogs

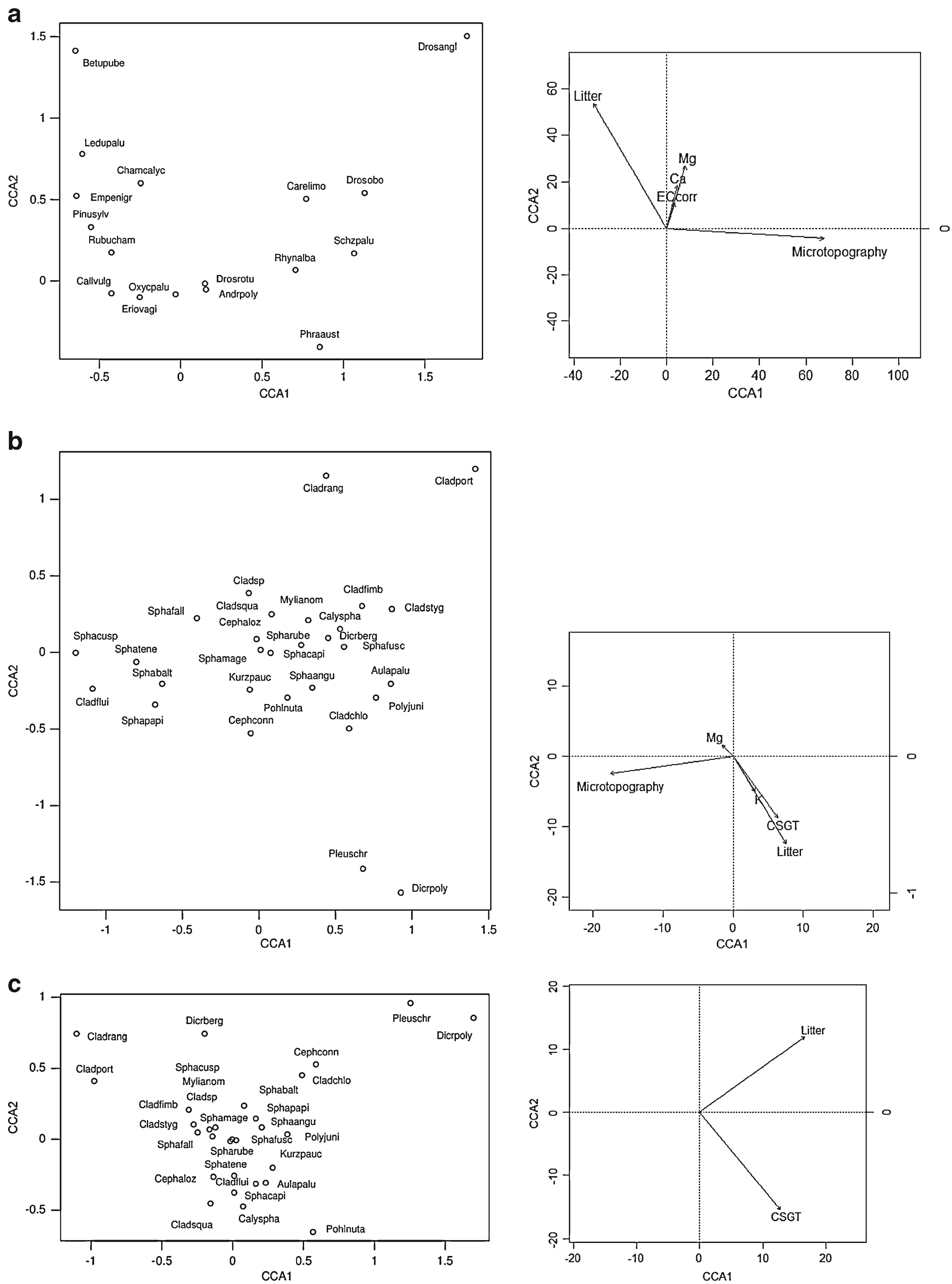
Vegetation group	Variables	Estimate	*SE*	AIC	*P*
Species richness					
Dwarf shrubs	Model (pH)	3.47	0.91	1475	< 0.01
	pH (−)	−0.68	0.22		< 0.01
Trees	Model (MT+pH+Ca)	−6.26	1.89	502	< 0.01
	MT (−)	−0.52	0.13		< 0.01
	pH (+)	1.00	0.40		< 0.01
	Ca (+)	0.29	0.08		< 0.01
Total	Model (MT)	2.22	0.06	2344	< 0.01
	MT (−)	−0.07	0.02		< 0.01
Species cover					
Graminoids	Model (MT)	3.61	0.09	4299	< 0.01
	MT (+)	0.10	0.02		< 0.01
Dwarf shrubs	Model (K+Mg+MT+EC)	3.97	0.10	3955	< 0.01
	K (+)	0.06	0.03		< 0.05
	Mg (−)	−0.29	0.12		< 0.05
	MT (−)	−0.43	0.02		< 0.01
	EC (+)	0.004	0.002		< 0.05
Trees	Model (Na+K+MT+pH)	−6.37	1.56	1983	< 0.01
	Na (+)	0.36	0.12		< 0.01
	K (−)	−0.27	0.07		< 0.01
	MT (−)	−0.61	0.05		< 0.01
	pH (+)	1.60	0.36		< 0.01
Total	Model (MT)	5.24	0.05	4883	< 0.05
	MT (−)	−0.04	0.02		< 0.05

Full models included MT, CSGT (only for lichens and bryophytes), pH, EC. The estimate for the models refers to the estimate for the intercept of the models. MT – microtopography (1 – means the driest conditions, and 4 – conditions with high water level), CSGT – cover of dwarf shrubs, trees and graminoids. In parenthesis the direction, (+) positive or (−) negative, of the parameter's influence is given. Only the final simplified models and variables are presented. Simplification was done according to the AIC – Akaike's Information Criterion. For *Sphagnum* and richness of graminoids no significant models could be constructed.. For lichens and bryophytes other than Sphagnum the very strong zero-inflation in the data and too few non-zero data did not allow for meaningful models (see Appendix 2 for the pattern)

plot. The highest lichen and bryophyte species richness was found on hummocks, with maximum number of four lichen and five bryophyte species, but the mean lichen species richness was lower because of many zero values, and for bryophytes mean species richness did not differ between microtopographical classes.

In the CCA of vascular-plant data, where microtopography was included as one of the variables, this variable showed a strong correlation with the first axis (r = 0.89), followed by litter (r = −0.41). The second axis was best explained by litter (r = 0.71), followed by Mg (r = 0.35) and Ca (r = 0.24 – Fig. 4a, Table 4). The same variables (except from microtopography) explained vascular plant composition in the CCA, where microtopography was set as a covariate (not shown). *Betula pubescens* took an extreme position on both axes, being associated with high litter cover. It appeared on the same extreme of the first CCA axis together with the other

Fig. 4 CCA ordination with vegetation data from Latvian raised bogs. A – vascular plant data, B – bryophyte and lichen data, C – bryophyte and lichen data (microtopography as covariate). ECcorr– electric conductivity [$\mu S \cdot cm^{-1}$], Mg [$mg \cdot l^{-1}$], K [$mg \cdot l^{-1}$], Ca [$mg \cdot l^{-1}$], CSGT – cover of dwarf shrubs, graminoids and trees. Species name abbreviations are given in Appendix 1 ▶


a
Drosangl
Betupube
Ledupalu
Chamcalyc
Empenigr
Pinusylv
Rubucham
Callvulg
Oxycpalu
Eriovagi
Drosrotu
Andrpoly
Carelimo
Drosobo
Schzpalu
Rhynalba
Phraaust
CCA1
CCA2
Litter
Mg
Ca
ECcorr
Microtopography
b
Cladrang
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Cladsp
Mylianom
Cladfimb
Cladstyg
Sphafall
Cladsqua
Calyspha
Cephaloz
Sphacusp
Sphatene
Sphamage
Sphabalt
Sphacapi
Sphafusc
Sphagangu
Kurzpauc
Aulapalu
Cladflui
Sphapapi
Pohlnuta
Polyjuni
Cephconn
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Pleuschr
Dicrpoly
Dicrberg
Sphangu
Sphagrube
Mg
Microtopography
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Sphaangu
Sphafall
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Kurzpauc
Sphatene
Cephaloz
Cladflui
Aulapalu
Sphacapi
Calyspha
Cladsqua
Pohlnuta
Litter
CSGT

Table 4 Significant correlations ($P < 0.05$) between environmental variables and CCA Axis 1 and Axis 2 for vascular plant, bryophyte and lichen species groups in Latvian raised bogs

Variables	Vascular plants		Bryophytes and lichens		Bryophytes and lichens (microtopography as a covariate)	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Microtopography	0.89	−0.0.06	−0.89	−0.13	–	–
EC	0.04	0.14	–	–	–	–
Litter	−0.41	0.71	0.39	−0.64	0.71	0.51
Mg	0.11	0.35	−0.08	0.08	–	–
K	–	–	0.16	−0.26	–	–
Ca	0.06	0.24	–	–	–	–
CSGT	–	–	0.33	−0.45	0.55	−0.66

EC electric conductivity, *CSGT* cover of dwarf shrubs, trees and graminoids

hummock indicators like *Empetrum nigrum*, *Calluna vulgaris*, *Ledum palustre*, *Pinus sylvestris* and *Rubus chamaemorus*. These tree and dwarf shrub species contribute strongly to the production of litter and thus also affect the chemical variables; this may partly explain the nature of the correlations found in our study, with vegetation and environment being involved in a continuous feedback.

In the CCA for bryophytes and lichens, where microtopography was included as a variable, this variable likewise had the strongest correlation with the first axis ($r = -0.89$), followed by litter ($r = 0.39$) and CSGT ($r = 0.33$). The second axis was most correlated with litter ($r = -0.64$), CSGT (−0.45) and K (−0.26). In the CCA, where microtopography was treated as covariate, litter ($r = 0.71$ for the first axis, $r = 0.51$ for the second axis) and CSGT ($r = 0.55$ for the first axis and $r = -0.66$ for the second axis) were also the most influential variables, while other variables did not contribute sufficient information to include them in the CCA models, according to the Akaike information criterion (Fig. 4c). The lichen *Cladonia portentosa* and the peat moss *Sphagnum cuspidatum* took the most extreme positions along the first axis, corresponding to contrasting microtopographical preferences. With microtopography excluded, these species were much less separated. On the second axis, *C. portentosa* again takes an extreme position, together with *C. rangiferina* at the end with low litter and vascular plant cover, contrasted with the bryophytes *Dicranum polysetum* and *Pleurozium schreberi*, which occurred in plots with high litter cover. This contrast was maintained in the CCA, where microtopography was a covariable (Fig. 4b,c; Table 4).

Discussion

The best explanation for total plant species richness, cover, and composition in Latvian raised bogs is the microtopography. The species composition is also correlated with litter cover and concentrations of alkaline ions (Ca, Mg), though the importance of the different nutrients differed between vascular plants vs. bryophytes and lichens. Microtopography, in turn, determines nearly all other environmental factors. The importance of microtopography we found agrees with reports from boreal or temperate mountain bogs where water level is considered a particularly important vegetation-forming factor (e.g. Anderson and Davis 1997; Rydin and Jeglum 2013; Jiroušek et al. 2013). The hummocks harboured a higher species richness than the hollows and the highest total cover overall, while the other microtopographical classes did not differ in this respect, though they did differ in species composition. The analysis per species group reveals, however, that groups vary strongly in their responses to environmental factors and that microtopography is not the main factor explaining species richness for all groups. Species richness and cover of most groups tended to be higher in hummocks, but graminoid species richness and cover were higher in lawns and hollows (Table 3, Table 5). Similar differences were found for other environmental variables in our study. For example, the tree diversity and abundance were more diverse in dry and less acidic sites, where the dwarf shrub diversity was higher at more acidic sites.

In our study, both chemical (mineral content of surface water, but not pH) and physical factors (microtopographic moisture, vascular-plant cover except from herbs, litter) were significant in explaining species composition of bryophytes. Belland and Vitt (1995) in their study on coastal bogs in northern Alberta (Canada) found that bryophyte vegetation was influenced mostly by dryness and shade and only to a lesser extent by pH. Bryophytes are considered as good indicators of water levels in peatlands (Goffinet and Shaw 2009). Vascular plant cover and litter were important for bryophyte and lichen species richness as well. They shade the lower strata and their litter can either prevent establishment or, on the other hand, provide a substrate for some species of bryophytes and lichens. For instance, small liverworts such as *Cephalozia* spp. prefer a specific microhabitat of decaying litter in small depressions at hummock margins. Pouliot et al. (2011) showed that vascular plants increase relative humidity, prevent temperature fluctuations, and reduce the light intensity at the *Sphagnum* surface, microclimatic modifications that may strongly influence bryophyte and lichen communities.

Lichen cover was highest in the highest and driest microtopographical positions, confirming the results of Anderson and Davis (1997) that lichen richness increased with hummock presence and decreased with humidity. Nevertheless, in our study the overall lichen diversity was too low to draw a sound conclusion.

We found only few species in the studied sample plots that might be associated with increased alkaline ion concentrations (e.g. *Betula pendula*, *Betula pubescens*, *Phragmites australis* and *Plagiomnium affine*). Their occurrence in the oligotrophic bogs, if not caused by stochastic processes such as mass effects, might be explained by nutrient input from outside the bogs, e.g. from anthropogenic activities, incoming dust or marine input (van Breemen 1995; Proctor 2003). Such extra inputs were also apparent in the chemical composition of the surface water of some bogs (Table 1). For example, the Aizkraukles purvs bog site encompasses several areas of mineral soils with deciduous forests as well as transitional mire patches with nutrient-rich substrates, and part of the bog is exploited for peat milling. Probably this explains the higher PO_4^{3-} and K contents in comparison to most other areas studied. The increased concentrations of Na in Tīrspurvs might be related to its closeness to the sea (~23 km). Some other studied bog sites were even closer to the sea – Cenas tīrelis (~13 km) and Laugas purvs (~16 km), but these bogs are located closer to the Gulf of Riga, where salt concentration is slightly lower than in the open Baltic Sea and where they are not in the predominant wind direction from the sea.

In spite of a ca 15-fold variation in PO_4^{3-} concentration between bogs, which is greater than e.g. the variation found in 'poor' (0.01–0.02 $mg \cdot l^{-1}$) vs 'extremely rich' fens (0.01 $mg \cdot l^{-1}$) in Canada (Vitt and Chee 1990), we did not find any relationship between PO_4^{3-} and vascular plant richness, cover or composition. Analogous results have been reported by Jiroušek et al. (2013) from Central-European mountain bogs, where PO_4^{3-} explained species composition only in one specific case – the variation in bryophyte species composition among individual bogs in the Jeseníky Mts (where bogs have been affected by aerial liming) have been partially explained by the five-year averages of PO_4^{3-} concentration. Generally, raised bog vegetation can be limited or co-limited by N, P or K (Rydin and Jeglum 2013; Bergsma and Quinlan 2009) We did not measure any form of nitrogen, but differences in N level can partially explain the variation in species data found in our study. In our study, K was a significant predictor of bryophyte and lichen composition and dwarf shrub cover "(correlating positively; Tab 3, Tab 4) confirming the results of Wendel et al. (2011), coming from ombrotrophic peatlands in Canada, and Anderson and Davis (1997), coming from Maine bogs and fens, that K is a significant predictor in the variance of vascular plant cover.

Jiroušek et al. (2013) found that the magnitude of the abiotic factors – water level, pH and Ca contents shaping the bog communities, might be assessed during single sampling, but the importance of PO_4^{3-}, Na and K can not be evaluated from a single sampling as in the case of our study. However, as we have data from the entire growing season for a large number of bogs, we expect only negligible biases caused by temporal variation in nutrient concentrations. Samples within individual bogs were generally taken in one occassion, so that relative differences within bogs should be reliably pictured in our data. However, it is possible that other elements are also important in shaping vegetation patterns and long-term studies are certainly recommendable to understand long-term influences on vegetation structure in raised bogs.

Conclusions

The present study describes the environmental controls of raised bog vegetation in the boreo-nemoral zone, providing a reference for comparing human-affected vs natural bog ecosystems that is needed for the implementation of nature conservation or restoration projects.

Chemical properties of surface waters were explained mainly by microtopography, and microtopography alone, in particular hummocks vs other microtopographical features, explained total species richness and cover better (i.e. most parsimoniously) than other factors. The importance of environmental variables varied between functional species groups and species richness, cover and composition of the same functional group were controlled by different factors. For species composition of vascular plants, alkaline ions and litter cover were the most important factors, and for bryophytes and lichens, vascular plant cover was additionally important. However, as many of the variables are highly correlated to each other and to microtopographical position, a real understanding of their effects would benefit from experimental studies that complement large-scale observational studies as presented here.

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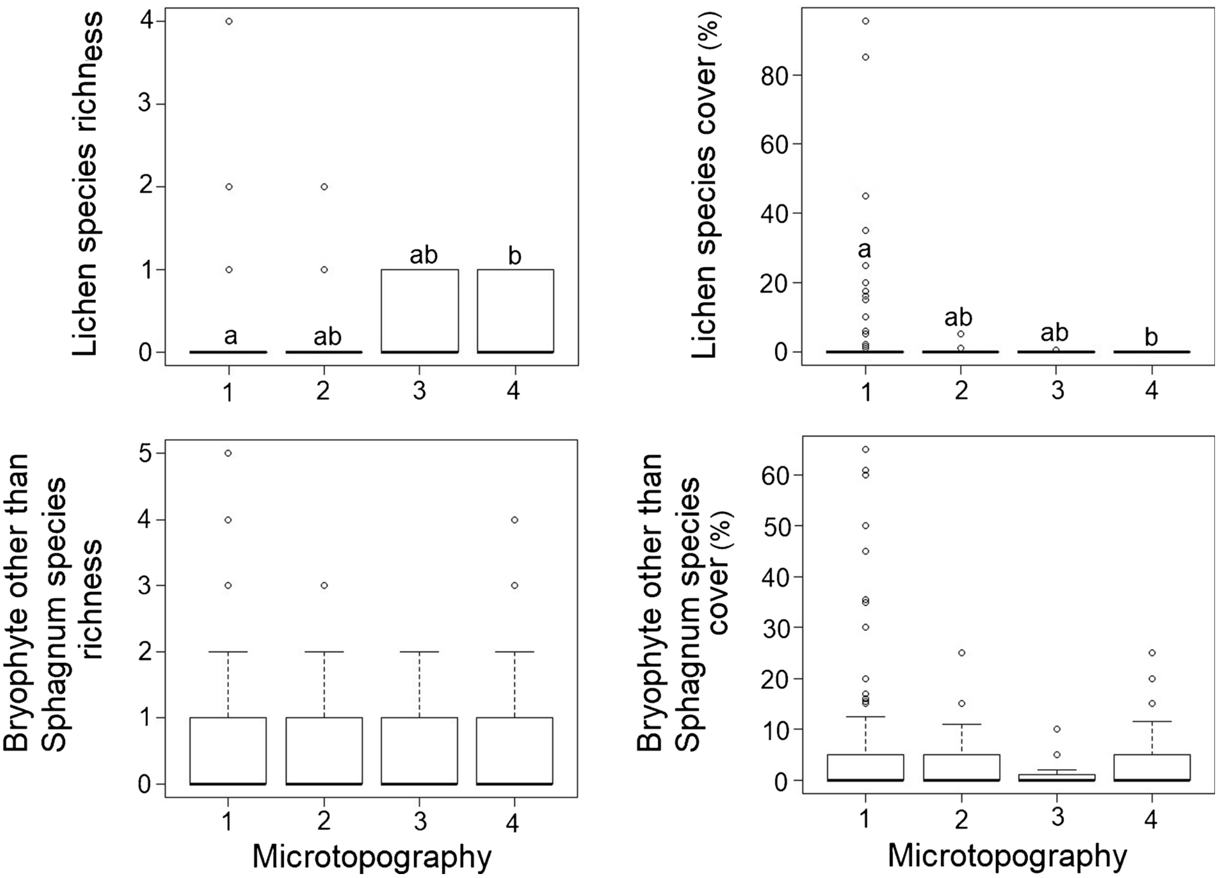
Appendix 1 Lichen, bryophyte and vascular plant species list with indicator-species analysis and frequency of occurrence in studied raised bogs

Abbreviation	Species name	Microtopographic preference	Frequency occurrence [%]
Vascular plants			
Andrpoly	*Andromeda polifolia*	n.s.	67. 3
Betupend	*Betula pendula*	n.s.	0.4
Betupube	*Betula pubescens*	n.s.	0.8
Callvulg	*Calluna vulgaris*	1*	65.6
Carelimo	*Carex limosa*	2*	2.9
Chamcaly	*Chamaedaphne calyculata*	n.s.	6.7
Drosangli	*Drosera anglica*	n.s.	1.5
Drosobo	*Drosera ×obovata*	3*	0.6
Drosrotu	*Drosera rotundifolia*	3*	31.7
Empenigr	*Empetrum nigrum*	1*	12.3
Eriovagi	*Eriophorum vaginatum*	1*	80.0
Ledupalu	*Ledum palustre*	1*	12.1
Oxycpalu	*Oxycoccus palustris*	3*	71.7
Phraaust	*Phragmites australis*	n.s.	1.3
Pinusylv	*Pinus sylvestris*	1*	23.3
Rhynalba	*Rhynchospora alba*	4*	37.5
Rubucham	*Rubus chamaemorus*	1*	23.3
Schzpalu	*Scheuchzeria palustris*	3*	12.3
Vacculig	*Vaccinium uliginosum*	n.s.	0.4
Bryophytes			
Aulapalu	*Aulacomnium palustre*	n.s.	2.9
Calyspha	*Calypogeia sphagnicola*	n.s.	1.7
Cephconn	*Cephalozia connivens*	n.s.	1.5
Cephaloz	*Cephalozia* sp.	n.s.	1.0
Cladflui	*Cladopodiella fluitans*	4*	16.9
Dicrberg	*Dicranum bergeri*	n.s.	1.5

Appendix 1 (continued)

Abbreviation	Species name	Microtopographic preference	Frequency occurrence [%]
Dicrpoly	*Dicranum polysetum*	n.s.	0.8
Dicrscop	*Dicranum scoparium*	n.s.	0.2
Kurzpauc	*Kurzia pauciflora*	n.s.	5.0
Mylianom	*Mylia anomala*	n.s.	13.1
Odonspha	*Odontoschisma sphagni*	n.s.	0.4
Plagaffi	*Plagiomnium affine*	n.s.	0.4
Pleuschr	*Pleurozium schreberi*	n.s.	1.0
Pohlnuta	*Pohlia nutans*	n.s.	1.5
Polycomm	*Polytrichum commune*	n.s.	0.2
Polyjuni	*Polytrichum juniperinum*	1*	15.4
Sphaangu	*Sphagnum angustifolium*	n.s.	31.9
Sphabalt	*Sphagnum balticum*	n.s.	4.4
Sphacapi	*Sphagnum capillifolium*	n.s.	2.7
Sphacusp	*Sphagnum cuspidatum*	4*	27.1
Sphafall	*Sphagnum fallax*	2*	24.6
Sphafusc	*Sphagnum fuscum*	1*	40.0
Sphamage	*Sphagnum magellanicum*	n.s.	67.9
Sphapapi	*Sphagnum papillosum*	n.s.	0.8
Spharube	*Sphagnum rubellum*	1*	61.0
Sphatene	*Sphagnum tenellum*	4*	18.5
Strastra	*Straminergon stramineum*	n.s.	0.2
Lichens			
Cladarbu	*Cladonia arbuscula*	n.s.	0.4
Cladchlo	*Cladonia chlorophaea*	n.s.	1.9
Cladcili	*Cladonia ciliata*	n.s.	0.4
Cladconi	*Cladonia coniocraea*	n.s.	0.2
Cladfimb	*Cladonia fimbriata*	n.s.	2.3
Cladglau	*Cladonia glauca*	n.s.	0.2
Claddigi	*Cladonia digitata*	n.s.	0.4
Cladmaci	*Cladonia macilenta*	n.s.	0.4
Cladport	*Cladonia portentosa*	n.s.	1.0
Cladrang	*Cladonia rangiferina*	n.s.	0.6
Cladstyg	*Cladonia stygia*	n.s.	4.6
Cladsp	*Cladonia* sp.	n.s.	1.6
Cladsqua	*Cladonia squamosa*	n.s.	0.6

The column 'Microtopographic preference' shows the class where the species was found the most frequently. Microtopography was recorded in four classes, where 1 – hummock, 2 – lawn, 3 – hollow with moderate water level, 4 – hollow with high water level, n.s. – no significant indicator value. A significant ($P < 0.05$) indicator value is indicated by *, implying an indicator value > 10. *Polytrichum juniperinum* may include *P. strictum*



Appendix 2 Boxplots of lichen and bryophyte species richness and cover [%] in Latvian bogs in relation to microtopographical classes. 1 – hummock (no visible water), 2 – lawn (sites where water appears after pressing the vegetation down), 3 – hollow with moderate water level (visible water patches appear), 4 – hollow with the highest water level (including submerged vegetation). Significant ($P < 0.05$) differences are indicated by small letters (Kruskall-Wallis rank sum tests). No significant influence of microtopography were found for bryophytes other than *Sphagnum* in terms of species richness and cover

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