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Species composition and structure of vascular plants and bryophytes on the water level gradient within a calcareous fen in North Estonia

Mati Ilomets✉, Laimdota Truus, Raimo Pajula, and Kairi Sepp

Institute of Ecology, Tallinn University, Uus-Sadama 5, 10120 Tallinn, Estonia

✉ Corresponding author, ilomets@tlu.ee

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Abstract. We examined the relationship between the composition and structure of vegetation and hydrology and microtopography within the Paraspõllu calcareous-rich fen (North Estonia). Species composition, depth to groundwater level (+6 to –40 cm), pH (6.1–7.1), and electrical conductivity (220–840 µS cm^{-1}) were recorded in 23 relevés of 1 m^2 along transects over the site. The species composition and coverage of vascular plants depended on the extent of water level fluctuations and water conductivity, those of moss species additionally also on microtopography. A total of 44 bryophyte and 57 vascular plant species were identified, including 14 protected and rare species. Nonmetric multidimensional scaling and the Monte Carlo test were used to describe compositional variation and identify significant habitat variables separately for vascular plant and bryophyte species. The relationship between the species composition of field and surface layers was nonsignificant. Three of the five assemblages distinguished by two-way cluster analysis, *Carex panicea–Schoenus ferrugineus–Drepanocladus cossonii*, *Phragmites australis–Calliergonella cuspidata*, and *Molinia caerulea–Carex davalliana*, represent the calcareous tufa-forming fen type. The other two are distributed on the moderately drained part of the fen. The number and coverage of rich fen species decreased sharply as the coverage of *M. caerulea* exceeded the 30% level and seasonal fluctuation of water level was over 25 cm.

Key words: calcareous fen, ordination, nonmetric multidimensional scaling, conductivity, pH, water level.

INTRODUCTION

Calcareous tufa-forming species-rich low-productive fens are among the most endangered wetland types in the world. This fen type can be characterized by precipitation of the calcite as consolidated tufa or unconsolidated marl on the surface (Hájek et al., 2006). The vegetation consists of many calcifuge specialist species that favour the low content of available phosphorus in a high-calcium substrate (Boyer & Wheeler, 1989; Wassen et al., 2005). Such an environment can develop in the conditions of a stable near-surface water level by recharge of calcium-rich groundwater. A drop of the water level and an increase in its seasonal fluctuation result in complete desiccation of the topsoil. This influences the redox status − the nitrogen availability increases, but phosphorus availability does not increase because of limited decomposition (Boomer & Bedford, 2008). Electrical conductivity decreases as recharged groundwater dilutes with precipitation but pH remains stable until the bicarbonate buffer system functions (Lamers et al., 1998). The water level drawdown is responsible for the decrease in plant species diversity as many specialist species are outcompeted by a few generalists like *Molinia caerulea* (Trass, 1957, 1986; Villems, 1996; Mälson et al., 2008) and for the encroachment of woody species (Middleton, 2002; Bootsma & Wassen, 1996; Mälson et al., 2008).

Rich fens have been used for haymaking and cattle grazing in Western Europe for a long time. Among other reasons the decrease in species richness on these undrained or slightly ameliorated fens is argued to be related with the cessation of the traditional management regime (Middleton et al., 2006), which is responsible for increasing litter accumulation (Weltzin et al., 2005; Peintinger & Bergamini, 2006).

Mineral-rich (mainly calcium, but also magnesium and iron) groundwater-fed fens are spread in regions where calcareous sediments lie close to the surface. In Estonia, calcareous-rich fens are concentrated in the western and northern areas and on the western island of Saaremaa (Laasimer, 1965), where the Silurian carbonate rock and Ordovician limestone and marls are covered by thin Quaternary sediments (Teedumäe, 1997).

Estonian fens have been mown and grazed by cattle, drained, and turned into pastures, hayfields, and crop fields since the middle of the 17th century. Since the 1950s the area of intact rich fens decreased from about 80 500 ha (Laasimer, 1965) to 5000–8000 ha in the 1990s (Ilomets, 1994). The rich fen sites left in the near-natural state are mostly fragmentary and even protected fens are under indirect drainage impact, although in many cases the characteristic species composition is largely preserved.

This study was conducted at a calcareous fen site of the Paraspõllu Nature Reserve (also a Natura 2000 site) in North Estonia, which was in part slightly drained and used for mowing and cattle grazing for a long time (at least from the end of the 19th century), but was abandoned in the early 1960s. The site is important because of its rich flora with many rare vascular and moss species that are protected regionally. In all, 19 rare and protected vascular plant species (incl. 17 orchid species; Kivistik, 2000) are known to inhabit the Paraspõllu Nature Reserve.

Our objective was to identify factors associated with the composition and structure of plant communities within the Paraspõllu calcareous-rich fen site. The more detailed purpose was to determine the relationships between vascular and moss species coverage, water table position and its seasonal fluctuations, water pH and electrical conductivity (EC), and litter, but also microtopography (coverage and height of tussocks) and coverage of *Molinia caerulea*. Three transects were established over the fen site, and vegetation, microtopography, water table position, and water pH and EC data were collected from 23 relevés of 1 m × 1 m. This pilot study is the first step towards finding effective ways of management that could help to decrease the predominance of the few ubiquitous species that evidently are outcompeting specialist species characteristic of calcareous-rich fens.

METHODS

Study site

The Paraspõllu Nature Reserve (253 ha) constitutes the south-eastern part of the Peningi mire complex (7552 ha), which lies on the Harju plateau in North Estonia (Fig. 1). It is surrounded by glaciofluvial ridges in the west and south and by a till plateau in the east and north. Fen communities are distributed in the southern and eastern parts of the mire complex. The gradient in moisture conditions and vegetation pattern can be well distinguished over the open calcareous fen site (ca 40 ha) (59°18′ N, 25°7′ E) selected for the study.

The peat deposit is formed of reed–sedge and reed–brown moss fen peats with a medium degree of decomposition, and is underlain by tufa in some parts of the site. The thickness of the peat layer reaches 3.2 m and that of tufa 1.1 m, underlain by a sandy–clayey till deposit.

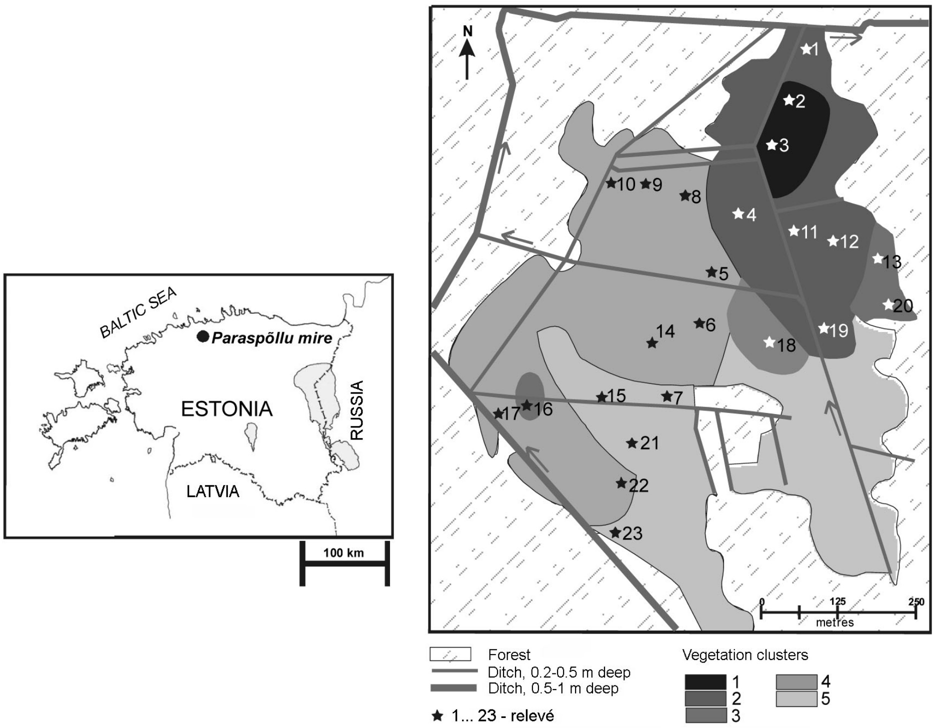

Fig. 1. Schematic map showing the position of the Peningi mire complex in Estonia (left) and the location of relevés and distribution of vegetation clusters 1–5 on the Paraspõllu fen site (right).

Four hand-cut ditches bordering and crossing the fen site can be found on a ‘One Verst Map’ (one verst = 1066.788 m) from as early as about 1900. A denser drainage network is marked on the map from the mid-1930s. In the 1950s the site (open fen) was bordered by deeper ditches in the west and south-west, but these are partly filled with sediments and the actual depth of most ditches is 0.2–0.5 m. The fen surface gradient and water flow are directed roughly to the north-west. The density of the drainage network of the area, including border ditches, is 106 m ha^{-1}.

The study site is open calcareous-rich fen with a sparse tree layer (mainly *Betula pubescens* and *Picea abies*), surrounded by paludified forest (in the east) and slightly drained bog pine forest (in the west). Trees and shrubs (*Pinus sylvestris*, *Picea abies*, *Betula pubescens*, *B. humilis*, *B. nana*) invade into the fen area mainly from its borders. The tree canopy is denser in the western and south-western parts of the fen close to deeper border ditches.

Vegetation sampling

In June 2007 the composition and coverage of vascular plant species of the field layer and bryophyte species of the surface layer were recorded in 23 relevés 1 m × 1 m in size along three transects (Fig. 1). As one plot contains on average 22% of the site’s vascular plant flora and some 16% of the moss flora, the size of the plot is adequate for ordination analyses. Additionally, the total species list of the area was compiled. The nomenclature of bryophytes follows Ingerpuu & Vellak (1998) and that of vascular plants, Leht (2007). The coverage of litter and the height and coverage of tussocks were estimated. The coverage of vascular plants and bryophytes was recorded using the percentage scale.

Pore water sampling

Flow directions in the ditches are indicated by arrows in Fig. 1. Depth to water level (DWL) from the ground surface between tussocks was measured (30 October 2007, 30 May and 30 July 2008), and the pore water samples were taken (1 November 2007, 1 June 2008) from piezometers (PVC tubes with the inner diameter of 22 mm, perforated by 10 cm and inserted into the surface to a depth of 50 cm) close to each relevé. Samples were taken to the laboratory, kept at room temperature for 24 h, and pH (Handylab pH11/SET, SCHOTT Instruments GmbH) and EC (Conductivity Meter Micrometer 900) were measured.

Data analyses

The Mantel test (Mantel, 1967) was used to evaluate the null hypothesis of no relationship between the field and surface layers. Standardized Mantel statistic (r)

was calculated using Mantel's asymptotic approximation method. The size of field and surface layer dissimilarity matrixes was 43 species by 23 plots and 24 species by 23 plots, respectively.

The classification and ordination of field and surface layer plant cover data were performed by PC-ORD software (McCune & Grace, 2002). Based on two-way cluster analysis of species cover data for all plots, five plant assemblages were identified. We used the Sørensen (Bray–Curtis) distance measure and the Flexible Beta group linkage method with the flexible beta value of −0.250. Of vascular plant species 13 and of moss species 20 were exluded from the matrix as rare species (found per one plot). The final data matrix consisted of 23 plots and 43 vascular plant (herbs, shrubs, and trees in the field layer) and 24 moss species. Nonmetric Multidimensional Scaling (NMS) ordinations (Kruskal, 1964; Mather, 1976) using random starting points were used to explore the relationships between the vegetation and environmental data. Data transformation by relativization by column maximum was performed to improve the assumption of normality and homogeneity of variance and to make units of environmental variables measured in different scales more comparable. This adjustment also tends to equalize common and uncommon species.

The proportion of variance represented by each axis was found based on the r^2 between the distance in the ordination space and the distance in the original space. In order to interpret the ordination, multiple correlations were calculated between ordination axes and the plant species coverage, and between the axes and each environmental variable.

RESULTS

Species density and coverage of species groups

Altogether, 44 species of bryophytes (incl. 9 hepatics) and 70 (57 in relevés) vascular plant species were found on the study site. Lichens were not identified to species level.

The total list contains 13 rare species, among others 11 in vegetation relevés (see Appendix). Species richness per plot was 19.3, evenness 0.50, Shannon's diversity index 1.46, and Simpson's diversity index for infinite population 0.65. The species density of bryophytes varied between 4 and 12, of graminoids between 4 and 14, and of woody species (trees, shrubs, and dwarf shrubs) between 0 and 4 per plot.

Description of clusters

Using two-way cluster analysis, we identified five groups (Fig. 1) from 23 plots.

Cluster 1, the *Phragmites australis–Calliergonella cuspidata* group, occurred only in two plots (2 and 3) in the northern part of the area. It consisted of 4 species in the shrub layer, 15 species in the surface layer, and 8 species in the ground layer (Appendix). Surface layer coverage was not high; *Carex lasiocarpa*, *Phragmites australis*, and *Menyanthes trifoliata* dominated. In the ground layer *Drepanocladus cossonii*, *Calliergonella cuspidata*, and *Campylium elodes* covered most part of submerged depressions between tussocks. The depth of the water level was rather stable close to the surface and fluctuated up to 5 cm between seasons.

Cluster 2, the *Carex panicea–Schoenus ferrugineus–Drepanocladus cossonii* group, was found in five plots (1, 4, 11, 12, and 19) and was distributed around cluster 1. This was the most species-rich cluster distinguished. The relevés of the cluster were represented by 5 species in the shrub and tree layers, 27 species in the surface layer, and 18 species in the ground layer. *Schoenus ferrugineus* dominated in the ground layer with *Carex davalliana*, *C. panicea* was the co-dominant. *Selaginella selaginoides* was found on a tussock in two relevés. The depressions between *S. ferrugineus*, *C. davalliana*, and *M. caerulea* tussocks were well covered by mosses, with *Drepanocladus cossonii* dominating with mean coverage of about 19% and *Campylium stellatum*, *Meesia triquetra*, and *Scorpidium scorpioides* being other more common species. At the end of October the depressions between tussocks were submerged. In May and July the water level was close to the surface (plots 11, 12, 19) or at a depth less than 20 cm (plots 1 and 4).

Cluster 3, the *Molinia caerulea–Carex davalliana* group, was found in four relevés (13, 16, 18, and 20). Tussocks covered some 20% and litter some 70% of the surface. We found 4 species in the shrub layer, 19 in the surface layer, and 14 in the ground layer. Tussock-forming graminoids *Molinia caerulea*, *Carex davalliana*, and *Sesleria caerulea* dominated. Moss coverage (13 ± 7%) was much lower than in clusters 1 (28 ± 18%) and 2 (37 ± 20). In the ground layer *Calliergonella cuspidata*, *Ctenidium molluscum*, *Drepanocladus cossonii*, and *Fissidens adianthoides* were most frequent but with a low coverage. At the end of October the water table was close to the surface in depressions between tussocks but the seasonal amplitude of fluctuation was 4−25 cm.

Cluster 4, the *Molinia caerulea–Schoenus ferrugineus*, was the most widely distributed group (relevés 5, 6, 8, 9, 10, 14, 17, 22), which occupied the central and western parts of the fen site. We found 9 species in the shrub layer, 26 in the surface layer, and 19 species of bryophytes in the ground layer. In contrast to clusters 2 and 3, the coverage of shrubs (*Betula humilis*) was high in this cluster and dwarf shrubs (*Andromeda polifolia*, *Empetrum nigrum*) were present. On average the coverage of *Molinia caerulea* increased up to 24%. Nevertheless, the moss species composition reflected the calcareous-rich fen situation, but the distribution of most species was sporadic, with the mean coverage below 1%. Only the coverage of *Ctenidium molluscum* was about 4% on average. *Selaginella selaginoides* was present in seven of the eight relevés and *Pinguicula alpina* in one relevé. In October 2007 the water level was at or up to 3 cm below the surface but seasonal fluctuations were notable (16–38 cm).

Cluster 5, the *Molinia caerulea* group, was distributed in the southern part of the area (relevés 7, 15, 21, 23). The tree layer was formed by three species (*Betula pubescens*, *Pinus sylvestris*, and *Populus tremula*). The luxurious shrub layer of the cluster consisted of 8 species. Herbaceous plants (a total of 16 species found) were mostly tussock-forming graminoids, among which *Molinia caerulea* dominated with the coverage of up to 65% (mean 37%) and up to 40 cm (mean 25 cm) high tussocks. Dwarf shrubs (*Ledum palustre*, *Vaccinium uliginosum*, *V. vitis-idaea*) occupied stump hummocks together with certain forest mosses (*Pleurozium schreberi*, *Rhizomnium punctatum*, *Rhytidiadelphus triquetrus*) and peat mosses (mostly *Sphagnum contortum*, *S. fallax*, *S. papillosum*, *S. warnstorfii*). Other fen bryophyte species were present very sparsely. We found a total of 24 moss species in the ground layer. The relevés of the cluster contained 12 moss species not present in other relevés. At the end of October the water table was close to the surface, the summer minimum was 22−28 cm below the surface and seasonal fluctuation some 17–25 cm.

Environmental conditions

At the end of October 2007 the water level between tussocks was close to the surface and varied rather little between plots. In the next spring (30 May 2008) and summer (30 July 2008) the DWL was from +3 to –24 cm and from –1 to –39 cm, respectively. In the northern, eastern, and central parts of the fen site (clusters 1, 2, and 3 in Fig. 1) the water table lay closer to the surface than around plots of clusters 4 and 5. The amplitude of the water level seasonal fluctuation (WLF) in plots between the three measurements varied from 1 to 38 cm. Pore water EC varied considerably between plots (from 220 to 840 $\mu S\ cm^{-1}$), whereas only slight differences were observed in the values measured in late autumn and in midsummer. Clusters 1, 2, and 3 had higher average EC values than clusters 4 and 5 (over 600 and less than 500 $\mu S\ cm^{-1}$, respectively). The pH of mire water varied only a little, from 6.1 to 7.1 between plots and between two years, 2007 and 2008. The coverage and height of tussocks formed by *Carex davalliana*, *Schoenus ferrugineus* (clusters 1, 2 and 3), or *Molinia caerulea* (clusters 4 and 5) varied from 15% to 60% and from 10 to 30 cm, respectively, between the plots. The coverage of *Molinia caerulea* was between 0.1% and 55%. The coverage of tussocks, their mean height, coverage of *Molinia*, depth to water table in July, and WLF between autumn maximum and summer minimum values were significantly interrelated (Table 1). The DWL autumn maximum was not related to the DWL measured in May and July or to other environmental variables. The spring and summer values of the DWL and water EC of the samples collected in October 2007 were significantly correlated. The coverage of litter had no significant correlation with other environmental variables measured.

Table 1. Pearson product–moment correlations between environmental variables on the Paraspõllu fen site (values in bold $p < 0.05$). WL = water level, WLF = water level fluctuation, EC = electrical conductivity

	Coverage of tussocks	Height of tussocks	WL, Oct. 2007	WL, May 2008	WL, July 2008	WLF	EC, Oct. 2007	pH, Oct. 2007	pH, June 2008	EC, June 2008
Height of tussocks	**0.75**									
WL, Oct. 2007	0.01	0.09								
WL, May 2008	–0.32	**0.54**	0.36							
WL, July 2008	**0.53**	0.46	0.36	**0.72**						
WLF	**0.56**	0.46	0.15	**0.68**	**0.98**					
EC, Oct. 2007	–0.34	–0.38	–0.31	**–0.71**	**–0.80**	**–0.78**				
PH, Oct. 2007	0.09	–0.05	–0.27	–0.21	–0.36	–0.30	**0.57**			
pH, June 2008	–0.20	0.00	0.18	–0.11	–0.37	–0.42	0.39	**0.54**		
EC, June 2008	–0.21	–0.18	–0.23	–0.44	**–0.58**	**–0.58**	**0.85**	0.46	0.22	
Coverage of *Molinia*	**0.60**	**0.63**	0.43	**0.60**	**0.79**	**0.73**	**–0.65**	–0.41	–0.16	**–0.58**

Ordination of vegetation analyses

We used the Mantel test to measure the relationship between the field and surface layer species compositions. No significant overall relationship was established between vascular plant and moss species coverage ($r = 0.09$ at $p = 0.18$ with $t = 1.33$) for the 23 plots. Therefore we applied NMS ordination separately for plant species from the field and the surface layer.

Vascular plant species

The ordination of 23 plots was achieved with a final stress of 13.64 and final instability of 0.014 after 25 iterations for the three-dimensional solution. The Monte Carlo test with 249 runs demonstrated that the final stress was significantly lower ($p = 0.004$) than that reached by chance. The proportion of variation, after rotation of the diagram by +10°, explained by axes 1, 2, and 3 was 19.7%, 27.7%, and 32.4%, respectively (total for three axes 79.8%). The first ordination axis was correlated significantly ($p < 0.05$) with the pore water pH measured in October ($r = –0.49$) and with the EC measured in June ($r = –0.35$). The second ordination axis did not correlate significantly with any variable considered. The third ordination axis correlated significantly with the EC measured in October 2007 ($r = -0.629$) and in June 2008 ($r = -0.458$) and with WLF ($r = 0.577$). Axes 1 and 3 explained approximately 51.9% of the variation on the ordination space. We also found a relationship between the field layer species composition and the four environmental variables. The standardized Mantel statistic r indicated a weak ($r = 0.19$) but significant (at $p = 0.034$) positive ($t = 2.12$) association between the two dissimilarity matrixes. The highest value of the standardized Mantel statistic was achieved when the EC in October and the WLF were fitted into the second matrix ($r = 0.23$, $p = 0.007$, $t = 2.70$). Clusters arrayed along the WLF−pore water EC gradient on axis 3 (Fig. 2). Virtually all plots from clusters 4 and 5 were widely distributed on the upper left and right quadrants of the ordination diagram. Plots from clusters 2 and 3 were distributed on the lower left quadrant, characterized by unimportant seasonal fluctuations of the water level and high pore water pH and EC values. The two plots belonging to cluster 1 were located on the lower right quadrant with a high pore water EC and stable water level.

Axis 3 of the NMS ordination separated a group of vascular plant species found in the part of the fen site where the DWL was the deepest and the pore water EC values were considerably low. The other separate group of species was located in the lower right quadrant. These species were frequent in the part of the site with a stable water level lying close to the surface and with high EC values. The species located near the centre, such as *Schoenus ferrugineus*, *Gymnadenia conopsea*, *Epipactis palustris*, *Saussurea esthonica*, *Primula farinose*, and *Selaginella selaginoides*, were well correlated with axis 2, but nonsignificantly related with any parameter considered.

Bryophytes

The ordination of 23 plots was achieved with the final stress of 15.4 and final instability of 0.0076 after 35 iterations for the three-dimensional solution. The Monte Carlo test with 249 runs demonstrated that the final stress was significantly lower ($p = 0.004$) than that reached by chance. The proportion of variation explained by axes 1, 2, and 3 was 11.1%, 15.1%, and 17.3%, respectively (total for three axes 43.5%). The first ordination axis correlated significantly ($p < 0.05$) with the pore water EC in October ($r = -0.61$) and with the DWL in July ($r = 0.60$) (Fig. 3). The third ordination axis correlated significantly with the coverage of tussocks ($r = 0.528$) and the mean height of tussocks ($r = 0.652$). The second ordination axis correlated significantly with the four variables considered and was well related to axes 1 and 3. Axes 1 and 3 explained about 28% of the variation on the ordination space. The standardized Mantel statistic r indicated that the dissimilarity matrixes of moss species and the four environmental variables were significantly (at $p = 0.034$) and positively ($t = 2.12$) associated ($r = 0.26$).

The species located in the lower left quadrant of the ordination diagram preferred a habitat with few low tussocks close to the summer level of surface water (Fig. 3). The pore water EC had high values. The upper right quadrant close to axis 3 represents a group of moss species from plots with a high mean height

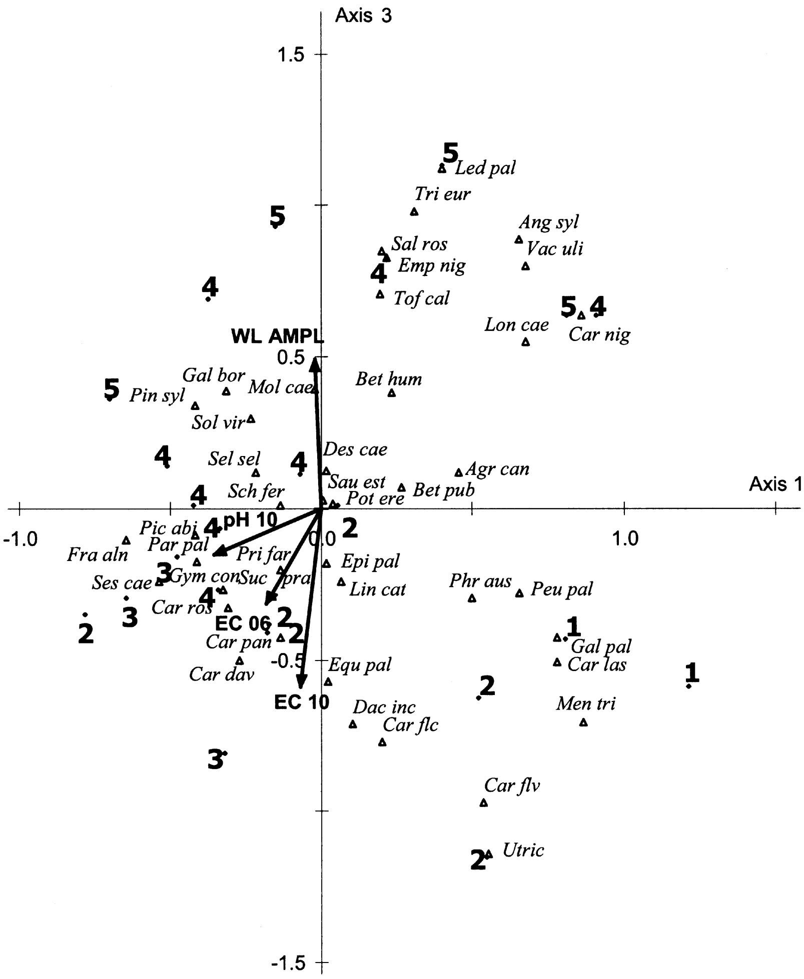

Fig. 2. Nonmetric Multidimensional Scaling (NMS) ordination of the vascular plant species and assemblages on the Paraspõllu fen (North Estonia), showing correlation between 23 plots, 43 vascular plant species, and four environmental variables, rotated by +10°. Symbols: **1–5** cluster number (for location see Fig. 1), Δ – plant species. Abbreviations: **environmental variables**: **WL AMPL** – range of water level seasonal amplitude, **pH 10** – pore water pH, samples collected in October 2007; **EC 10** – conductivity of pore water, samples collected in October 2007; **EC 06** – conductivity of water, samples collected in June 2008; **vascular plant species**: *Agr can – Agrostis canina*, *Ang syl – Angelica sylvestris*, *Bet hum – Betula humilis*, *Bet pub – Betula pubescens*, *Car dav – Carex davalliana*, *Car flc – Carex flacca*, *Car flv – Carex flava*, *Car las – Carex lasiocarpa*, *Car nig – Carex nigra*, *Car pan – Carex panicea*, *Car ros – Carex rostrata*, *Dac inc – Dactylorhiza incarnata*, *Des cae – Deschampsia caespitosa*, *Emp nig – Empetrum nigrum*, *Epi pal – Epipactis palustris*, *Equ pal – Equisetum palustre*, *Fra aln – Frangula alnus*, *Gal bor – Galium boreale*, *Gal pal – Galium palustre*, *Gym con – Gymnadenia conopsea*, *Led pal – Ledum palustre*, *Lin cat – Linum catharcticum*, *Lon cae – Lonicera caerulea*, *Men tri – Menyanthes trifoliata*, *Mol cae – Molinia caerulea*, *Par pal – Parnassia palustris*, *Peu pal – Peucedanum palustre*, *Phr aus – Phragmites australis*, *Pic abi – Picea abies*, *Pin syl – Pinus sylvestris*, *Pot ere – Potentilla erecta*, *Pri far – Primula farinosa*, *Sal ros – Salix rosmarinifolia*, *Sau est – Saussurea alpina* subsp. *esthonica*, *Sch fer – Schoenus ferrugineus*, *Sel sel – Selaginella selaginoides*, *Ses cae – Sesleria caerulea*, *Sol vir – Solidago virgaurea*, *Suc pra – Succisa pratensis*, *Tof cal – Tofieldia calyculata*, *Tri eur – Trientalis europaea*, *Utric – Utricularia intermedia*, *Vac uli – Vaccinium uliginosum*.

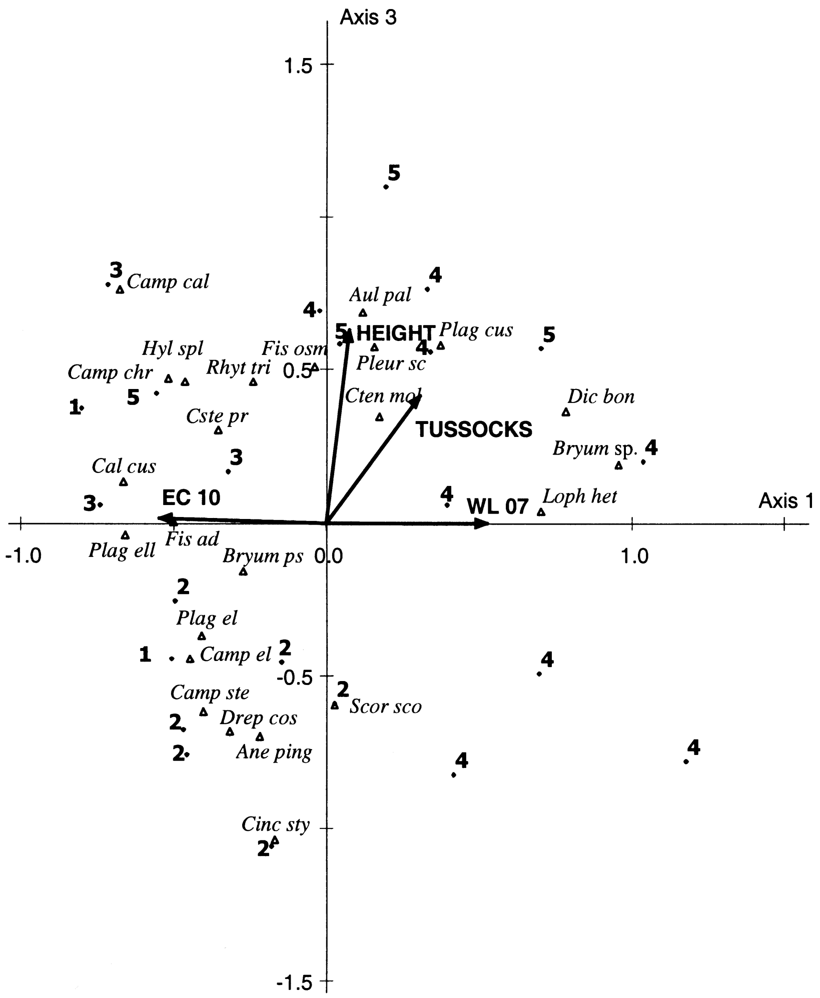

Fig. 3. Nonmetric Multidimensional Scaling (NMS) ordination of the moss species and assemblages on the Paraspõllu fen (North Estonia), showing correlation between 23 plots, 24 moss species, and four environmental variables. Symbols: **1–5** cluster number; Δ – plant species. Abbreviations: **environmental variables**: **TUSSOCKS** – coverage of tussocks per plot, **HEIGHT** – mean height of tussocks per plot, **EC 10** – conductivity of water samples collected in October 2007, **WL 07** – depth to water level on 30 July 2008; **moss species**: *Ane ping* – *Aneura pinguis*, *Aul pal* – *Aulacomnium palustre*, *Bryum* sp. – *Bryum* sp., *Bryum ps* – *Bryum pseudotriquetrus*, *Cal cus* – *Calliergonella cuspidata*, *Camp cal* – *Campylium calcareum*, *Camp chr* – *Campylium chrysophyllum*, *Camp el* – *Campylium elodes*, *Camp ste* – *Campylium stellatum*, *Cinc sty* – *Cinclidium stygium*, *Cste pr* – *Campylium stellatum* var. *protensum*, *Cten mol* – *Ctenidium molluscum*, *Dic bon* – *Dicranum bonjeanii*, *Drep cos* – *Drepanocladus cossonii*, *Fis ad* – *Fissidens adianthoides*, *Fis osm* – *Fissidens osmundoides*, *Hyl spl* – *Hylocomium splendens*, *Loph het* – *Lophozia heterocolpos*, *Plag cus* – *Plagiomnium cuspidatum*, *Plag el* – *Plagiomnium elatum*, *Plag ell* – *Plagiomnium ellipticum*, *Pleur sc* – *Pleurozium schreberi*, *Rhyt tri* – *Rhytidiadelphus triquetrus*, *Scor sco* – *Scorpidium scorpioides*.

of tussocks. Three species in the same quadrant (*Dicranum bonjeanii*, *Lophocolea heterophylla*, *Bryum* sp.) were found to occupy tussocks in the driest part of the fen site. The species in the upper left quadrant preferred near-surface midsummer water level with high EC values of pore water. The lower right quadrant contains no moss species located around the three plots (9, 10, and 17) that belonged to cluster 4. These plots were very poor in moss species and the number of individuals was low.

DISCUSSION

Habitat conditions

Hydrologically the Paraspõllu fen site includes sections of two types. In the northern and eastern sections the water level is high and stable (around clusters 1, 2, and partly 3). This phenomenon can be explained by the stable source of water inflow – a spring on the eastern slope of the mire depression – and by recharging groundwater. This part of the fen site showed a significant negative correlation between the amplitude of WLF and EC of pore water.

The southern and western sections of the site belong to the discharge zone as the water table drops down to about 40 cm in summer and shows great seasonal fluctuations. The EC values of pore water were quite low and more variable between the plots than in the plots of the recharge zone, which was possibly caused by the dilution effect of pure rainwaters. The pore water pH varied insignificantly from 6 to 7 units between plots and had somewhat higher values at the beginning of summer than in late autumn. One of the causes of the spatial and temporal stability of the pore water pH is the buffering effect of bicarbonates (Lamers et al., 1998).

The density and coverage of calcicole species in relation to habitat conditions

The proportions of calcicole vascular plant and bryophyte species were not related to the number of plots per cluster. The inter-plot differences in species diversity were most strongly related to differences in habitat conditions. The number of calcicole moss species was higher in plots of clusters 2 and 3 than in other clusters.

The coverage of calcicole vascular plant and moss species differed largely between the clusters. The much higher coverage of calcicole moss species in plots of cluster 2 than in other parts of the fen may be due to the stable and near-surface calcium-rich waters (as reflected by high EC values) and to the relatively low coverage of the field layer. The notably lower coverage of calcicole vascular plant species in cluster 5 and to a lesser extent in cluster 4 compared to clusters 2 and 3 is most probably connected with a significantly higher coverage of *Molinia* *caerulea* in the former. The expansion of *M. caerulea* in turn is caused by increasing DWL during the vegetation period. The optimum conditions for most of the calcicole vascular plant species represented in the Paraspõllu fen site are the seasonal fluctuation of the water table by less than 20−25 cm and the midsummer water level not lower than 15 cm below the surface. Unlike vascular plants, calcicole moss species depend more on the water chemistry than on the substrate chemistry (Vitt & Chee, 1990). Calcicole bryophytes probably require even a more stable and closer to the surface water level (9−10 cm and 4−5 cm, respectively, on the study site).

The coverage of litter varied largely between the plots (from 15% to 80%). Surprisingly, the effect of litter on the species composition and coverage of both vascular plants and bryophytes was insignificant. Hájková & Hájek (2003) confirmed that high quantities of litter cause a decrease in bryophyte biomass but not in species richness. Peintinger & Bergamini (2006) found that in Swiss calcareous fens litter mass explains differences in the species composition of vascular plants equally well with the effect of abandonment, whereas the influence of litter on bryophytes is much less important. The experiment conducted in a Minnesota fen (USA) demonstrated that litter addition has a minor effect on the composition and production of plant cover species (Weltzin et al., 2005). Instead, litter removal, mainly because of increased light availability and soil temperature, leads to changes in the plant community in the fen. Our study site was abandoned at least some 40–50 years ago. Therefore, we may believe that such a time interval was sufficiently long for the system to reach a stable state between the rate of litter accumulation, plant species composition, and vegetation coverage.

Environmental effect on the distribution of plant groups

The Paraspõllu fen site is characterized by a high variability in species composition and vegetation structure, depth of the water level, seasonal amplitude of water level fluctuations, and water conductivity gradients.

About 52% of the vascular plant species variance was due to four environmental variables – amplitude of WLF, water pH, and conductivity measured in late autumn and early summer. More than 28% of the variance can be explained by other habitat conditions, not measured by us, possibly by substrate chemistry (e.g. phosphorus availability).

It is often reported that the compositional pattern of the plant cover in fens is most importantly controlled by the water level and its stability (Bootsma & Wassen 1996; Johnson & Steingraeber, 2003; Hájková et al., 2004; Nekola, 2004; Barry et al., 2008) or by the length of the period when the water level drops in summer (Wilcox & Nichols, 2008). On a small scale (across a mire) also the soil organic matter content is of importance (Hájková et al., 2004).

For bryophytes, the surface microtopography has equally important control with hydrology and water conductivity, as the height and coverage of tussocks, EC of pore water, and midsummer minimum DWL describe some 43.5% of the compositional variation of moss species. Where the tussocks occupied about half of the surface and leaves of sedges and grasses shaded almost totally the inter-tussock small depressions (clusters 4 and 5), the shade-intolerant moss species were able to inhabit only the tops and sides of tussocks. In such a situation the effect of the midsummer minimum DWL was not as great as in plots of clusters 2 and 3 where the water level was at almost the same depth but differences in vascular plant cover were significant.

The absence of a relationship in the species compositional variation between vascular plants and bryophytes can be explained by the more rapid response of moss species to changes in the habitat conditions compared to vascular species (Mälson et al., 2008).

Clusters 1, 2, and 3 represent the near-natural calcareous-rich fen state. The *Carex panicea–Schoenus ferrugineus–Drepanocladus cossonii* assemblage of cluster 2 corresponds well to the calcareous tufa-forming fen type according to Hájek et al. (2006). In small depressions between tussocks calcium carbonate precipitates and forms unconsolidated marl. The number and coverage of calcareous species, especially moss species, was higher in the *Carex panicea–Schoenus ferrugineus–Drepanocladus cossonii* assemblage compared to the other assemblages distinguished on the Paraspõllu fen. In the moss cover the typically calcicole species *D. cossonii* dominated with *Campylium stellatum* as a co-dominant.

The *Phragmites australis–Calliergonella cuspidata* assemblage (cluster 2) is distributed in almost the same hydrological conditions as the *Carex panicea–Schoenus ferrugineus–Drepanocladus cossonii* assemblage. *Phragmites australis* forms a rather dense cover and calcium does not precipitate, most likely because of mobile but stable near-surface groundwater. Moss layer dominants *Calliergonella cuspidata* and *Campylium elodes* indicate calcareous and extremely rich fen according to Hájek et al. (2006). The *Molinia caerulea–Carex davalliana* assemblage (cluster 3) can also be classified as calcareous and extremely rich fen type but weakly affected by drainage.

Two assemblages, namely *Molinia caerulea–Schoenus ferrugineus* (cluster 4) and *Molinia caerulea* (cluster 5), demonstrate that even moderate drainage promotes the expansion of *M. caerulea*. The principal difference between these assemblages is that *S. ferrugineus* was frequent in the former but occasional in the latter assemblage. In the *Molinia caerulea* assemblage certain forest floor species such as *Hylocomnium splendes* and *Pleurozium schreberi* dominated among the bryophytes and several *Sphagnum* species (*S. contortum*, *S. fallax*, *S. papillosum*, *S. warnstorfii*) had formed small patches on stump hummocks. The long-term (over 20 years) monitoring of the drainage effect on the vegetation of a rich fen in Central Sweden (Mälson et al., 2008) showed that rapid emergence of a few dominants such as *M. caerulea*, *Betula pubescens*, and *Sphagnum* spp. may start at different times after drainage. The *Molinia* cover made up a few per cent just after drainage in 1979, but over 50% 10−30 years later.

Distribution of rare species

The rarest species among vascular plants on the Paraspõllu fen site were *Malaxis monophyllos*, *Selaginella selaginoides*, and *Pinguicula alpina*, which are listed in category II of protected species in Estonia. *Malaxis monophyllos* is a sporadic species growing in moist or flooded sites of fens and mire forests. In Estonia its distribution has decreased due to extensive drainage activities (Kull & Tuulik, 2002). On the Paraspõllu fen this species was found in one relevé of cluster 2 in a wet habitat with negligible seasonal fluctuations of the water table around the ground surface.

Selaginella selaginoides is a relict of the post-glacial period, which is on the southern border of its distribution area in Estonia (Kukk & Kull, 2005). On our study site *S. selaginoides* was closely related to the tussock-forming graminoid *Schoenus ferrugineus* growing on the top and sides of its tussocks.

Pinguicula alpina, a very rare species in Estonia, grows in calcareous fens. On the Paraspõllu fen it was found in one relevé in cluster 4 on the sides of *S. ferrugineus* and *Carex davalliana* tussocks.

Our data are consistent with the results of Trass (1986) indicating that *Epipactis palustris* gains from weak drainage. *Saussurea alpina* subsp. *esthonica* also seems to benefit from weak drainage and increasing shade provided by a sparse tree and shrub layer.

The orchid species present on the Paraspõllu fen site prefer wet areas or those moderately affected by drainage. The water level there was not deeper than 20−25 cm during the midsummer minimum.

The bryophyte list of the studied fen contains several rare and protected species preferring calcareous substrate, such as *Campylium calcareum*, *C. halleri*, and *Catoscopium nigritum*. Only the last species was identified in wetter conditions, whereas the two *Campylium* species with a very low coverage were found in the driest, *Molinia*-rich part of the fen site.

CONCLUSIONS

We distinguished five assemblages on the Paraspõllu fen well arranged on the gradient of the midsummer water level minimum together with the respective late autumn pore water conductivity pattern. The proportion of calcareous moss species decreased rapidly when the seasonal amplitude of the water level fluctuation reached 9–10 cm and midsummer water level minimum was more than 4–5 cm. Calcareous vascular plant species were more tolerant to water level instability and still dominated in plots where the water level fluctuated with an amplitude of up to 25 cm. The microtopography had also a strong effect on the coverage and species composition of mosses. Obviously different responses to hydrology and microtopography are among the main reasons for the weak (statistically non-significant) correspondence between the compositional variance of field and surface layer plant species on the Paraspõllu calcareous fen site. The fen site, weakly drained in part, is a habitat of many rare and endangered vascular and moss species. The drainage of the abandoned calcareous fen site favours the expansion of *Molinia caerulea* and encroachment of woody species. There is an urgent need to develop a well-defined management plan to restore the calcareous rich fen plant cover and create respective habitat conditions over the site based on good knowledge of nutritional requirements of plant species, interspecies relationships, and substrate biogeochemistry.

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APPENDIX

Coverage (%) of vascular plants and bryophytes at vegetation clusters (see also Table 1). The asterisks mark species that are rare or protected in Estonia

No.	Species	Cluster				
		1	2	3	4	5
1	*Agrostis canina* L.	<1			<1	
2	*Andromeda polifolia* L.				<1	
3	*Angelica sylvestris* L.				<1	<1
4	*Betula humilis* Schrank	<1	<1	<1	3	1
5	*Betula nana* L.					<1
6	*Betula pubescens* Ehrh.	2	<1	<1	<1	<1
7	*Calluna vulgaris* L.					<1
8	*Carex davalliana* J. E. Sm.		<1	11		<1
9	*Carex digitata* L.				<1	
10	*Carex flacca* Schreb.		1	<1		
11	*Carex flava* L.	<1	<1			
12	*Carex lasiocarpa* Ehrh.	5	1			
13	*Carex nigra* (L.) Reichard				<1	<1
14	*Carex panicea* L.		6			
15	*Carex rostrata* Stokes		1	1		
16	*Dactylorhiza incarnata* (L.) Soó*		<1	<1	<1	
17	*Deschampsia cespitosa* (L.) P. Beauv.		<1			<1
18	*Empetrum nigrum* L. subsp. *nigrum*				<1	
19	*Epipactis palustris* (L.) Crantz*		<1	<1	<1	
20	*Equisetum palustre* L.	<1	<1	<1		
21	*Filipendula ulmaria* (L.) Maxim.				<1	
22	*Frangula alnus* Mill.		<1		<1	
23	*Galium boreale* L.			<1		<1
24	*Galium palustre* L.	<1	<1		<1	
25	*Gymnadenia conopsea* (L.) R. Br.*		<1	<1		

APPENDIX. *Continued*

No.	Species	Cluster				
		1	2	3	4	5
26	*Ledum palustre* L.				<1	<1
27	*Linum catharcticum* L.	<1	<1	<1	<1	
28	*Lonicera caerulea* L.					<1
29	*Malaxis monophyllos* (L.) Sw.*	<1				
30	*Menyanthes trifoliata* L.	6	2		<1	
31	*Molinia caerulea* (L.) Moench	<1	1	16	24	37
32	*Parnassia palustris* L.		<1	<1	<1	<1
33	*Pedicularis palustris* L.				<1	
34	*Peucedanum palustre* (L.) Moench	<1	<1		<1	
35	*Phragmites australis* (Cav.) Trin. ex Steud.	7	<1		<1	<1
36	*Picea abies* (L.) H. Karst.	<1	<1	1	<1	
37	*Pinguicula alpina* L.*				<1	
38	*Pinguicula vulgaris* L.		<1			
39	*Pinus sylvestris* L.			<1	1	1
40	*Platanthera bifolia* (L.) Rich.*	<1				
41	*Populus tremula* L.					<1
42	*Potentilla erecta* (L.) Räusch.		<1	<1	<1	<1
43	*Primula farinosa* L.	<1	<1	<1	<1	<1
44	*Salix fragilis* L.	<1				
45	*Salix rosmarinifolia* L.		<1		1	1
46	*Saussurea alpina* (L.) DC. subsp. *esthonica* (Baer ex Rupr.) Kupffer*			<1	<1	
47	*Schoenus ferrugineus* L.		5	3	11	<1
48	*Selaginella selaginoides* (L.) Beauv. ex Schrank & Mart*		<1	<1	<1	
49	*Sesleria caerulea* (L.) Ard.		1	5	<1	<1
50	*Solidago virgaurea* L.			<1	<1	<1
51	*Succisa pratensis* Moench		<1		<1	<1
52	*Tofieldia calyculata* (L.) Wahlenb.	<1	<1	<1	<1	
53	*Trientalis europaea* L.				<1	<1
54	*Utricularia intermedia* Hayne	<1	<1			
55	*Vaccinium uliginosum* L.					1
56	*Vaccinium vitis-idaea* L.					<1
57	*Viola* sp.					<1
58	*Aneura pinguis* (L.) Dumort.	<1	<1			
59	*Calypogeia integristipula* Steph.					<1
60	*Cephalozia* sp.				<1	
61	*Lophocolea heterophylla* (Schrad.) Dumort.				<1	<1
62	*Lophozia bantriensis* (Hook.) Steph.				<1	
63	*Pellia* sp.				<1	
64	*Pellia endiviifolia* (Dicks.) Dumort.		<1			
65	*Preissia quadrata* (Scop.) Nees		<1			
66	*Aulacomnium palustre* (Hedw.) Schwägr.				<1	<1
67	*Brachythecium albicans* (Hedw.) Schimp.					<1
68	*Bryum* sp.		<1		<1	
69	*Bryum pseudotriquetrum* (Hedw.) P. Gaertn. et al.		2	<1	<1	<1
70	*Calliergonella cuspidata* (Hedw.) Loeske	13	<1	3		1
71	*Campylium calcareum* Crundw. & Nyholm*			1		<1
72	*Campylium chrysophyllum* (Brid.) Lange			<1		

Continued overleaf

APPENDIX. *Continued*

No.	Species	Cluster				
		1	2	3	4	5
73	*Campylium elodes* (Lindb.) Kindb.	10	<1	1	<1	
74	*Campylium halleri* (Hedw.) Lindb.*					<1
75	*Campylium polygamum* (Schimp.) Lange & C. E. O. Jensen				<1	
76	*Campylium stellatum* (Hedw.) Lange & C. E. O. Jensen	<1	8	3	<1	
77	*Campylium stellatum* (Hedw.) Lange & C. E. O. Jensen var. *protensum* (Brid.) Bryhn ex Grout		<1	<1	<1	<1
78	*Catoscopium nigritum* (Hedw.) Brid.*		<1			
79	*Cinclidium stygium* Sw.		<1			
80	*Ctenidium molluscum* (Hedw.) Mitt.		<1	2	4	<1
81	*Dicranum bonjeanii* De Not.				1	1
82	*Drepanocladus cossonii* (Schimp.) Loeske	5	19	4	1	
83	*Fissidens adianthoides* Hedw.	<1	<1	2	<1	<1
84	*Fissidens dubius* P. Beauv.			<1		
85	*Fissidens osmundoides* Hedw.			<1	1	<1
86	*Fissidens taxifolius* Hedw.				<1	
87	*Hylocomium splendens* (Hedw.) Schimp.					6
88	*Meesia triquetra* (L. ex Jolycl.) Ångstr.		3			
89	*Philonotis calcarea* (Bruch & Schimp.) Schimp.	<1				
90	*Plagiomnium cuspidatum* (Hedw.) T. J. Kop.					<1
91	*Plagiomnium elatum* (Bruch & Schimp.) T. J. Kop.		<1	<1		<1
92	*Plagiomnium ellipticum* (Brid.) T. J. Kop.	<1	<1	1	<1	
93	*Pleurozium schreberi* (Willd. ex Brid.) Mitt.				<1	3
94	*Polytrichum juniperinum* Hedw.					<1
95	*Rhizomnium punctatum* (Hedw.) T. J. Kop.					<1
96	*Rhytidiadelphus triquetrus* (Hedw.) Warnst.					1
97	*Scorpidium scorpioides* (Hedw.) Limpr.		5			
98	*Sphagnum contortum* Schultz					<1
99	*Sphagnum fallax* (H. Klinggr.) H. Klinggr.					<1
100	*Sphagnum papillosum* Lindb.					1
101	*Sphagnum warnstorfii* Russow					1

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Põhja-Eesti kaltsiumirikka madalsoo soontaime- ja samblaliikide koostis ning struktuur veetaseme gradiendil

Mati Ilomets, Laimdota Truus, Raimo Pajula ja Kairi Sepp

On uuritud Põhja-Eesti allikalise toitega kaltsiumirikka Paraspõllu madalsoo (pindala 40 ha) taimestiku koostise ja struktuuri seoseid hüdroloogiliste tingimuste ning mikrotopograafiaga. Liigiline koostis, liikide katvus, mätaste katvus ja keskmine kõrgus, varise katvus, veetaseme sügavus, poorivee pH ning erielektrijuhtivus määrati 23 prooviruudus (à 1 m^2). Leiti 57 soontaime ja 44 samblaliiki, sh 14 kaitsealust või haruldast liiki. Seos rohu- ja samblarinde koostise vahel ei olnud oluline. Soontaimede liigilist koostist määrasid eelkõige veetaseme sesoonse fluktueerumise amplituud ja poorivee erielektrijuhtivus, samblaliikide puhul lisandus mikrotopograafia. Klasteranalüüsi abil eraldatud viiest kooslusest kolm (*Carex panicea–Schoenus ferrugineus–Drepanocladus cossonii*, *Phragmites australis–Calliergonella cuspidata* ja *Molinia caerulea–Carex davalliana*) iseloomustasid (allika)lubjarikast madalsood. Teised kaks taimekooslust (*Schoenus ferrugineus–Molinia caerulea* ja *Molinia caerulea*) levivad nõrgalt kuivendatud madalsoo osal. Nii kaltsifiilsete liikide arv kui katvus vähenevad järsult, kui *M. caerulea* katvus ületab 30% taseme ja veetaseme sesoonne fluktueerumine on üle 25 cm.