

Article

The Vertical Structure of Rich Fen Vegetation and the Development of Bryophyte Cover

Monika Kalvaitienė *  and Ilona Jukonienė 

State Scientific Research Institute Nature Research Centre, Akademijos St. 2, LT-08412 Vilnius, Lithuania; ilona.jukonienė@gamtc.lt

* Correspondence: monika.kalvaitiene@gamtc.lt; Tel.: +370-64177716

Abstract

The vertical structure of fen vegetation has received little attention, despite its obvious relevance to interactions between herbaceous plants and bryophytes. The main objective of this study was to determine relationships among the vertical herbaceous-rich-fen vegetation structure and the overall cover and species diversity of bryophytes. The study was conducted in eight fens in Lithuania and covered 210 subplots (0.5 m × 0.5 m). Within each subplot, the total and individual percentages of bryophyte and vascular plant cover, and of each visually distinct vertical vegetation layer, were estimated. In vertical vegetation structure, five distinct structural groups were identified, ranging from a simple two-layer group to a four-layer group. Vertical structural differences in herb cover were primarily associated with water level and microrelief. Our results revealed that an open structure is favourable for entire bryophyte cover; shading does not necessarily lead to a decline in total bryophyte cover but rather drives a structural rearrangement of the bryophyte community. The abundant development of higher vegetation layers in highly hummocky areas negatively affects the bryophyte cover. Monitoring visually distinct vertical structures can help predict negative trends in plant community structure, including shifts in bryophyte diversity and cover.

Keywords: hollows; hummocks; lawns; Lithuania; microtopography; mires; plant communities; surface water; vegetation layers

1. Introduction

Rich fens are among the most biodiverse and highly threatened wetland ecosystems in Europe, sustained by a unique combination of mineral-rich groundwater and low nutrient availability [1–3]. Because of this specific ecological regime, these habitats develop a complex vertical and spatial structure that supports both diverse vegetation and a detailed mosaic [4,5]. This structural complexity creates a multitude of distinct microclimatic and hydrological niches, allowing numerous rare, highly specialised, and endangered plant species to coexist [1,6]. However, since botanically rich fens are widely degraded by drainage and land-use abandonment, understanding their vertical stratification is crucial for predicting community shifts and guiding effective conservation strategies [7–9].

A distinguished feature of rich fens is a well-developed layer of bryophytes, especially brown mosses. In fens, bryophytes always constitute the lower (bottom) layer of vegetation, whether they form continuous ground cover or are scattered in different microhabitats on hummocks or in hollows. The ecological relationship between bryophytes and vascular plants remains a subject of debate in previous research [10]. Nutrients arriving throughfall



Academic Editors: Lele Liu, Yaolin Guo, Youzheng Zhang and Weihua Guo

Received: 9 June 2026

Revised: 14 July 2026

Accepted: 15 July 2026

Published: 20 July 2026

Copyright: © 2026 by the authors.

Licensee MDPI, Basel, Switzerland.

This article is an open access article distributed under the terms and conditions of the [Creative Commons Attribution \(CC BY\)](https://creativecommons.org/licenses/by/4.0/) license.

from the vascular plant canopy can facilitate bryophyte growth [11–13], as can evaporation and reduced shade under moderate vascular plant cover. On the other hand, a lack of light and space often suppresses bryophytes, as illustrated by the predominantly negative correlation between bryophyte cover and that of vascular plants [14,15]. This competitive or facilitative balance is largely driven by the composition of the upper vegetation layer [8].

The herb layer of rich fens may be dominated not only by different species in terms of their taxonomy, but also by different species with contrasting life traits: small or large graminoids (*Carex* spp., *Eleocharis* spp., *Juncus* spp., *Molinia caerulea*, *Phragmites australis*, etc.) and low (*Drosera* spp., *Cardamine* spp.) or tall herbs (*Eupatorium cannabinum*, *Ranunculus lingua*). Different plant species with various traits combined to form certain species pools and different physiognomically distinct vertical structures. Thus, plants act as ecosystem engineers by creating specific habitat niches, e.g., as light patches in canopies and undergrowth [16]. An example of this is the orientation of leaves in different plant groups: in broadleaf plants, it is more horizontal (planophilic), whereas in grasses it is more vertical (erectophilic) [17]. In turn, this variation in physical structure shapes a range of microenvironments relevant to other organisms. The distribution of various organisms, especially arthropods, across ecosystems indicates that vegetation structures may be more important than previously suggested [18,19].

However, most studies assessing vertical vegetation structure have focused primarily on forested habitats [16,20–22]. In contrast, the canopy architecture of herbaceous communities has received little attention, despite its obvious relevance to interactions between herbaceous vascular plants [23,24] and between herbaceous plants and bryophytes [25]. Furthermore, the overall productivity of the herb layer remains an understudied factor controlling the patterns of non-forest fen vegetation [8]. Shading by vascular plants may also contribute to the decline in brown mosses [26]. However, the mechanism by which specific structural variations within the herbaceous canopy mediate this relationship remains poorly understood. Therefore, this study focuses on the intricate relationship between the vertical structure of herbaceous plants and the bryophyte layer in rich fens. Our main objective is to determine the processes occurring in rich fens by combining vertical herbaceous vegetation structure with bryophyte cover development and species diversity. To address this, we sought to answer the following research questions: (1) What vertical structures of herbaceous vegetation are formed in different habitats of rich fens? (2) What effect do these structures have on total bryophyte cover? (3) Are these structures related to the composition of bryophyte species? These data will be used to assess vegetation trends in fens across Lithuania, a country uniquely positioned at the transition between the boreal and continental biogeographical zones. Recent research highlights that Lithuanian fens exhibit highly distinct environmental and structural characteristics [5]. Based on the literature review, we set up the following hypotheses: H1: The increasing vertical complexity would be associated with lower bryophyte cover due to increased shading. H2: Different structural groups would support distinct bryophyte assemblages. H3: Structural groups with greater broadleaf plant cover have a greater influence on bryophyte cover than those dominated by narrow-leaved plants. Consequently, understanding these dynamics is essential for identifying the most appropriate conservation measures and evaluating the success of ongoing restoration projects.

2. Materials and Methods

2.1. Study Sites

The investigations were conducted between 2016 and 2019 across eight fens distributed throughout various regions of Lithuania (Figure 1). These sites were selected to characterise the region's characteristic vertical structures of fen ecosystems. The overarching study

matrix belongs to the Lithuanian landscape, a territory positioned within the maritime-continental transitional climate of Northeastern Europe and the eastern part of the Baltic Sea basin [27,28]. According to the Geiger Köppen global climate classification, which divides regions based on seasonal temperature, precipitation, and vegetation [29], the area mostly experiences a humid continental climate with warm summers (16–18 °C) and relatively cold winters (−3 to −6 °C), except for a narrow, more temperate coastal zone [30]. This geographic setting determines distinct seasonal variations and a positive moisture balance, with average annual precipitation typically ranging between 600 and 800 mm, though historically fluctuating from 355 to 950 mm [31,32]. The regional macro-relief, primarily formed by the deglaciation phases of the Last Glacial Period, exhibits an intricate arrangement of lowlands, glacial basins, and undulating uplands with restricted natural drainage [33,34]. Although diverse mire types historically covered substantial portions of the country, intensive 20th-century agricultural drainage transformed the landscape, confining intact, non-degraded rich fens to isolated wetland refugia [3,8]. Currently, these minerotrophic systems are highly critical for sustaining structurally diverse vegetation communities reliant on stable, base-rich groundwater discharge. The eight selected fens are distributed across three climatic subregions that differ in their mean annual temperature (MAT) and mean annual precipitation (MAP) [35] (Figure 1).

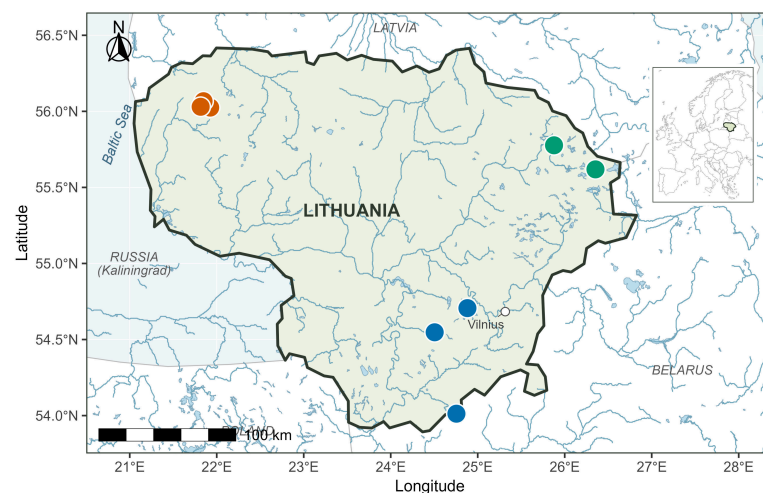


Figure 1. Map of the study sites. Fens marked with orange dots are located in the Žemaičių subarea of the Žemaičių Highland region (MAT: 6.3–6.7 °C; MAP: 810–820 mm); those marked with blue dots are located in the Dzūkų subarea of the Southeast Highland region (MAT: 6.8 °C; MAP: 700 mm); and those marked with green dots are located in the Aukštaičių subarea of the Southeast Highland region (MAT: 6.1–6.7 °C; MAP: 610–690 mm).

2.2. Field Sampling and Vegetation Records

At each of the eight study sites along randomly selected transects, 4 m × 4 m study plots [36] focusing on microrelief forms, vertical layer development, and dominant plant and bryophyte species were established. Within each study plot, five smaller 0.5 m × 0.5 m subplots (a total of 210 subplots) were positioned at the corners and in the centre of the study plot. Within each subplot, the total percentage cover of bryophytes and vascular plants was estimated; all bryophyte species were recorded along with their individual percentage cover. Subsequently, the vegetation's vertical structure was analysed (Figure 2). Visually distinct vertical layers were identified (scaled from layer I as the lowest stratum adjacent to bryophytes to layer IV as the uppermost stratum), and the total percentage cover of each layer was estimated.

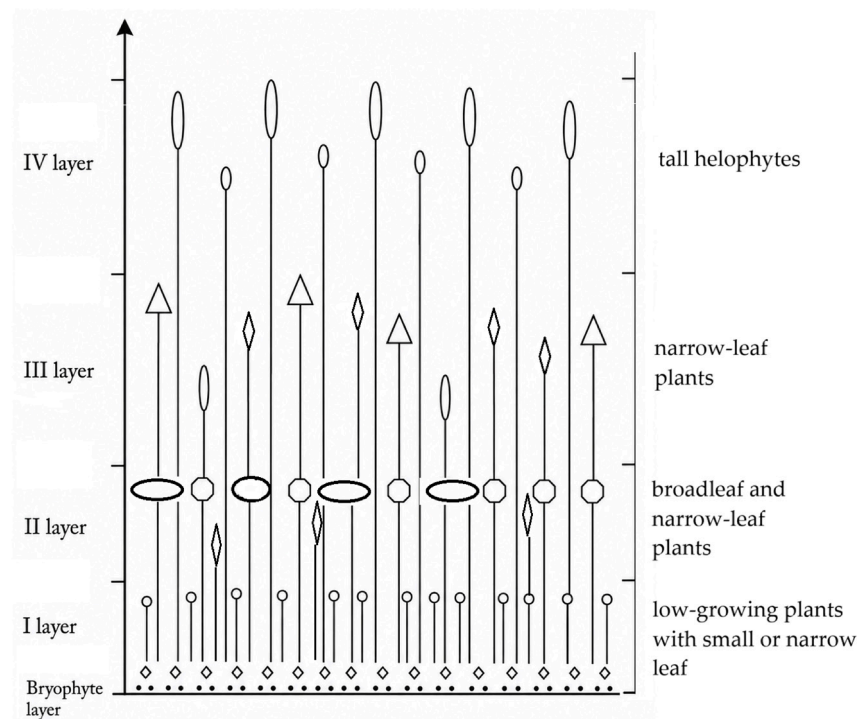


Figure 2. Schematic representation of the vertical vegetation structure in rich fens.

Within each layer, all present plant species were recorded, their individual percentage cover was determined, and the height from the bryophyte surface was measured. The height range for each layer was determined based on the minimum and maximum heights of the species presented. The microtopographical surface percentage cover (%) of hummocks and water-filled depressions (hollows) was evaluated within each subplot. Water samples were collected in autumn (September–October) to determine the concentrations of calcium (Ca^{2+}), magnesium (Mg^{2+}), iron (Fe^{3+}), nitrate (NO_3^-), ammonium (NH_4^+), and phosphate (PO_4^{3-}) in study plots. These chemical parameters were chosen to assess the trophic status and hydrological feeding characteristics of the fen ecosystems. The samples were kept frozen until chemical analysis, which was performed by the accredited laboratory CJSC “EKOMETRIJA” (Vilnius, Lithuania) using standardised ISO and EN ISO methods [37–42]. A total of 88 vascular plant species and 22 bryophyte species were recorded during the field study. Most of them were identified during field surveys. Unidentified specimens were collected for more accurate species identification in the laboratory. The voucher specimens are deposited at the Herbarium of the Nature Research Centre (BILAS). The data were collected by the authors of the paper between 2016 and 2019. The taxonomic nomenclature of bryophytes followed the latest European checklist [43], while vascular plants were classified according to the World Checklist of Vascular Plants [44].

2.3. Data Analysis

Initially, based on the number of identified vertical layers, vegetation descriptions were categorised into three major structural groups: group A comprised communities with two layers, group B included those with three layers, and group C represented communities with four layers. Because Group B (three-layered communities) was the largest group and showed high internal heterogeneity, it was further subdivided into three sub-groups (B-1, B-2, and B-3). This heterogeneity was mainly driven by differences in the development, fragmentation, or degradation of the layers across certain subplots. To identify these subgroups, a hierarchical clustering analysis was performed using PAST statistical software, version 5.3 [45], based on the Bray–Curtis similarity coefficient and

Ward's linkage method, incorporating variables such as total bryophyte cover, total herb cover, layers (I–IV) cover (%), mean weighted height, maximum layer height, and height variance (Figure 3). The optimal number of sub-clusters was determined based on the linkage distance threshold and the ecological interpretability of the resulting groups. A cutting height (linkage distance ≈ 25) was selected on the dendrogram, as it represented a significant jump in dissimilarity between the branches.

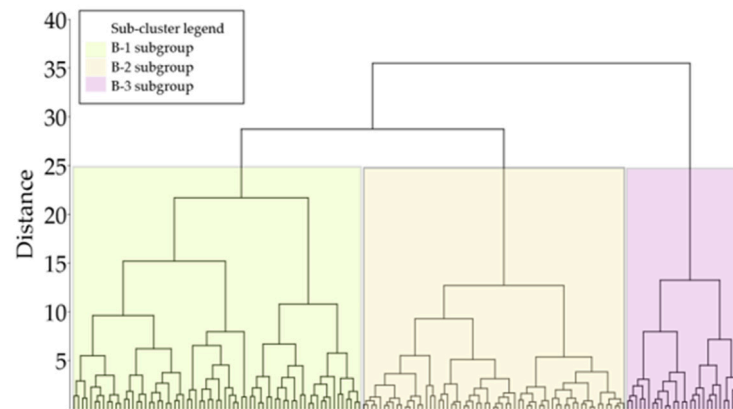


Figure 3. Dendrogram of the hierarchical cluster analysis identifying vegetation sub-clusters (B-1, B-2, and B-3) in PAST software, based on the Bray–Curtis similarity coefficient and Ward's linkage method.

To characterise the environmental conditions associated with the different vertical structures, an environmental parameter comparison was conducted among them. The analysis utilised hummock and surface water cover (determined as micro-habitat structures at the subplot level) and concentrations of Ca^{2+} , Mg^{2+} , Fe^{3+} , NO_3^- , NH_4^+ , and PO_4^{3-} (determined as macro-environmental background parameters captured at the plot level to characterise site-specific hydrochemical baseline conditions). To illustrate the overarching abiotic context without scale-induced statistical artefacts, the study plot-level hydrochemical concentrations are presented as descriptive background profiles to visually assess environmental homogeneity across the structural groups. First, the normality of the subplot-level variables (hummock and surface water cover) was evaluated using the Kolmogorov–Smirnov test. Because micro-habitat predictors were not normally distributed, their differences within groups were determined using the non-parametric Kruskal–Wallis test. Upon identifying significant overall differences, the Mann–Whitney U test was used for subsequent pairwise comparisons of the subplot physical structures. Statistical evaluations were considered significant at $p < 0.05$.

To characterise the vertical layers (I–IV) based on their floristic composition, a summary table was constructed focusing on the dominant vascular plant species for each group. Within each individual layer, species achieving the maximum percentage cover value in at least one given relevé were designated as dominants. To ensure data legibility and focus on the main structural components, only these dominant species were included in the final summary table, omitting rare or low-cover species. To assess the structural and compositional divergence specifically within the bryophyte cover, a Permutational Multivariate Analysis of Variance (PERMANOVA) based on Bray–Curtis distances was performed to test for significant differences in bryophyte assemblages among the groups, followed by a Permutational Analysis of Multivariate Dispersions (PERMDISP) to evaluate homogeneity of variance. A Principal Coordinates Analysis (PCoA) was applied to project the compositional gradient in multivariate space. Additionally, a Similarity Percentage (SIMPER) analysis was conducted to identify the diagnostic bryophyte species responsible for the observed dissimilarity between groups.

To evaluate the overall distribution of bryophyte species in relation to environmental parameters, subplot-level data were averaged to the study plot level, resulting in 42 plot-level observations. Bryophyte species cover data were Hellinger-transformed prior to the analysis. Environmental variables were standardised (z-score) to account for differences in measurement units and scale among predictors. To select the most appropriate ordination method, the gradient length along the first axis was evaluated using Detrended Correspondence Analysis (DCA). The resulting gradient length of 2.51 standard deviation (SD) units indicated a linear response, justifying the choice of Redundancy Analysis (RDA) over Canonical Correspondence Analysis (CCA). Before model fitting, multicollinearity among environmental variables (I–IV layer cover, I–IV layer height, surface water cover, hummock cover and concentrations of Ca^{2+} , Mg^{2+} , Fe^{3+} , NO_3^- , NH_4^+ , and PO_4^{3-}) was assessed using variance inflation factors (VIF); all variables showed low collinearity ($\text{VIF} < 3$); the highest VIF values were 2.19 for Fe^{3+} , 1.81 for Ca^{2+} , 1.77 for layer IV cover, and 1.73 and 1.70 for Mg^{2+} and layer IV height, respectively. Therefore, all variables were retained for further analysis. To identify which environmental parameters contributed significantly to the ordination, the marginal (unique) effect of each variable was tested using a permutation procedure (999 permutations), analogous to a Type III test, in which the significance of each predictor was evaluated while controlling for the effects of all remaining variables. Only environmental variables with a significant marginal effect ($p < 0.01$) were retained in the final model and displayed in the ordination biplot. To improve the interpretability of the biplot, moss species were filtered based on their goodness-of-fit to the first two RDA axes (R^2), and only species with $R^2 > 0.3$ were displayed, since these were considered to be reasonably well represented by the two-dimensional ordination.

Finally, to assess the relationship between vegetation structure and bryophyte cover, two complementary analyses were performed. First, the influence of upper vegetation layer development on the total coverage of the bryophyte layer was evaluated within each structural group separately, using Spearman's rank correlation coefficients. Correlations were tested between total bryophyte cover, total vascular cover, and the individual covers of layers I, II, III, and IV (conditioned by the layer count of the respective group). This analysis quantified the competitive or suppressive effects between the upper vegetation canopy and the ground-layer bryophytes across varying structural complexities. Second, because the group-specific correlation analysis suggested that the relationship between vegetation layers and bryophyte cover was inconsistent across structural groups, a Generalised Linear Mixed-Effects Model (GLMM) was additionally used to assess this relationship across all subplots simultaneously ($n = 210$), while accounting for the nested sampling design (Site/Study plot) and testing all vegetation layer variables jointly rather than individually. The total percentage cover of the bryophyte layer was introduced as the response variable. The fixed predictors included the individual percentage covers and average heights of vascular plant layers I–IV, the total number of vegetation layers, and the percentage covers of surface water and hummock cover. To accommodate the bounded nature of percentage data, the GLMM was modelled using a Beta error distribution with a logit link function. To account for the nested sampling hierarchy and potential spatial dependency across different localities, 'Site' and 'Study plot' were incorporated into the model structure as nested random intercepts ($1 \mid \text{Site/Study plot}$). This mixed-model approach effectively accounted for potential pseudoreplication and isolated the direct vertical suppression, facilitation, or microhabitat partitioning effects.

Univariate non-parametric tests (Kolmogorov–Smirnov, Kruskal–Wallis, Mann–Whitney U), hierarchical cluster analysis, PCA, and Spearman correlation analyses, as well as multivariate community analyses—including PERMANOVA, PERMDISP, DCA, PCoA, and SIMPER—were conducted using PAST software, version 5.3 [39]. Linear constrained

ordinations (RDA) and Generalised Linear Mixed-Effects Models (GLMMs) were executed within the R statistical environment (version 4.3.1) using the vegan (version 2.6-4) [46] and glmmTMB (version 1.1.7) [47] packages, with statistical significance for all evaluations set at $p = 0.05$.

3. Results

3.1. Characteristics of Vertical Structural Groups

To represent the variation in vertical vegetation structure across the studied fens, five distinct structural groups (A, B-1, B-2, B-3, and C) were identified (Table 1). These categories reflected the inherent complexity of the vertical layers, ranging from simple structures to multi-layered communities with varying bryophyte cover.

Table 1. Structural characteristics, species richness, and layer cover values of the identified vegetation groups (A, B-1, B-2, B-3, and C). Total layer cover data are presented as mean $\pm$ standard deviation, with minimum and maximum values indicated in parentheses (min–max %).

Parameters	Groups				
	A	B			C
	<i>n</i> = 25	B-1 <i>n</i> = 79	B-2 <i>n</i> = 47	B-3 <i>n</i> = 35	<i>n</i> = 24
Number of layers	2	3	3	3	4
Total herb cover (%)	35.1 $\pm$ 9.4 (20–60)	44.9 $\pm$ 15.1 (14–80)	83 $\pm$ 9.1 (60–100)	60.8 $\pm$ 14.1 (32–90)	70.5 $\pm$ 19.0 (30–100)
Total bryophyte cover (%)	95.1 $\pm$ 6.9 (80–100)	91.2 $\pm$ 12.5 (52–100)	64.6 $\pm$ 26.5 (16–100)	58.6 $\pm$ 29.4 (7–100)	48.2 $\pm$ 27.8 (6–90)
Total herb species richness (per plot)	6.9 $\pm$ 1.6 (3–10)	8.1 $\pm$ 2.5 (4–16)	9.3 $\pm$ 2.5 (3–17)	9.3 $\pm$ 2.1 (4–14)	11.8 $\pm$ 2.2 (8–16)
Total bryophyte species richness (per plot)	2.9 $\pm$ 0.9 (2–5)	3.4 $\pm$ 1.2 (2–6)	3.5 $\pm$ 1.3 (2–7)	3.5 $\pm$ 1.3 (2–7)	4.1 $\pm$ 1.3 (2–6)
Mean weighted height (cm)	15.6 $\pm$ 4.4 (8.5–25.6)	20.2 $\pm$ 3.9 (11.5–29.5)	23.2 $\pm$ 5.2 (12.7–40.1)	41.1 $\pm$ 10.1 (25–66)	32.4 $\pm$ 8.8 (18.7–59.1)
Maximum layer height (cm)	30.3 $\pm$ 8.7 (18–50)	53.1 $\pm$ 8.3 (32–75)	58 $\pm$ 10.4 (40–90)	67.1 $\pm$ 5.9 (50–75)	80.5 $\pm$ 14.5 (60–120)

The vertical structure of the identified groups became more complex from a simple two-layer structure in Group A to a distinct four-layer canopy in Group C. Group A represented the most basic structural form, characterised by only two layers, where vegetation is almost entirely compressed into the bryophyte and the lowest vascular plant layer (layer I). In this group, higher layers (III and IV) were virtually absent, and the mean weighted height was the lowest among all groups. Groups B-1, B-2, and B-3 formed a three-layer structure; however, they differed significantly in the extent of their coverage of the layers and overall height profiles. Group B-1 represented plant communities in which the third layer emerged with a low mean cover (8.2%), while the overall community remained dominated by a dense bryophyte layer. In group B-2, vertical development was heavily concentrated in layer II, with a mean cover of 52.1%, creating a dense but low-growing profile which also contributes to the highest total herb cover observed across all structural groups. A further shift in verticality was observed in group B-3, where the dominance of herb cover began to migrate upwards, with layer III becoming the most prominent vascular layer (mean cover 29.2%), resulting in a significantly higher mean weighted height. Group C stood out as the most complex because it was the only group with four distinct layers. The uppermost layers (III and IV) coincided with a notable reduction in the lowest vascular layer (layer I),

which dropped to a mean cover of less than 14% while exhibiting the highest maximum layer height and the most advanced vertical differentiation.

3.2. Microrelief and Hydrochemistry of Structural Groups

We observed significant changes in microrelief across the groups, alongside some apparent visual shifts in groundwater chemistry. Group A was characterised by flat lawns with high surface water cover and almost no hummock formation (Figure 4). This simple structure coincided with the hydrochemical profile, which visually displayed the lowest levels and narrowest ranges of Fe^{3+} and PO_4^{3-} , pointing to a stable, highly flooded environment.

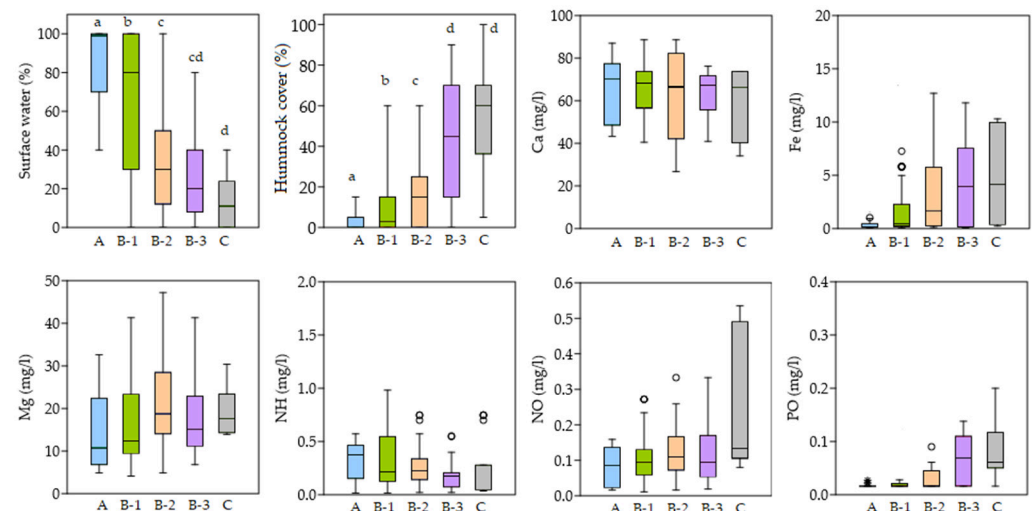


Figure 4. Comparison of environmental variables across the identified groups (A, B-1, B-2, B-3, and C): surface water, hummock cover, Ca^{2+} (indicated as Ca in the figure), Fe^{3+} (Fe), Mg^{2+} (Mg), NH_4^+ (NH), NO_3^- (NO), and PO_4^{3-} (PO). For microrelief parameters (surface water and hummock cover), different letters indicate statistically significant differences based on the Mann–Whitney U test ($p < 0.05$). Hydrochemical parameters represent plot-level baseline concentrations projected onto the structural groups. The circles indicate outliers.

Group B-1 also maintained a high average surface water, but its hydrological parameters varied widely—surface water dropped from almost 100% to nearly 40% at certain sites, which aligned with wide ranges in Ca^{2+} , Mg^{2+} , and Fe^{3+} concentrations. In Group B-2, mineral levels stayed consistently high for both Ca^{2+} and Mg^{2+} , accompanied by a broad spread of Fe^{3+} . However, the microrelief began to differentiate, showing an emerging overlap between initial hummock cover and fluctuating surface water. Groups B-3 and C shifted towards drier, semi-waterlogged conditions. Group B-3 was notable for an extreme spike in PO_4^{3-} variation, with specific sites acting as significant outliers compared to the relatively low and stable levels in earlier groups. Finally, Group C displayed the most developed microrelief, with hummock cover reaching up to 60–70% and a corresponding decline in surface water cover. Hydrochemically, group C exhibited a distinct visual shift in nitrogen dynamics: while the previous groups (A and B) maintained a uniformly low, flat baseline, group C displayed a visibly elevated NO_3^- concentration and a wide amplitude of NH_4^+ . Such trends suggest a potential acceleration of nutrient cycling and increased oxygenation within the developed hummock-hollow complex.

3.3. Species Composition of Vegetation Layers Between Groups

The development of layer I varied inconsistently between the studied groups. In groups A and B-1, layer I was characterised by a stable mean cover ranging from 18.8% to 20.6% (Table 2). While group A was floristically dominated by *Vaccinium oxycoccos*, *Menyanthes trifoliata*, and *Drosera anglica*, group B-1 exhibited a shift toward a slightly

different structure; there, the layer was primarily dominated by *Rumex acetosa*, *Vaccinium oxycoccos*, and *D. anglica*. Following this baseline, a distinct peak was observed in group B-2, where the mean layer I cover reached 26.8% (individual plots reaching up to 70%). This peak was dominated by *Rumex acetosa* and *Cardamine pratensis*. However, a significant reduction in mean cover was recorded in the subsequent groups (B-3, C). Although group B-3 shared the same key dominant species at identical frequencies as group B-2 (*R. acetosa* and *C. pratensis*), its mean cover was substantially lower. This declining trend was partially reversed in terms of cover in group C, where layer I recovered to a mean cover of 13.6%, with *R. acetosa*, *C. pratensis*, and *Galium uliginosum* emerging as the dominant taxa.

Table 2. Structural and compositional characteristics of vertical vegetation layers (I–IV) across the identified vertical structural groups. Data are presented as mean percentage cover % and standard deviation, with minimum and maximum values in parentheses. Dominant species (and their percentage frequency) within each layer are listed based on maximum stratal cover, incorporating only taxa with a frequency threshold of $\geq 10\%$.

Group	Layer	Total Cover %	Dominant Species
A	II	18.9 $\pm$ 8.7 (5–40)	<i>Carex panicea</i> (35%), <i>Carex lepidocarpa</i> (24%), <i>Trichophorum alpinum</i> (18%), <i>Carex limosa</i> (18%)
	I	20.6 $\pm$ 10.4 (5–55)	<i>Vaccinium oxycoccos</i> (29%), <i>Menyanthes trifoliata</i> (24%), <i>Drosera anglica</i> (18%)
B-1	III	8.2 $\pm$ 4.5 (1–20)	<i>Carex lepidocarpa</i> (44.6%), <i>Carex lasiocarpa</i> (13.8), <i>Carex limosa</i> (10.8%)
	II	27.7 $\pm$ 17.6 (2–90)	<i>Menyanthes trifoliata</i> (61.5%), <i>Carex chorrhiza</i> (12.3%)
	I	18.8 $\pm$ 12.5 (2–50)	<i>Rumex acetosa</i> (33.8%), <i>Vaccinium oxycoccos</i> (29%), <i>Drosera anglica</i> (18.5%)
B-2	III	17.3 $\pm$ 9.1 (4–40)	<i>Carex rostrata</i> (32%), <i>Carex lepidocarpa</i> (26%)
	II	52.1 $\pm$ 23 (18–95)	<i>Menyanthes trifoliata</i> (72.5%), <i>Caltha palustris</i> (11%)
	I	26.8 $\pm$ 16.8 (2–70)	<i>Rumex acetosa</i> (33.8%), <i>Cardamine pratensis</i> (19%), <i>Galium palustre</i> (13%)
B-3	III	29.2 $\pm$ 13.3 (10–58)	<i>Carex rostrata</i> (34%), <i>Carex lasiocarpa</i> (21%), <i>Juncus</i> sp. (17%)
	II	20.3 $\pm$ 15.3 (1–55)	<i>Menyanthes trifoliata</i> (47%), <i>Caltha palustris</i> (24.5%)
	I	11.1 $\pm$ 9.5 (1–45)	<i>Rumex acetosa</i> (33.8%), <i>Cardamine pratensis</i> (19%)
C	IV	11.3 $\pm$ 9.7 (1–35)	<i>Typha</i> sp. (53%), <i>Phragmites australis</i> (25%)
	III	28.7 $\pm$ 15.4 (7–70)	<i>Carex rostrata</i> (31%), <i>Carex diandra</i> (25%), <i>Festuca rubra</i> (13%), <i>Thelypteris palustris</i> (13%)
	II	27.1 $\pm$ 21.9 (2–75)	<i>Menyanthes trifoliata</i> (69%)
	I	13.6 $\pm$ 11.3 (1–50)	<i>Rumex acetosa</i> (31%), <i>Cardamine pratensis</i> (28%), <i>Galium uliginosum</i> (13%)

The development of layer II served as a primary indicator of vertical structural reorganisation across the studied groups. Group A represented a distinct baseline, in which layer II had a mean cover of 18.9% and was primarily defined by the frequent occurrence of *Carex panicea* and *C. lepidocarpa* (Table 2). These dominants were accompanied by less frequent occurrences of *Menyanthes trifoliata* and *Trichophorum alpinum*. As vertical complexity increased in Group B-1, a significant compositional shift occurred. While the mean cover increased to 27.7%, the relative dominance of *C. panicea* was reduced, and the layer became increasingly dominated by *M. trifoliata* (61.5%) alongside *Carex chordorrhiza* (12.3%). The peak of vertical intensification for this layer was reached in group B-2, which exhibited the highest mean cover (52.1%). In sharp contrast to the heterogeneity of group A, group B-2 was defined by extreme floral homogenisation, marked by the massive dominance of *M. trifoliata*, establishing a nearly monodominant mid-layer. In groups B-3 and C, layer II

underwent a structural decline or stabilisation, with mean cover dropping to 20.3% and 27.1%, respectively. While *M. trifoliata* remained a constant dominant across both groups (47% in B-3 and 69% in C), group B-3 was further characterised by a substantial presence of *Caltha palustris* (24.5%).

The emergence and maturation of layer III mark the transition toward advanced stratification. Absent in group A, the III layer first appeared in group B-1 with a low mean cover of 8.2%, dominated by *Carex lepidocarpa*, *C. lasiocarpa*, and *C. limosa*. In group B-2, the mean cover of layer III increased to 17.3%, with *Carex rostrata* and *C. lepidocarpa* taking over the dominance. Layer III became the most prominent in group B-3, reaching its maximum mean cover of 29.2%, driven by the codominance of *Carex rostrata* and *C. lasiocarpa*. In group C, layer III maintained a high mean cover and remained dominated by *C. rostrata*, but was further diversified by *C. diandra*, *Festuca rubra*, and *Thelypteris palustris*.

Layer IV was uniquely characteristic of group C, providing a consistent mean cover of 11.3%. The composition of this uppermost canopy was distinct, dominated by tall helophytes, such as *Typha* sp. (53%) and *Phragmites australis* (25%).

Significant differences in bryophyte species composition were detected across the structural vegetation groups (PERMANOVA, $F = 16.57$, $p = 0.0001$) (Table 3). Pairwise comparisons showed that Groups A, B-1, and B-2 differed significantly in bryophyte assemblage composition ($p < 0.01$), whereas no significant compositional difference was detected between Groups B-3 and C ($p = 0.95$), indicating pronounced stabilisation and compositional homogeneity in the final stages of the structural gradient. Although significant heteroscedasticity was present across the dataset (PERMDISP, $F = 14.76$, $p = 0.001$), the PCoA ordination confirmed a consistent compositional gradient, showing a clear spatial separation between the open (Groups A and B-1) and shaded assemblages (Groups B-3 and C), while Group B-2 occupied an intermediate position in the multivariate space (Figure 5).

Table 3. Pairwise PERMANOVA comparisons of bryophyte species composition (based on Bray–Curtis’s dissimilarities) among the five vertical structural groups (A, B-1, B-2, B-3, and C). Values are p -values from pairwise permutational multivariate analysis of variance (9999 permutations); significant differences ($p < 0.05$) are shown in bold.

Group	A	B-1	B-2	B-3	C
A	–	0.00	0.00	0.00	0.00
B-1	0.00	–	0.00	0.00	0.00
B-2	0.00	0.00	–	0.00	0.00
B-3	0.00	0.00	0.00	–	0.95
C	0.00	0.00	0.00	0.95	–

Global PERMANOVA: total sum of squares = 79.65; within-group sum of squares = 61.83; $F = 16.57$; p (same) = 0.00.

Over three-quarters of the total compositional dissimilarity (82.27%) was attributable to changes in the abundance of six species: *Scorpidium cossonii* (25.91%), *S. scorpioides* (17.90%), *Calliergonella cuspidata* (14.06%), *Plagiomnium ellipticum* (8.44%), *Hamatocaulis vernicosus* (8.12%), and *Marchantia polymorpha* (7.84%) (Table A1). These species showed a clearly contrasting distribution pattern along the gradient. *Scorpidium cossonii*, *S. scorpioides*, and *C. stellatum* were most abundant in the waterlogged, open conditions of group A and group B-1 but declined markedly and were largely absent from the remaining groups. In contrast, *C. cuspidata*, *M. polymorpha*, and *H. vernicosus* were absent or near-absent in group A but increased progressively in abundance, with *C. cuspidata* and *H. vernicosus* both reaching their highest mean abundance in group B-2. A similar pattern toward more shaded, hummocky microtopography under a more developed vascular canopy was

observed for *P. ellipticum*, which increased consistently across the gradient and reached its highest mean abundance in Group B-3.

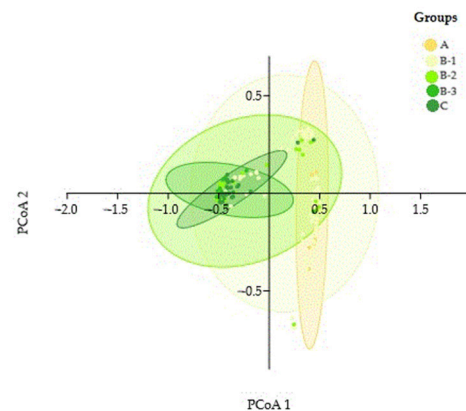


Figure 5. Principal Coordinates Analysis (PCoA) ordination, based on Bray–Curtis distances, illustrating the compositional gradient of bryophyte assemblages across the structural vegetation groups (A, B-1, B-2, B-3, and C).

While the SIMPER analysis identified which species drove compositional differences between structural groups, redundancy analysis (RDA) was subsequently used to determine which environmental parameters most strongly shaped bryophyte species distribution across all study plots. Redundancy analysis showed that bryophyte species composition was significantly related to environmental conditions across the study plots, with the first two RDA axes explaining 43.0% and 7.8% of the total variance, respectively (Figure 6). Of the sixteen environmental parameters considered, seven contributed significantly to the ordination ($p < 0.01$): first- and third-layer cover, surface water, hummock cover, and concentrations of iron, magnesium, and phosphorus. While the preceding classification indicated that bryophyte species differed mainly by structural group, the RDA suggested that, across all plots, species distribution was more strongly linked to hydrological and chemical conditions than to vegetation structure alone. Along the first axis, *Scorpidium cossonii* and *Campylium stellatum* were associated with surface water, indicating a preference for wetter microhabitats, whereas *Calliergonella cuspidata*, *Marchantia polymorpha*, and *Hamatocaulis vernicosus* were linked to higher Fe^{3+} and Mg^{2+} concentrations and greater first-layer cover, indicating more mineral-rich, structurally denser conditions. *Plagiomnium ellipticum* was primarily related to hummock cover along the second axis.

3.4. Relationship Between Vegetation Layer Development and Bryophyte Cover

In terms of bryophyte cover, the results show a progressive decline from group A to group C, reflecting a clear response to changing habitat conditions. Group A exhibited the highest and most consistent bryophyte cover values, indicating stable fen conditions in which bryophytes dominate the ground layer (Table 2).

Group B formed an ecologically diverse mosaic, with bryophyte cover and species diversity varying considerably among its distinct subgroups (B-1, B-2, and B-3), reflecting a wide range of micro-habitat conditions. While group C recorded the lowest overall bryophyte cover, coupled with high variability. Based on the correlation analysis for all data, total bryophyte cover was negatively associated with total herb cover ($p = -0.56$), III layer cover ($p = -0.51$), and IV layer cover ($p = -0.43$) (Figure 7). At the group level, however, the impact of these individual layers varied markedly. In Group A, no variables reached the significance threshold for bryophyte cover. Within Group B, subgroup B-1 showed no significant layer-to-bryophyte correlations either. Subgroups B-2 and B-3 showed opposite trends in the upper plant layers. In subgroup B-2, the III layer cover

was the only variable that had a significant positive correlation with total bryophyte cover ($p = 0.51$). At the same time, although the II layer cover was high, we did not find any significant negative relationship between this layer and the bryophytes. In contrast, in subgroup B-3, the III layer cover showed a strong negative correlation with bryophytes, matching the negative trend of total herb cover. For the C group, the correlation analysis highlighted the importance of the lowest herb layers. Total bryophyte cover showed a strong, significant positive correlation exclusively with I layer cover ($p = 0.61$). In contrast, the upper layers showed negative tendencies: IV layer cover had a correlation of -0.49 , and the total herb cover was -0.41 , though neither crossed the 0.5 significance threshold. For the remaining variables, such as the II and III layer cover, the correlations with bryophytes were very weak and not significant.

To further assess this relationship across the full dataset, a generalised linear mixed-effects model (GLMM) was used, accounting for the nested sampling design and testing all vegetation layer variables jointly (Table 4). The model confirmed that bryophyte cover was significantly negatively affected by the development of the upper vegetation layers. The strongest negative effects were associated with IV layer cover (estimate = -0.0599 , $p < 0.001$), followed by III layer cover (estimate = -0.0207 , $p = 0.0017$) and III layer height (estimate = -0.0150 , $p = 0.0175$). I layer height also showed a significant negative effect on bryophyte cover (estimate = -0.0973 , $p = 0.0061$), while II layer cover and height showed only marginally significant negative effects ($p = 0.072$ and $p = 0.051$, respectively), suggesting a weaker influence of mid-canopy layers. In contrast, neither surface water nor hummock cover had a significant effect in the model, nor did the total number of vegetation layers.

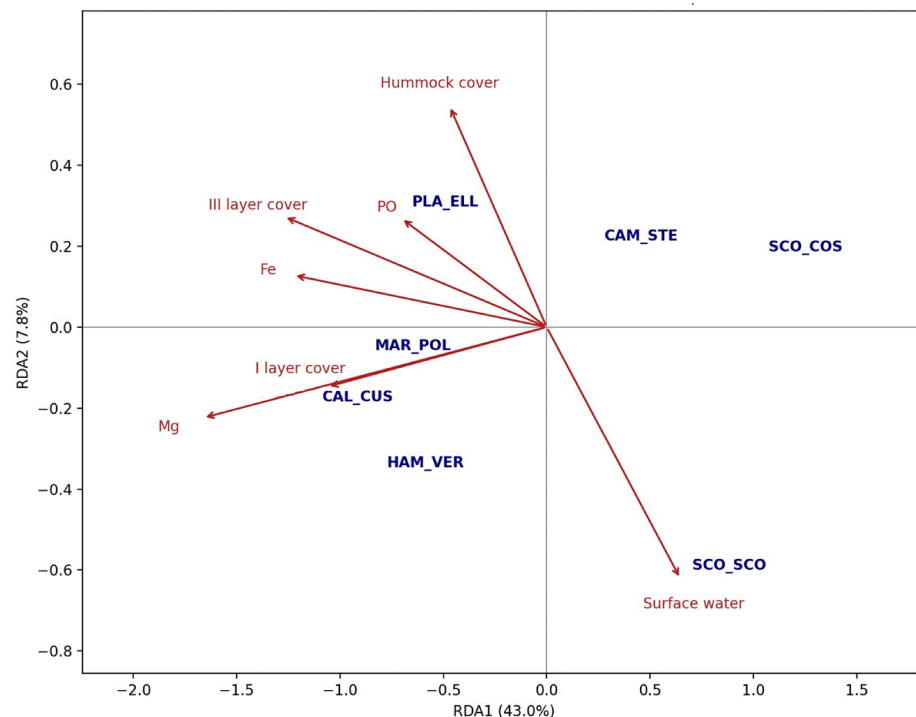


Figure 6. RDA biplot of bryophyte species composition constrained by environmental variables. Arrows represent the seven environmental parameters with significant marginal effects ($p < 0.01$, permutation test, 999 permutations) out of sixteen tested. Only bryophyte species with goodness-of-fit $R^2 > 0.3$ to the first two RDA axes are displayed.

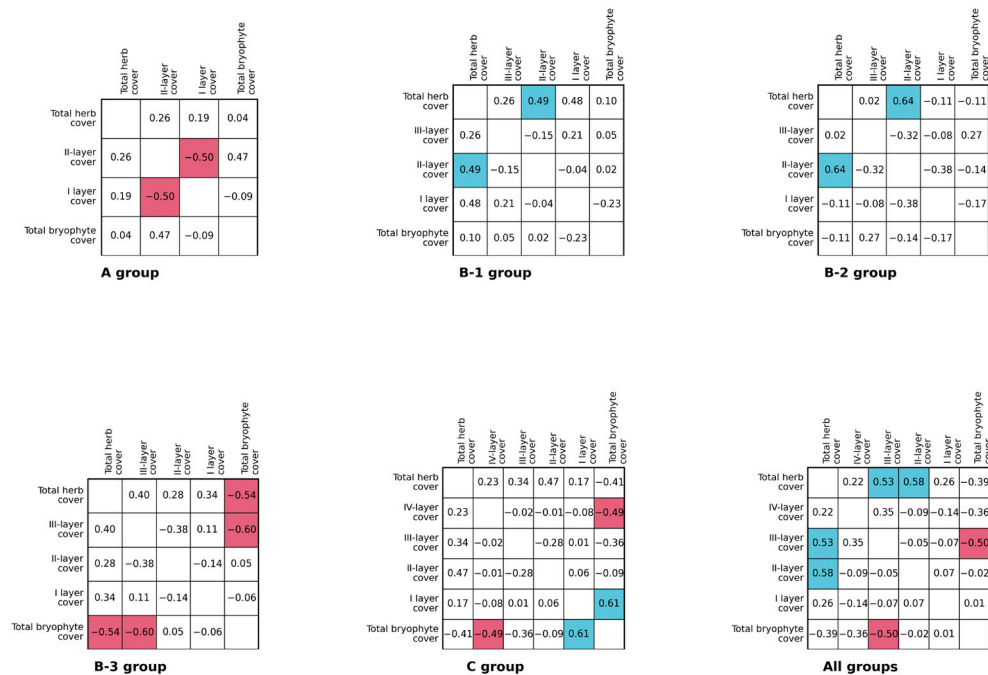


Figure 7. Results of Spearman's rank correlation analysis across all study subplots and within individual groups, showing the relationships between total bryophyte cover and vegetation layer development. Values equal to or greater than 0.5 (blue) (or -0.5 (red)) were considered to indicate a significant correlation.

Table 4. Results of the generalised linear mixed-effects model (GLMM) testing the effects of vertical vegetation structure and microrelief on total bryophyte cover. Significance codes: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; $p < 0.1$.

Parameter	Estimate	SE	Z	p
(Intercept)	3.95	1.11	3.53	***
Layer I cover	−0.00	0.00	−0.01	
Layer I height	−0.09	0.03	−2.73	**
Layer II cover	−0.00	0.00	−1.79	
Layer II height	−0.02	0.01	−1.95	
Layer III cover	−0.02	0.00	−3.13	**
Layer III height	−0.01	0.00	−2.37	*
Layer IV cover	−0.05	0.01	−3.35	***
Layer IV height	0.00	0.00	0.62	
Surface water	−0.00	0.00	−0.05	
Hummock cover	0.00	0.00	0.92	
Number of layers	−0.01	0.36	−0.04	

Taken together, the GLMM results support and extend the group-level correlation patterns: while I layer cover itself was not a significant predictor once all layers and the nested sampling structure were accounted for, the height of the lowest layer, together with the cover and height of the III and IV layers, emerged as the main factors suppressing bryophyte cover across the full dataset. This indicates that bryophyte cover is primarily governed by the vertical development of the upper vascular vegetation, rather than by hydrological or microtopographic gradients, which—although important for shaping species composition (see RDA results above)—did not significantly affect total bryophyte cover.

4. Discussion

Our results show that vertical structural differences in herb cover of rich fens in Lithuania are primarily aligned with the same factors as differences in species diversity, i.e., water level and microrelief conditions [5]—key drivers that concurrently shape species richness [48].

Two specific topographic configurations, an even microrelief and a high water level, are favourable for the development of plant communities of low sedges (*Carex limosa*, *C. panicea*), characterised by low total herb cover [5]. Such an open structure of herb vegetation is favourable for the development of a complete bryophyte cover by reducing interspecific competition [49]. These conditions usually support hygrophilous bryophyte communities dominated by *Scorpidium scorpioides*, *Scorpidium cossonii*, and *Campylium stellatum* (Groups A and B-1), species characteristic of stable, calcium-rich, waterlogged fen conditions. This is evident when analysing both species-poor two-layered plant communities and communities differentiated into three layers: neither the second nor the third layer is abundant, so neither affects bryophyte coverage.

Further, our results illustrate how changes in microtopography, alongside hydrological and hydrochemical changes, are associated with the vertical structure of vegetation. As the fen becomes more hummocky, higher vascular plant species richness co-occurs with a greater differentiation of the herb layers. In addition to the layer of herbs growing close to the bryophytes, which consists of rosette and creeping plants, layers of broad-leaved herbs and tall sedges, as well as layers of grasses, become differentiated. On the one hand, this microtopographic diversity and the resulting heterogeneity in hydrological conditions promote higher bryophyte species richness, as specialised species colonise distinct hummock, lawn, and hollow biotopes [48,49]. On the other hand, this vertical complexity introduces intense competition for light. Lacking roots and low in stature, bryophytes are highly susceptible to shading by taller plants [50]. Consequently, our first hypothesis (H1), which posited that increasing vertical complexity is associated with lower bryophyte cover due to increased shading, was only partially supported. Our results reveal that this shading does not necessarily lead to a decline in total bryophyte cover in all structural groups but rather drives a structural rearrangement of the bryophyte community.

In habitats where hummocks alternate with depressions filled with water, the second layer is composed of broad-leaved herbs such as *Menyanthes trifoliata* and *Caltha palustris* (as observed in group B-2), which cast dense shade. Traditionally, it is widely accepted that at the highest values of vascular plant cover, light availability becomes insufficient to maintain bryophyte viability [51], often resulting in a strong negative correlation between the two groups, e.g., in deciduous forests [14] and alvars and meadows [10]. Interestingly, in our fen communities, despite the intense canopy cover of group B-2, the total bryophyte layer does not collapse but instead undergoes compositional turnover while retaining substantial cover. This is also confirmed by Ingerpuu's [10] statement that the correlation between vascular plant and bryophyte cover in fens is not significant, as the relationship between the two plant groups is often contradictory; while excessive shading suppresses light-demanding taxa, a moderate canopy can facilitate bryophytes by creating a humid microclimate. Because bryophytes lack roots and rely on external water held between their stems and leaves, shade reduces evaporation and shields them from drying winds [52,53]. Consequently, the high coverage in group B-2 is achieved through a near-complete turnover of species rather than a decline in total coverage. This species turnover strongly supports our second hypothesis (H2), confirming that different structural groups indeed support distinct bryophyte assemblages. The dense shade, largely from *M. trifoliata*, filters out photophilous fen specialists like *Scorpidium cossonii*—which thrives under the more open canopy of group B-1—and facilitates the establishment of shade-tolerant species, most

notably *Calliergonella cuspidata* [54]. Furthermore, this phenomenon directly refutes our third hypothesis (H3), which assumed that structural groups dominated by broadleaf plants (such as the *M. trifoliata*-dominated group B-2) would exert a stronger negative influence on total bryophyte cover than those dominated by narrow-leaf plants. Instead, the broadleaf canopy facilitated a high cover of shade-tolerant bryophytes by maintaining a humid microclimate, whereas narrow-leaf graminoids in other groups proved to be more detrimental to the bryophyte layer. It is important to consider this when managing wetlands with rising water levels. The rapid expansion of *M. trifoliata* and other herbaceous species with similar ecological requirements can significantly alter the characteristic species composition of fen bryophyte cover.

The communities of groups B-3 and C, characterised by a well-developed higher layer, represent progressively advanced microrelief stages—with hummock development most pronounced in group C—and exhibit several atypical hydrochemical shifts, linked to microtopographic aeration and peat mineralisation. In line with H1, the analysis of the relationship between vertical structure and bryophyte cover in groups B3 and C demonstrates that the abundant development of higher vegetation layers eventually crosses a threshold, beyond which it negatively affects the bryophyte cover. This occurs even in areas with a less abundant layer of broadleaf herbs in more hummocky locations. The reduction in bryophyte cover in these groups is more closely associated with the overall vascular plant cover: in group B-3, the dense graminoid canopy of the third layer showed the strongest negative association, while in group C the group-level correlations instead pointed to the tallest, helophyte-dominated fourth layer—consistent with the overall GLMM, in which IV layer cover was the strongest negative predictor of bryophyte cover across the full dataset (estimate = -0.0599 , $p < 0.001$). This further clarifies H3, demonstrating that tall, narrow-leaf, and dense graminoid or helophyte layers (III and IV layers) actually exert a far more severe limiting effect on total bryophyte cover than the lower broadleaf herb layer (II layer).

A parallel hydrochemical shift was recorded, which may signal a potential decoupling of the surface layer from the calcareous groundwater as hummocks elevate. Moreover, group B-3 was marked by a pronounced spike in PO_4^{3-} concentration at specific outlier sites, while group C displayed elevated NO_3^- concentrations alongside a wide amplitude of NH_4^+ . That is a clear indicator of enhanced nitrification processes occurring in the better-aerated upper layers of the hummocks, while high PO_4^{3-} levels point to intense organic matter decomposition in these drier microhabitats [9,55,56]. Under these progressively eutrophic and drier conditions, competitive and highly competitive species thrive. *Calliergonella cuspidata*, frequently documented as an indicator of eutrophic, disturbed, or highly mineralised fen habitats, exhibits a strong tolerance for such nutrient flushes [57]. Similarly, productive helophytes, such as *Phragmites australis* and *Typha* sp., can rapidly expand through rhizomatous growth under these conditions. The literature indicates that under enriched conditions, *P. australis* and *Typha* sp. communities significantly enhance nitrogen and phosphorus cycling in wetland soils, forming dense monocultures that reduce overall biodiversity [58–60]. Although these large helophytes are not yet dominant in our studied habitats, their potential expansion poses a severe shading and space risk. This hydrochemical and physical shift shifts the bryophyte layer away from specialised, rich-fen true bryophytes toward more opportunistic, nutrient-loving species such as *Calliergonella cuspidata*, *Marchantia polymorpha*, *Drepanocladus aduncus*, and *Brachythecium mildeanum* [54]. This divergence in species composition across different microtopographical and structural states provides further robust evidence in support of H2. Our findings are important because there is little information available on how the structure of vertical vegetation

influences the distribution of rare bryophytes and the maintenance of species-rich fen communities [61].

It is important to emphasise that, according to the GLMM results, hydrological and microrelief conditions did not significantly affect total bryophyte cover, which was primarily governed by the vertical development of the upper vascular layers, a pattern consistent with the partial support for H1 noted above; hydrochemistry and microtopography instead played a decisive role in shaping bryophyte species composition (see RDA results above) and in the significant variation in other abiotic factors observed among these physiognomically distinct plant communities. The distinct hydrochemical signatures, particularly the combination of high mineral content and localised nutrient flushes, suggest that these habitats are intimately linked to spring flushes and groundwater seepage points. This environmental heterogeneity highlights that soil and water chemistry act as indirect but powerful filters, working in tandem with microtopography to dictate the fine-scale patchiness and vertical stratification of both the vascular plant and bryophyte layers.

Overall, our results fully support H2, while H1 and H3 were only partially supported, highlighting that bryophyte responses depend not only on vegetation complexity itself but also on the identity of the dominant vascular plant layer and the associated environmental context.

5. Conclusions

This study shows that the vertical structure of herbaceous vegetation in rich fens is closely linked to total bryophyte cover and species diversity. Instead of a simple negative relationship with the total herb layer, bryophyte abundance and distribution correspond with the development of specific vegetation layers, indicating these groups share the vertical space. Ultimately, examining the vertical structure of fen plant communities provides valuable additional information for evaluating habitat conditions. Monitoring these visually distinct structures can help us predict negative changes in the community, including drops in bryophyte diversity and cover caused by environmental changes or habitat management.

Author Contributions: Conceptualization, I.J.; methodology, I.J. and M.K.; software, M.K.; validation, I.J. and M.K.; formal analysis, I.J. and M.K.; investigation, I.J. and M.K.; data curation, M.K.; writing—original draft preparation, I.J. and M.K.; writing—review and editing, I.J. and M.K.; visualisation, M.K.; supervision, I.J. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Institutional Review Board Statement: Not applicable.

Data Availability Statement: The data presented in this study are available upon request from the corresponding author. The data are not publicly available due to privacy concerns.

Acknowledgments: The authors sincerely thank Zofija Sinkevičienė, Dalytė Matulevičiūtė, and Lukas Petrulaitis for their valuable assistance with vascular plant species identification. We are also grateful to Zofija Sinkevičienė for providing additional insights into fen ecosystems, and to Laurynas Tauras for his expert assistance in preparing the study site map. We also thank the anonymous reviewers for their valuable comments and suggestions, which significantly improved the quality of this manuscript.

Conflicts of Interest: The authors declare no conflicts of interest.

Appendix A

Table A1. SIMPER analysis showing the bryophyte species contributing most to the dissimilarity in species composition among the five vertical structural groups (A, B-1, B-2, B-3, C). Av. dissim.—average dissimilarity contributed by the taxon; Contrib. %—percentage contribution to overall dissimilarity; Cumulative %—cumulative contribution; A–C—mean abundance (cover-derived index) of the species within each group.

Species	Av. dissim.	Contrib. %	Cumulative %	A	B-1	B-2	B-3	C
<i>Scorpidium cossonii</i>	0.22	25.91	25.91	49.95	33.15	8.90	4.71	2.29
<i>Scorpidium scorpioides</i>	0.15	17.90	43.81	39.35	21.19	1.92	0.71	0.00
<i>Calliergonella cuspidata</i>	0.12	14.06	57.87	0.00	5.51	21.74	8.59	14.77
<i>Plagiomnium ellipticum</i>	0.07	8.44	66.31	0.00	0.15	3.38	12.35	8.66
<i>Hamatocaulis vernicosus</i>	0.07	8.12	74.43	0.00	6.48	7.36	1.59	1.17
<i>Marchantia polymorpha</i>	0.07	7.84	82.27	0.00	2.79	4.00	7.94	11.77
<i>Campylium stellatum</i>	0.03	4.10	86.37	4.70	6.71	1.90	0.00	0.29
<i>Tomentypnum nitens</i>	0.03	3.30	89.67	0.00	6.69	1.74	0.94	0.17
<i>Aulacomnium palustre</i>	0.03	3.01	92.68	0.15	1.50	0.22	2.71	3.91
<i>Plagiomnium elatum</i>	0.02	2.64	95.32	0.10	3.36	3.08	0.00	0.86
<i>Sphagnum warnstorffii</i>	0.01	1.05	96.37	0.00	3.26	0.00	0.00	0.09
<i>Drepanocladus trifarius</i>	0.01	0.70	97.07	0.40	0.21	0.18	0.54	0.90
<i>Calliergon trifarium</i>	0.00	0.56	97.63	0.00	0.10	1.54	0.00	0.00
<i>Brachythecium mildeanum</i>	0.00	0.55	98.18	0.00	0.03	0.00	0.12	1.11
<i>Cinclidium stygium</i>	0.00	0.53	98.71	0.95	0.20	0.51	0.00	0.00
<i>Drepanocladus aduncus</i>	0.00	0.44	99.15	0.00	0.00	0.10	0.12	0.63
<i>Climacium dendroides</i>	0.00	0.42	99.57	0.00	0.02	0.00	0.00	1.14
<i>Helodium blandowii</i>	0.00	0.20	99.77	0.00	0.29	0.00	0.03	0.20
<i>Calliergon giganteum</i>	0.00	0.13	99.90	0.00	0.10	0.05	0.00	0.26
<i>Meesia triquetra</i>	0.00	0.08	99.98	0.00	0.11	0.00	0.18	0.00
<i>Sphagnum divinum</i>	0.00	0.01	99.99	0.00	0.04	0.00	0.00	0.00
<i>Polytrichum stricyum</i>	0.00	0.01	100.00	0.00	0.02	0.00	0.00	0.00

References

- Hájek, M.; Horsák, M.; Hájková, P.; Dítě, D. Habitat diversity of Central European fens in relation to environmental gradients and an effort to standardise fen terminology in ecological studies. *Perspect. Plant Ecol. Evol. Syst.* **2006**, *8*, 89–114. [\[CrossRef\]](#)
- Janssen, J.A.; Rodwell, J.S.; García Criado, M.; Gubbay, S.; Haynes, T.; Nieto, A.; Sanders, N.; Landucci, F.; Loidi, J.; Ssymank, A.; et al. *European Red List of Habitats. Part 2. Terrestrial and Freshwater Habitats*; Publications Office of the European Union: Luxembourg, 2016; pp. 1–38. Available online: <https://data.europa.eu/doi/10.2779/091372> (accessed on 15 May 2026).
- Joosten, H.; Tanneberger, F.; Moen, A. (Eds.) *Mires and Peatlands of Europe: Status, Distribution and Conservation*; Schweizerbart Science Publishers: Stuttgart, Germany, 2017; pp. 1–780.
- Sjörs, H.; Gunnarsson, U. Calcium and pH in north and central Swedish mire waters. *J. Ecol.* **2002**, *90*, 650–657. [\[CrossRef\]](#)
- Kalvaitienė, M.; Jukonienė, I. The ecological drivers of the mosaic structure of bryophyte and vascular plant cover in the rich fens of Lithuania. *Plants* **2025**, *14*, 2662. [\[CrossRef\]](#) [\[PubMed\]](#)
- Bergamini, A.; Pauli, D.; Peintinger, M.; Schmid, B. Relationships between productivity, number of shoots and number of species in bryophytes and vascular plants. *J. Ecol.* **2001**, *89*, 920–929. [\[CrossRef\]](#)
- Joosten, H.; Clarke, D. *Wise Use of Peatlands*; International Mire Conservation Group, International Peat Society: Jyväskylä, Finland, 2002; pp. 1–302.
- Kotowski, W.; van Diggelen, R. Light as an environmental filter in fen vegetation. *J. Veg. Sci.* **2004**, *17*, 583–594. [\[CrossRef\]](#)
- Lamers, L.P.M.; Vile, M.A.; Grootjans, A.P.; Acreman, M.C.; van Diggelen, R.; Evans, M.G.; Richardson, C.J.; Rochefort, L.; Kooijman, A.M.; Roelofs, J.G.M.; et al. Ecological restoration of rich fens in Europe and North America: From trial and error to an evidence-based approach. *Biol. Rev.* **2015**, *90*, 182–203. [\[CrossRef\]](#) [\[PubMed\]](#)
- Ingerpuu, N. Bryophyte Diversity and Vascular Plants. Ph.D. Thesis, University of Tartu, Tartu, Estonia, 2002.
- Weibull, H. Influence of tree species on the epilithic bryophyte flora in deciduous forests of Sweden. *J. Bryol.* **2001**, *23*, 55–66. [\[CrossRef\]](#)
- Nordén, U. Acid deposition and throughfall fluxes of elements as related to tree species in deciduous forests of South Sweden. *Water Air Soil Pollut.* **1991**, *60*, 209–230. [\[CrossRef\]](#)

13. Nordén, U. Leaf litterfall concentrations and fluxes of elements in deciduous tree species. *Scand. J. For. Res.* **1994**, *9*, 9–16. [CrossRef]
14. Ingerpuu, N.; Vellak, K.; Liira, J.; Pärtel, M. Relationships between species richness patterns in deciduous forests at the North Estonian Limestone Escarpment. *J. Veg. Sci.* **2003**, *14*, 773–780. [CrossRef]
15. Ingerpuu, N.; Liira, J.; Pärtel, M. Vascular plants facilitated bryophytes in a grassland experiment. *Plant Ecol.* **2005**, *180*, 69–75. [CrossRef]
16. Rutten, G.; Ensslin, A.; Hemp, A.; Fischer, M. Vertical and horizontal vegetation structure across natural and modified habitat types at Mount Kilimanjaro. *PLoS ONE* **2015**, *10*, e0138822. [CrossRef] [PubMed]
17. Ross, J. *The Radiation Regime and Architecture of Plant Stands*; Dr W. Junk Publishers: The Hague, The Netherlands, 1981.
18. Brose, U. Bottom-up control of carabid beetle communities in early successional wetlands: Mediated by vegetation structure or plant diversity? *Oecologia* **2003**, *135*, 407–413. [CrossRef] [PubMed]
19. Borges, P.A.; Brown, V.K. Arthropod community structure in pastures of an island archipelago (Azores): Looking for local–regional species richness patterns at fine-scales. *Bull. Entomol. Res.* **2004**, *94*, 111–121. [CrossRef] [PubMed]
20. Mitchell, M.G.E.; Wu, D.; Johansen, K.; Maron, M.; McAlpine, C.; Rhodes, J.R. Landscape structure influences urban vegetation vertical structure. *J. Appl. Ecol.* **2016**, *53*, 1477–1488. [CrossRef]
21. Yang, H.; Deng, R.; Jing, X.; Dong, Z.; Yang, X.; Li, J.; Mei, Z. The novel models for identifying the vertical structure of urban vegetation from UAV LiDAR Data. *Remote Sens.* **2026**, *18*, 692. [CrossRef]
22. Cheng, C.; Zhang, J.; Li, M.; Liu, C.; Xu, L.; Niu, K. Vertical structural complexity of plant communities represents the combined effects of resource acquisition and environmental stress on the Tibetan Plateau. *Commun. Biol.* **2024**, *7*, 395. [CrossRef] [PubMed]
23. Emsens, W.J.; Aggenbach, C.J.S.; Rydin, H.; Smolders, A.J.P.; van Diggelen, R. Competition for light as a bottleneck for endangered fen species: An introduction experiment. *Biol. Conserv.* **2018**, *220*, 76–83. [CrossRef]
24. Liira, J.; Zobel, K. Vertical structure of a species-rich grassland canopy, treated with additional illumination, fertilization and mowing. *Plant Ecol.* **2000**, *146*, 183–193. [CrossRef]
25. Chollet, S.; Baltzinger, C.; Le Saout, S.; Martin, J.L. A better world for bryophytes? A rare and overlooked case of positive community-wide effects of browsing by overabundant deer. *Écoscience* **2013**, *20*, 352–360. [CrossRef]
26. Hájek, M.; Jiroušek, M.; Navrátilová, J.; Horodyská, E.; Peterka, T.; Plesková, Z.; Navrátil, J.; Hájková, P.; Hájek, T. Changes in the bryophyte layer of Czech fens indicate early succession triggered by nutrient enrichment. *Preslia* **2015**, *87*, 279–301.
27. Jaagus, J.; Briede, A.; Rimkus, E.; Remm, K. Precipitation pattern in the Baltic countries under the influence of large-scale atmospheric circulation and local landscape factors. *Int. J. Climatol.* **2010**, *30*, 705–720. [CrossRef]
28. Kavaliauskas, P. *Kraštovaizdžio Samprata ir Analizė [The Concept and Analysis of Landscape]*; Vilniaus Universiteto Leidykla: Vilnius, Lithuania, 2011; pp. 1–245.
29. Geiger, R. Klassifikation der Klimate nach W. Köppen [Classification of climates after W. Köppen]. In *Landolt-Börnstein—Zahlenwerte und Funktionen aus Physik, Chemie, Astronomie, Geophysik und Technik*; Springer: Berlin/Heidelberg, Germany, 1954; Volume 3S, pp. 603–607.
30. Kottek, M.; Grieser, J.; Beck, C.; Rudolf, B.; Rubel, F. World map of the Köppen-Geiger climate classification updated. *Meteorol. Z.* **2006**, *15*, 259–263. [CrossRef] [PubMed]
31. Galvonaitė, A.; Misiūnienė, M.; Valiukas, D.; Pipiraitė, B. *Lietuvos klimatas [Climate of Lithuania]*; Lietuvos Hidrometeorologijos Tarnyba: Vilnius, Lithuania, 2007; pp. 1–207.
32. Klimavičius, L.; Rimkus, E.; Stonevičius, E.; Mačiulytė, V. Seasonality and long-term trends of NDVI values in different land use types in the eastern part of the Baltic Sea basin. *Oceanologia* **2023**, *65*, 171–181. [CrossRef]
33. Guobytė, R.; Satkūnas, J. Pleistocene glaciations in Lithuania. *Dev. Quat. Sci.* **2011**, *15*, 231–246. [CrossRef]
34. Česnulevičius, A. The morphometric structure of Lithuanian relief and its influence on erosion processes. *Baltica* **2011**, *24*, 137–142.
35. Lietuvos Hidrometeorologijos Tarnyba. Climatic Regions of Lithuania. Available online: <https://www.meteo.lt/en/climate/lithuanian-climate/climate-regions-of-lithuania/> (accessed on 26 June 2026).
36. Štechová, T.; Kučera, J. The requirements of the rare bryophyte, *Hamatocaulis vernicosus* (Calliergonaceae, Musci) in the Czech Republic in relation to vegetation, water chemistry and management. *Biol. Conserv.* **2007**, *135*, 443–452. [CrossRef]
37. *LST ISO 6058:1998/P:2008*; Water Quality—Determination of Calcium Content—EDTA Titrimetric Method (ISO 6058:1984, Identical). Lietuvos Standartizacijos Departamentas: Vilnius, Lithuania, 2008.
38. *LST ISO 6332:1995*; Water Quality. Determination of Iron. Spectrometric Method Using 1,10—Phenanthroline. Lietuvos Standartizacijos Departamentas: Vilnius, Lithuania, 1995.
39. *LST ISO 7150-1:1998*; Water Quality. Determination of Ammonium. Part 1: Manual Spectrometric Method. Lietuvos Standartizacijos Departamentas: Vilnius, Lithuania, 1998.
40. *LST ISO 7890-3:1998*; Water Quality. Determination of Nitrate. Part 3: Spectrometric Method Using Sulfosalicylic Acid. Lietuvos Standartizacijos Departamentas: Vilnius, Lithuania, 1998.

41. LST ISO 6059:1998; Water Quality—Determination of the Sum of Calcium and Magnesium—EDTA Titrimetric Method (ISO 6059:1984, Identical). Lietuvos Standartizacijos Departamentas: Vilnius, Lithuania, 1998.
42. LST EN ISO 6878:2004; Water Quality—Determination of Phosphorus—Ammonium Molybdate Spectrometric Method (ISO 6878:2004). Lietuvos Standartizacijos Departamentas: Vilnius, Lithuania, 2004.
43. Hodgetts, N.G.; Söderström, L.; Blockeel, T.L.; Caspari, S.; Ignatov, M.S.; Konstantinova, N.A.; Lockhart, N.; Papp, B.; Schröck, C.; Sim-Sim, M.; et al. An annotated checklist of bryophytes of Europe, Macaronesia and Cyprus. *J. Bryol.* **2020**, *42*, 1–116. [[CrossRef](#)]
44. Govaerts, R.; Nic Lughadha, E.; Black, N.; Turner, R.; Paton, A. The World Checklist of Vascular Plants, a continuously updated resource for exploring global plant diversity. *Sci. Data* **2021**, *8*, 215. [[CrossRef](#)] [[PubMed](#)]
45. Hammer, Ø.; Harper, D.A.T.; Ryan, P.D. PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontol. Electron.* **2001**, *4*, 9.
46. Oksanen, J.; Simpson, G.L.; Blanchet, F.G.; Kindt, R.; Legendre, P.; Minchin, P.R.; O'Hara, R.B.; Solymos, P.; Stevens, M.H.H.; Szoecs, E.; et al. *Vegan: Community Ecology Package*, R Package Version 2.6-10. 2026. Available online: <https://CRAN.R-project.org/package=vegan> (accessed on 22 June 2026).
47. Bates, D.; Mächler, M.; Bolker, B.; Walker, S. Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Softw.* **2015**, *67*, 1–48. [[CrossRef](#)]
48. Vitt, D.H.; Li, Y.; Belland, R.J. Patterns of bryophyte diversity in peatlands of continental western Canada. *Bryologist* **1995**, *98*, 218–227. [[CrossRef](#)]
49. Gignac, L.D. Niche structure, resource partitioning and species interactions of mire bryophytes relative to climatic and ecological gradients in Western Canada. *Bryologist* **1992**, *95*, 406–418. [[CrossRef](#)]
50. Udd, D.; Sundberg, S.; Rydin, H. Multi-species competition experiments with peatland bryophytes. *J. Veg. Sci.* **2016**, *27*, 165–175.
51. van der Wal, R.; Pearce, I.S.K.; Brooker, R.W. Mosses and the struggle for light in a nitrogen-polluted world. *Oecologia* **2005**, *142*, 159–168. [[CrossRef](#)] [[PubMed](#)]
52. Proctor, M.C.F. Physiological ecology: Water relations, light and temperature responses, carbon balance. In *Bryophyte Ecology*; Smith, A.J.E., Ed.; Chapman and Hall: London, UK, 1982; pp. 333–381.
53. Valanne, N. Photosynthesis and photosynthetic products in bryophytes. In *The Experimental Biology of Bryophytes*; Dyer, A.F., Duckett, J.G., Eds.; Academic Press: London, UK, 1984; pp. 257–273.
54. Dierßen, K. *Distribution, Ecological Amplitude and Phytosociological Characterization of European Bryophytes*; Bryophytorum Bibliotheca, Band 56; J. Cramer in der Gebrüder Borntraeger Verlagsbuchhandlung: Stuttgart, Germany, 2001; pp. 1–289.
55. Wassen, M.J.; van der Vliet, R.E.; Verhoeven, J.T.A. Nutrient limitation in the Biebrza fens and floodplain (Poland). *Acta Bot. Neerl.* **1998**, *47*, 241–253.
56. Mettrop, I.S.; Cusell, C.; Kooijman, A.M.; Lamers, L.P.M. Nutrient and carbon dynamics in peat from rich fens and *Sphagnum*-fens during different gradations of drought. *Soil Biol. Biochem.* **2014**, *68*, 317–328. [[CrossRef](#)]
57. Aggenbach, C.J.S.; Backx, H.; Emsens, W.J.; Grootjans, A.P.; Lamers, L.P.M.; Smolders, A.J.P.; Stuyfzand, P.J.; Wołejko, L.; van Diggelen, R. Do high iron concentrations in rewetted rich fens hamper restoration? *Preslia* **2013**, *85*, 405–420.
58. Güsewell, S.; Edwards, P. Shading by *Phragmites australis*: A threat for species-rich fen meadows? *Appl. Veg. Sci.* **1999**, *2*, 61–70. [[CrossRef](#)]
59. Ge, Z.; An, R.; Fang, S.; Lin, P.; Li, C.; Xue, J.; Yu, S. *Phragmites australis* + *Typha latifolia* community enhanced the enrichment of nitrogen and phosphorus in the soil of Qin Lake Wetland. *Scientifica* **2017**, *2017*, 8539093. [[CrossRef](#)] [[PubMed](#)]
60. Stratoulas, D.; Tóth, V.R. Photophysiology and Spectroscopy of Sun and Shade Leaves of *Phragmites australis* and the Effect on Patches of Different Densities. *Remote Sens.* **2020**, *12*, 200. [[CrossRef](#)]
61. Ilomets, M.; Truus, L.; Pajula, R.; Sepp, K. Species composition and structure of vascular plants and bryophytes on the water level gradient within a calcareous fen in North Estonia. *Est. J. Ecol.* **2010**, *59*, 19. [[CrossRef](#)]

Disclaimer/Publisher's Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.