# Quagmires around southern and southeastern Estonian lakes

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## SUMMARY

We studied quagmires around 17 soft-water lakes in southern and southeastern Estonia. Vegetation analysis was carried out at the level of moss and field layer synusiae and plant communities. The aims of the current study were to elucidate the main factors determining the species richness of these quagmires, in order to ascertain what types of synusiae and plant communities form their vegetation, and what are their indicator species. Increasing the pH of peat-water increased the number of bryophyte species and the total number of species. The number of bryophyte species was positively related to through-flowing lakes and neighbouring forest vegetation. In total nine societies of bryophyte synusiae, 14 societies of vascular plants and eight community types were distinguished. Six community types represented minerotrophic quaking fen, and two types were classified as mixotrophic quaking bog. Our results show clearly a relative independency of synusiae; similar moss synusiae can associate with synusiae of various vascular plant societies and *vice versa.*

**KEY WORDS:** community types, minerotrophy, mixotrophy, societies, soft-water lakes, synusiae

**Nomenclature**: the Plant List (http://www.theplantlist.org) for vascular plants, Ingerpuu & Vellak (1998) for bryophytes.

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## INTRODUCTION

Terrestrialisation of shallow lakes is one of the main processes of mire formation (Succow 2001). About 60 % of Estonian mires have developed in this way (Orru 1995). In the course of terrestrialisation the floating mat will start to develop at the shallowest shores, then expand gradually over the deeper parts of the lake, the roots of living plants and the increasing peat layer forming a tight raft although the water level frequently reaches its surface. The component vascular plants obtain nutrients from the underlying water body or from groundwater flowing in from the surroundings. Such mires are classified as limnogenous/minerotrophic floating fens, quagmires (Moore & Bellamy 1974, Masing 1975, Joosten *et al*. 2017) or quagfens (Van Wirdum 1990). When the peat layer becomes thicker and the plants form hummocks, some species lose contact with the fen/lake water and the vegetation becomes bog-like with *Sphagnum* spp., *Calluna vulgaris*, *Empetrum nigrum* and other typical bog species (Sjörs 1948); quagmires of this successional stage could be classified as mixotrophic or transitional quagmires (Paal 1997). The speed and course of terrestrialisation depends on features of the lake, mainly the trophic level, but factors such as the presence of inflow or throughflow, water depth, pH, etc. are also important (Laasimer 1965, Marek 1992, Succow 2001, Roelofs *et al*. 2002).

According to Laasimer (1965), the extent of minerotrophic quagmires in Estonia was 1,300 ha in the 1950s. According to the latest inventory of Estonian mires (Paal & Leibak 2011, 2013), the number of minerotrophic quagmires larger than 1 ha is now 306 and their total area is 2,076 ha. Additionally, 128 smaller quagmires exist in the marginal parts of mires of other types. Thus, the total area of habitats belonging to this site type may have been under-estimated by nearly 40 % because tens or even hundreds of lakes and pools have narrow strips of quagmire on their banks. During the last century, the total area of minerotrophic quagmires has increased due to terrestrialisation/infilling of lakes and pools, especially if they have been influenced by nitrogen pollution or drainage. Also, many minerotrophic quagmires have appeared after artificial lowering of lake water levels. Thus, the number and total area of minerotrophic quagmires is predicted to increase in the future due to both natural processes (ageing of lakes) and human influences. Even if causative human activities are no longer practised, the processes will continue once they have been initiated.

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Minerotrophic quagmires are distributed unevenly in Estonia. Their number and density are highest on the southeastern uplands (Otepää, Karula, Haanja), in the northern part of central Estonia (Lahemaa, Kõrvemaa), in the northwestern part of the mainland, and locally on Hiiumaa Island. Most of them are relatively small in area. Only one example exceeds 100 hectares (122 ha) and the three next largest extend to 60 ha; about one-third of the total are less than 1 ha each (Paal & Leibak 2011, 2013).

Mixotrophic quagmires are formed, like minerotrophic ones, as a result of terrestrialisation of lakes and ponds, but they occur also at the margins of bogs where water is infiltrating from neighbouring bogs at higher levels. Water is often present on or quite close to the surface. The soils are Eutri-Dystric Histosols. The herb and moss layers of both minerotrophic and mixotrophic quagmires are species-poor and often monodominant.

The surface areas of mixotrophic quagmires vary widely. There are about ten large sites (more than 50 ha) in northern Estonia, outside of the study area, but the majority of mixotrophic quagmires are small and similar in area to minerotrophic ones. They are almost absent in western, central and northeastern Estonia, as well as on islands (except Saaremaa Island). In total, 406 sites (4,628 ha) have been registered as mixotrophic quagmires. Of these, 312 (2,330 ha) include only habitats of this mire type, while the remainder also contain habitats of other types (mainly mixotrophic grass mires and/or minerotrophic quagmires) in their marginal parts; and 165 are themselves marginal habitats. Thus, the total area of mixotrophic quagmire habitats in Estonia is not less than 2,200 ha (Paal & Leibak 2011, 2013).

Quagmires are also well represented in nearby countries, e.g. in Finland (Lindholm & Heikkilä 2017), Latvia (Pakalne & Aleksāns 2017), Lithuania (Mierauskas & Taminskas 2017), Poland (Kotowski *et al*. 2017) and northwestern Russia (Botch & Smagin 1993); in western (Van Wirdum 1990), northern (Pålson 1998) and southern Europe (EC 2013); as well as in Canada (Jeglum 1993) and the USA (Damman & French 1987). They encompass ecosystems of various trophic and pH status, depending on bedrock chemistry (Van Wirdum 1990, Kotowski *et al*. 2017), water chemistry and, presumably, the species pools in their surroundings. According to the European Union Habitats Directive (EU 1992) they belong to the type 7140 ‘Transition mires and quaking bogs’ which has pan-European importance.

The layers of natural plant communities react to changing environmental conditions somewhat independently (e.g. During & Vershuren 1988, Paal 1995, Ewald 2000). The elemental structural units expressing the internal variability of plant communities are synusiae (Lippmaa 1939, Du Rietz 1965, Norin 1979, Decocq 2002, Paal & Degtjarenko 2015). Barkman (1973; page 452) has defined the synusia as a structural part of a plant community “inhabiting (a) a special microhabitat, with (b) a specific floristic composition and consisting of species that (c) belong to the same stratum and that do not differ fundamentally in either (d) periodicity or (e) way of exploitation of their environment”. The more or less stable combinations of synusiae of different layers constitute microcoenoses (Barkman 1973, Korchagin 1976). On the basis of this assumption, detailed studies of the syntaxonomical structure of plant communities should be conducted also at the level of their lower structural units, i.e. synusiae and/or microcoenoses (Norin 1979, Masing 1982, Dierschke 1994, Werffeli *et al*. 1997, Decoq 2002). Taking into account these considerations, the aims of the current study were to: (i) investigate the species richness of quagmires surrounding the small soft-water lakes in southeastern and southern Estonia; (ii) ascertain what types of synusiae (i.e. societies) form the vegetation of these plant communities; (iii) establish a typology for the plant communities found in the quagmires studied; and (iv) determine the indicator species for all types of synusiae and communities identified.

## METHODS

### Study area

We restricted our study to parts of southern and southeastern Estonia where the water hardness of lakes is less than 80 mg $HCO_3$ $L^{-1}$ (Mäemets 1977; database of small lakes at the Chair of Hydrobiology and Fishery, Estonian University of Life Sciences; Figure 1). The presence of quagmires around the lakes was checked using aerial photographs. Seventeen lakes were selected to represent all limnological types of soft-water lakes in Estonia (according to Ott & Kõiv 1999 and Tamre 2006; Table 1); their water exchange type was recorded according to Mäemets (1977). It should be noted here that the Estonian typology of lakes (Mäemets 1974, Ott & Kõiv 1999) is based on the natural accumulation type and differs fundamentally from classifications that consider only trophic state. Soft-water lakes with low content of humic compounds are naturally oligotrophic, while soft-water eutrophic lakes have been formed due to anthropogenic eutrophication. Low alkalinity determines the specific assemblage of submerged macrophytes

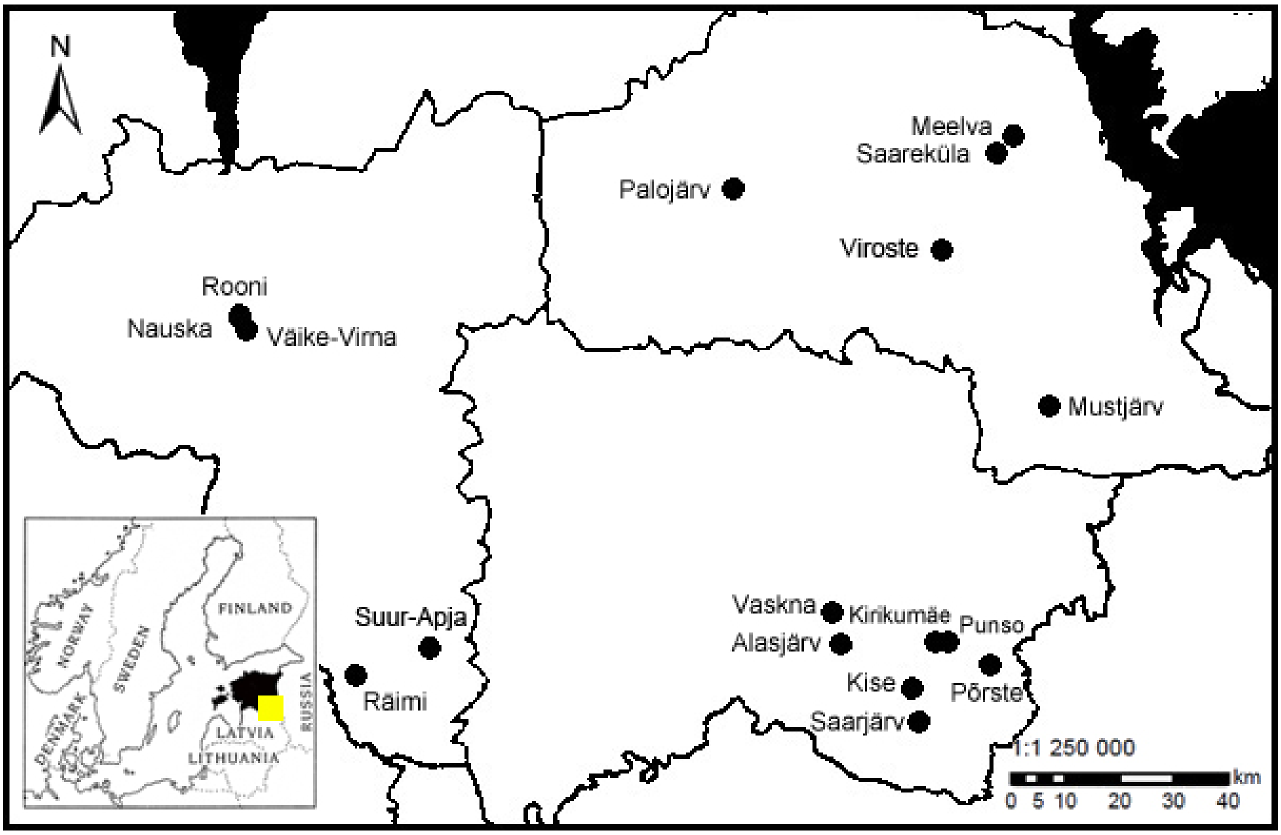

Figure 1. Locations of the selected lakes around which quagmires were studied.

(mainly mosses and isoetids) that can grow in these lakes. However, many examples have turned into other types of soft-water ecosystems due to accumulation of humic compounds from adjacent forests, quagmires and peatlands.

### Field data

Plant communities were delineated visually according to their general physiognomy and dominant plant species. Percent cover of species in the field layer and their presence in the moss layer, as well as the total cover of the layers considered, were recorded within five 1×1 m sample quadrats in each community. Sample quadrats were located randomly except where they occurred on a boundary between two microcoenoses, in which case they were moved into the larger microcoenosis. In this way we could regard the data collected in the 1 $m^2$ sample quadrats as representive of microcoenoses, as well as of the synusiae of moss and field layers (Barkman 1968, 1973, Korchagin 1976, Dierschke 1994, Paal & Degtjarenko 2015).

In every sample quadrat the peat-water temperature and pH were measured at a depth of 10 cm below the ground surface. For collection of water from higher and drier hummocks, a small hole was made in the hummock and measurements were carried out there. Similar measurements were carried out in lake water at the edges of the study sites.

The type of vegetation on the landward side of each quagmire was recorded as follows: 1 = forest, 2 = grassland, 3 = mire.

### Data processing

Relationships between species richness and environmental variables, as well as cover of field and moss layers at community level, were ascertained using General Regression Model (GRM) analyses based on the forward stepwise entry of variables (StatSoft Inc. 2011).

Cluster analysis was performed on the species presence data for both moss and field layers using the β-flexible (β = -0.8) algorithm (McCune & Mefford 2011) and the Sørensen distance as the measure of dissimilarity (McCune & Grace 2002). Analysis was carried out separately at the levels of sample quadrats (i.e. synusiae) and plant communities (i.e. using averaged data for sample quadrats of every community). To test the differences in species composition among the clusters, we used the non-parametric multi-response permutation procedure (MRPP; McCune & Mefford 2011); the Bonferroni corrections for multiple comparison were also considered.

Table 1. Characteristics of the selected lakes. Notation: Latitude and Longitude = lake centre coordinates; Perimeter = lake shoreline length; Limnological type (OL = oligotropic, DY = dystrophic, SD = semidystrophic, SM = soft-water mixotrophic, SE = soft-water eutrophic (due to anthropogenic eutrophication), AT = acidotrophic). WET = lake water exchange type (1 = endorheic (seepage) lake, 2 = outflow lake, 3 = throughflow lake); AverD = average depth; MaxD = maximum depth; pH = lake-water pH, Temp = lake-water temperature; No spp. = total number of species in quagmires; nd = no data.

| **Lake** | **Latitude** | **Longitude** | **Area (ha)** | **Perimeter (m)** | **Limnological type** | **WET** | **AverD (m)** | **MaxD (m)** | **pH** | **Temp (°C)** | **No spp.** |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Kise** | 57° 38' 31" | 27° 12' 21" | 44.3 | 4384 | OL | 1 | 2.9 | 5.1 | 6.1 | 26.6 | 34 |
| **Saarjärv (Misso)** | 57° 36' 49" | 27° 13' 10" | 23.8 | 2934 | OL | 2 | 2.4 | 4.4 | 7.0 | 24.4 | 53 |
| **Väike-Virna** | 57° 57' 37" | 26° 6' 14" | 1.6 | 504 | DY | 2 | nd | 1.2 | 6.3 | 25.7 | 24 |
| **Alasjärv** | 57° 40' 53" | 27° 5' 23" | 7.2 | 1124 | SD | 3 | 2.8 | 7.1 | 7.8 | 25.9 | 41 |
| **Kirikumäe** | 57° 41' 2" | 27° 14' 58" | 62 | 3201 | SD | 1 | 2.8 | 3.5 | 6.0 | 27.6 | 24 |
| **Palojärv (Ihamaru)** | 58° 5' 1" | 26° 54' 42" | 8.2 | 1180 | SD | 1 | nd | 10 | 6.5 | 26.0 | 35 |
| **Põrste** | 57° 39' 47" | 27° 20' 11" | 8.9 | 1533 | SD | 2 | 4 | 5 | 6.2 | 23.7 | 30 |
| **Vaskna** | 57° 42' 36" | 27° 4' 31" | 37.1 | 9503 | SD | 2 | 2.8 | 9.5 | 7.3 | 24.9 | 9 |
| **Suur-Apja** | 57° 40' 47" | 26° 24' 32" | 41.4 | 2791 | SM | 2 | 2 | 4.9 | 7.0 | 24.5 | 34 |
| **Mustjärv (Orava)** | 57° 53' 32" | 27° 26' 2" | 5.5 | 1719 | SM | 1 | 3.3 | 9.2 | 5.5 | 24.3 | 31 |
| **Punso** | 57° 41' 5" | 27° 15' 34" | 3.6 | 855 | SM | 1 | nd | nd | 6.0 | 26.9 | 17 |
| **Nauska** | 57° 58' 18" | 26° 5' 36" | 5.5 | 1158 | SE | 1 | nd | 3 | 8.6 | 24.8 | 34 |
| **Rooni** | 57° 58' 11" | 26° 5' 31" | 4.6 | 1400 | SE | 1 | nd | 17 | 7.3 | 26.2 | 43 |
| **Räimi** | 57° 39' 16" | 26° 17' 1" | 9.6 | 1156 | SE | 1 | 3.5 | 5 | 7.1 | 25.2 | 27 |
| **Meelva** | 58° 7' 51" | 27° 22' 33" | 75.4 | 6638 | AT | 2 | 2 | 3.2 | 5.4 | 30.2 | 27 |
| **Saareküla** | 58° 6' 53" | 27° 20' 49" | 6.2 | 1520 | AT | 3 | nd | 14.3 | 5.8 | 29.1 | 13 |
| **Viroste** | 58° 1' 47" | 27° 15' 19" | 11.3 | 3023 | AT | 3 | 4 | 10 | 5.3 | 28.8 | 44 |

For every sample quadrat (microcenosis) the Ellenberg indicator values of habitat environment conditions (Ellenberg 1974, revised by Chytrý *et al*. 2018) were calculated from the field layer species cover values. The difference in median values of pH for synusiae types (societies) was tested by the Kruskal-Wallis ANOVA and Duncan's test, and the difference in average values of other environmental variables by univariate analysis of variance (ANOVA) and Fischer LSD post-hoc test (StatSoft Inc. 2011).

The main gradients of the species data were summarised by detrended correspondence analysis (PC-ORD ver. 6, McCune & Mefford 2011) with a rescaling threshold of 0.1 and 26 segments, axes rescaled proportionally to the longest axis. Prior to data analysis, species recorded less than three times in the whole dataset were filtered out. The shared patterns of species occurrence and environmental variables were portrayed using ordination biplots.

Species indicator values for societies of synusiae and community types were calculated using the Dufrêne & Legrendre (1997) method as implemented in the PC-ORD statistical package (McCune & Mefford 2011). The statistical significance of the indicator values obtained was evaluated by the Monte Carlo permutation tests (N = 499).

## RESULTS

### Species richness

Altogether we registered 90 species of vascular plants and 23 species of bryophytes. The most common vascular species were *Carex rostrata*, *Potentilla palustris*, *Peucedanum palustre*, *Oxycoccus palustris*, *Scheuchzeria palustris*, *Carex lasiocarpa*, *Calla palustris*, *Menyanthes trifoliata*, *Lycopus europaeus*, *Agrostis canina*, *Lysimachia thyrsiflora*, *Drosera rotundifolia* and *Carex limosa*; and the most frequently recorded bryophytes were *Sphagnum flexuosum*, *Sphagnum fallax*, *Sphagnum squarrosum*, *Sphagnum magellanicum*, *Sphagnum cuspidatum*, *Sphagnum centrale*, *Calliergon stramineum*, *Calliergon cordifolium* and *Calliergonella cuspidata.*

In quagmires around lakes of the same limnological type, the total number of species was rather dissimilar; e.g. in quagmires connected with semidystrophic lakes it varied from 9 to 41 or 4.5 times and in mires associated with acidotrophic lakes it varied from 13 to 44 or 3.4 times (Table 1). The lowest total number of species (9) was found in a mire at semidystrophic Lake Vaskna and the maximal number (53) was recorded around oligotrophic Lake Saarjärv. The average number of species was also highest (44) in mires around oligotrophic lakes, but lowest (24) in the mire surrounding dystrophic Lake Väike-Virna (the smallest lake that we studied).

The GRM analysis confirmed that the number of species in both moss and field layers was significantly promoted by the higher peat-water pH (Table 2). Moreover, the number of bryophyte species was positively related to throughflow lakes and neighbouring forest vegetation. The significant relationship of bryophyte species number and total species number with longitude indicate, presumably, the importance of mesolandscape or even macrolandscape features for quagmire vegetation; since the uplands in southeastern Estonia alternate with lowlands in accordance with the longitude (Raukas & Rõuk 1995, Arold 2005).

### Syntaxonomic structure

*Bryophyte synusiae and societies*

Using cluster analysis we identified nine types of bryophyte synusiae, i.e. societies (Table 3), all with significantly different species composition ($p_{MRPP} < 0.01$), both before and after Bonferroni correction for multiple comparisons. In terms of their indicator species, these societies are:

1) *Calliergonella cuspidata*,
2) *Calliergon cordifolium*,
3) *Sphagnum magellanicum* - *Sphagnum fuscum*,
4) *Sphagnum squarrosum*,
5) *Sphagnum flexuosum*,
6) *Calliergon stramineum*,
7) *Sphagnum centrale* - *Sphagnum cuspidatum*,
8) *Sphagnum angustifolium*,
9) *Sphagnum fallax*.

The range of median peat-water pH amongst these societies was 2.5 units. In some societies the amplitude of variation was even larger, e.g. the *Sphagnum squarrosum* society had pH limits of 2.7–7.3, and the *Sphagnum flexuosum* society 2.9–6.4; the smallest range of these limits (1.3 units) was in synusiae belonging to the *Sphagnum centrale* - *Sphagnum cuspidatum* society. The synusiae of *Sphagnum fallax* and *Sphagnum magellanicum* - *Sphagnum fuscum* societies were abundant in habitats with the lowest median pH, while the synusiae of the *Calliergonella cuspidata* society were most common in habitats with the highest median pH (Table 4).

The indicator values for reaction and nutrients appeared to be rather well correlated; the lowest were those for microhabitats of *Sphagnum magellanicum* - *Sphagnum fuscum* synusiae and the highest were for *Calliergonella cuspidata* synusiae. The field layer had the lowest total cover in *Sphagnum centrale* -

Table 2. Effects of environmental factors on the species richness in quagmire communities according to the General Regression Model analyses. Notation: t = value of the t-criterion by stepwise inclusion of variables into the GRM model; p = significance level; ß = standardised regression coefficient; $\text{SE}_{\text{ß}}$ = its standard error; Multiple $R^2$, Adjusted $R^2$ and $p_{model}$ = statistics and significance level of the whole GRM model; Longitude = plant community centre longitude coordinates; pH = peat-water pH; WET = lake water exchange type; AVT = adjacent vegetation type.

| Variable | t | p | ß | $\text{SE}_{\text{ß}}$ | Multiple $R^2$ | Adjusted $R^2$ | $p_{model}$ |
|---|---|---|---|---|---|---|---|
| Bryophytes | | | | | 0.623 | 0.584 | <0.001 |
| Intercept | 8.31 | < 0.001 | | | | | |
| Longitude | -7.03 | < 0.001 | -0.75 | 0.11 | | | |
| WET | 3.56 | < 0.001 | 0.42 | 0.12 | | | |
| AVT | -4.34 | < 0.001 | -0.46 | 0.11 | | | |
| pH | 2.56 | 0.014 | -0.27 | 0.11 | | | |
| Vascular plants | | | | | 0.276 | 0.259 | < 0.001 |
| Intercept | -1.21 | 0.234 | | | | | |
| pH | 4.00 | < 0.001 | 0.53 | 0.13 | | | |
| All species | | | | | 0.290 | 0.255 | 0.001 |
| Intercept | 2.70 | < 0.001 | | | | | |
| pH | 3.43 | 0.001 | 0.46 | 0.13 | | | |
| Longitude | -2.69 | 0.010 | -0.36 | 0.13 | | | |

Table 3. Centroids (species frequency) of bryophyte societies and their significant ($p \leq 0.05$) indicator species (marked with asterisks).

| Species | Society | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
| *Aulacomnium palustre* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.2* | 0.0 | 0.0 |
| *Brachythecium oedipodium* | 0.0 | 0.0 | 0.0 | < 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Brachythecium salebrosum* | 0.0 | 0.0 | 0.0 | < 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Calliergonella cuspidata* | 1.0* | 0.0 | < 0.1 | < 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | < 0.1 |
| *Calliergon cordifolium* | 0.3 | 1.0* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Calliergon stramineum* | 0.0 | 0.3 | 0.0 | < 0.1 | 0.0 | 1.0* | 0.2 | 0.2 | < 0.1 |
| *Calypogia muelleriana* | 0.0 | 0.1* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Campylium polygamum* | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Dicranum polysetum* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 |
| *Plagiomnium elatum* | 0.0 | 0.0 | 0.0 | < 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Pleurozium schreberi* | 0.0 | 0.0 | 0.0 | < 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Polytrichum strictum* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.1 | 0.0 | 0.0 |
| *Sphagnum angustifolium* | 0.0 | 0.0 | < 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 1.0* | 0.0 |
| *Sphagnum centrale* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5* | 0.0 | 0.1 |
| *Sphagnum cuspidatum* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.4* | 0.0 | 0.2 |
| *Sphagnum fallax* | 0.0 | 0.0 | 0.3 | 0.2 | 0.3 | 0.0 | 0.0 | 0.0 | 1.0* |
| *Sphagnum flexuosum* | 0.5 | 0.5 | 0.6 | 0.7 | 1.0* | 0.9 | 1.0 | 1.0 | 0.0 |
| *Sphagnum fuscum* | 0.0 | 0.0 | 0.4* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Sphagnum magellanicum* | 0.0 | 0.0 | 0.8* | 0.1 | 0.0 | 0.1 | 0.0 | 0.0 | < 0.1 |
| *Sphagnum rubellum* | 0.0 | 0.0 | 0.3* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Sphagnum squarrosum* | 0.4 | 0.1 | 0.0 | 1.0* | 0.0 | 0.5 | 0.3 | 0.4 | < 0.1 |
| *Sphagnum subnitens* | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Warnstorfia exannulatus* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1* | 0.0 | 0.0 |

Table 4. Median values of pH and average values of other environmental variables of bryophyte societies. Notation: pH = peat-water pH; Temp = peat water temperature; L, T, M, R, N = Ellenberg indicator values of light, temperature, moisture, reaction and nutrients for synusiae microhabitats, respectively; CovF = field layer (dwarf shrubs + forbs + grasses + sedges) projective cover (%), CovM = moss layer projective cover (%); Min, Max = minimal and maximal values. Superscript letters indicate similar medians according to Duncan's (for pH values) or Ficher LSD post-hoc tests (for average values of other variables); p = significance level of Kruskal-Wallis median test for pH values, significance level of univariate ANOVA for other variables.

| Society | Statistic | Variable | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | pH | Temp | L | T | M | R | N | CovF | CovM |
| 1) *Calliergonella cuspidata* | Med/Aver | $6.1^{d}$ | $21.6^{ab}$ | $7.1^{a}$ | $4.8^{e}$ | $9.5^{c}$ | $4.7^{e}$ | $3.9^{e}$ | $86^{d}$ | $25^{a}$ |
| | Min | 4.3 | 17.5 | 6.5 | 4.1 | 9.1 | 3.5 | 2.9 | 60 | 2 |
| | Max | 6.9 | 26.5 | 7.8 | 5.6 | 10.0 | 5.9 | 4.8 | 100 | 80 |
| 2) *Calliergon cordifolium* | Med/Aver | $5.0^{c}$ | $22.6^{abc}$ | $7.4^{ab}$ | $4.4^{bcde}$ | $9.6^{c}$ | $4.5^{de}$ | $3.6^{de}$ | $78^{cd}$ | $32^{a}$ |
| | Min | 4.0 | 19.2 | 6.9 | 4.0 | 9.2 | 2.8 | 2.2 | 60 | 1 |
| | Max | 5.8 | 29.3 | 8.0 | 5.0 | 9.8 | 5.9 | 4.9 | 100 | 100 |
| 3) *Sphagnum magellanicum - S. fuscum* | Med/Aver | $3.7^{a}$ | $21.4^{ab}$ | $7.6^{bc}$ | $3.8^{a}$ | $8.8^{a}$ | $2.4^{a}$ | $1.5^{a}$ | $51^{b}$ | $91^{bc}$ |
| | Min | 3.5 | 17.7 | 7.0 | 3.2 | 8.2 | 1.3 | 1.0 | 25 | 2 |
| | Max | 6.2 | 26.1 | 8.8 | 4.5 | 10.0 | 4.3 | 2.9 | 80 | 100 |
| 4) *Sphagnum squarrosum* | Med/Aver | $4.6^{bc}$ | $22.6^{abc}$ | $7.3^{ab}$ | $4.5^{d}$ | $9.1^{b}$ | $3.9^{cd}$ | $3.0^{cd}$ | $66^{c}$ | $86^{b}$ |
| | Min | 2.7 | 17.5 | 6.2 | 3.1 | 7.4 | 1.5 | 1.0 | 30 | 1 |
| | Max | 7.3 | 26.9 | 8.6 | 5.8 | 10.0 | 6.5 | 6.9 | 100 | 100 |
| 5) *Sphagnum flexuosum* | Med/Aver | $3.9^{ab}$ | $22.8^{bc}$ | $7.4^{b}$ | $4.2^{b}$ | $9.3^{bc}$ | $3.1^{b}$ | $2.3^{b}$ | $51^{b}$ | $96^{c}$ |
| | Min | 2.9 | 18.1 | 6.2 | 3.3 | 7.6 | 1.9 | 1.0 | 20 | 20 |
| | Max | 6.4 | 30.5 | 8.6 | 4.9 | 10.0 | 5.8 | 4.8 | 98 | 100 |
| 6) *Calliergon stramineum* | Med/Aver | $4.3^{bc}$ | $21.4^{ab}$ | $7.4^{ab}$ | $4.4^{cd}$ | $9.2^{bc}$ | $3.5^{bc}$ | $2.5^{bc}$ | $71^{cd}$ | $86^{bc}$ |
| | Min | 3.8 | 18.7 | 6.9 | 4.0 | 8.8 | 2.4 | 1.4 | 40 | 1 |
| | Max | 5.6 | 25.7 | 8.1 | 5.1 | 9.5 | 5.0 | 3.4 | 100 | 100 |
| 7) *Sphagnum centrale - S. cuspidatum* | Med/Aver | $3.8^{a}$ | $24.3^{cd}$ | $7.4^{ab}$ | $3.9^{a}$ | $9.3^{bc}$ | $3.3^{bc}$ | $2.4^{b}$ | $36^{a}$ | $97^{bc}$ |
| | Min | 3.3 | 17.2 | 6.7 | 3.1 | 8.2 | 1.9 | 1.0 | 8 | 63 |
| | Max | 4.6 | 29.2 | 8.4 | 4.8 | 9.8 | 6.3 | 5.3 | 70 | 100 |
| 8) *Sphagnum angustifolium* | Med/Aver | $4.9^{c}$ | $21.0^{a}$ | $7.9^{c}$ | $4.2^{bc}$ | $9.1^{ab}$ | $3.3^{bc}$ | $2.2^{b}$ | $86^{d}$ | $96^{bc}$ |
| | Min | 4.1 | 16.6 | 7.2 | 4.1 | 9.0 | 2.4 | 1.7 | 70 | 80 |
| | Max | 5.2 | 25.0 | 8.4 | 4.6 | 9.3 | 4.1 | 3.2 | 90 | 100 |
| 9) *Sphagnum fallax* | Med/Aver | $3.6^{a}$ | $25.4^{d}$ | $7.3^{ab}$ | $4.3^{bcd}$ | $9.1^{b}$ | $3.3^{b}$ | $2.4^{b}$ | $52^{b}$ | $88^{bc}$ |
| | Min | 3.4 | 19.1 | 6.4 | 3.6 | 7.5 | 1.7 | 1.0 | 15 | 1 |
| | Max | 5.8 | 31.5 | 8.5 | 5.3 | 9.9 | 5.5 | 5.4 | 100 | 100 |
| p | | $< 0.001$ | $< 0.001$ | 0.008 | $< 0.001$ | 0.001 | $< 0.001$ | $< 0.001$ | $< 0.001$ | $< 0.001$ |

*Sphagnum cuspidatum* synusiae, while it was densest in synusiae of *Calliergonella cuspidata* and *Sphagnum angustifolium* societies. Total cover of the moss layer was comparatively low in *Calliergonella cuspidata* and *Calliergon cordifolium* synusiae; whereas the moss cover in *Sphagnum flexuosum*, *Sphagnum centrale* - *Sphagnum cuspidatum* and *Sphagnum angustifolium* synusiae was almost 100 % (Table 4).

### *Field layer synusiae and societies*

The field layer of quagmires proved to be more diverse than the moss layer, comprising 14 societies. All of these had different species content according to the MRPP test and significant indicator species (Table 5). On this basis the vascular plant societies were:

1) *Carex rostrata* - *Potentilla palustris*,
2) *Carex lasiocarpa* - *Typha latifolia*,
3) *Carex canescens* - *Menyanthes trifoliata*,
4) *Chamaedaphne calyculata* - *Lysimachia vulgaris*,
5) *Eriophorum angustifolium* - *Oxycoccus palustris*,
6) *Menyanthes trifoliata* - *Thelypteris palustris*,
7) *Lycopus europaeus* - *Peucedanum palustre*,
8) *Phragmites australis* - *Carex vesicaria*,
9) *Calla palustris* - *Carex rostrata*,
10) *Agrostis canina* - *Lysimachia thyrsiflora*,
11) *Carex nigra* - *Molinia caerulea*,

Table 5. Centroids (species frequency) of vascular plant societies and their significant ($p \leq 0.05$) indicator species (marked with asterisks).

| Species | Society | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 |
| *Andromeda polifolia* | 0.3* | 0.0 | 0.0 | 0.0 | 0.0 | <0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.3 | 0.0 | 0.2 |
| *Agrostis canina* | 0.2 | 0.0 | <0.1 | 0.5 | 0.0 | 0.3 | 0.2 | 0.0 | 0.0 | 0.7* | 0.0 | <0.1 | 0.2 | 0.0 |
| *Agrostis stolonifera* | 0.0 | 0.2* | 0.0 | 0.0 | 0.0 | 0.0 | <0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Alisma plantago-aquatica* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | <0.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Bidens cernua* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | <0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Calamagrostis neglecta* | 0.1 | 0.2 | 0.0 | 0.2 | 0.0 | 0.3* | 0.2 | 0.0 | 0.1 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Calamagrostis purpurea* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | <0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Calla palustris* | <0.1 | 0.1 | 0.5 | 0.1 | 0.0 | 0.2 | 0.7 | 0.6 | 1.0* | 0.7 | 0.1 | <0.1 | 0.3 | 0.0 |
| *Calluna vulgaris* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1* |
| *Cardamine pratensis* subsp. *paludosa* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | <0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Carex acuta* | 0.1 | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Carex acutiformis* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | <0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Carex canescens* | 0.0 | 0.1 | 0.4* | 0.2 | 0.0 | <0.1 | 0.1 | 0.0 | 0.0 | 0.2 | 0.1 | <0.1 | 0.0 | 0.0 |
| *Carex disticha* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Carex diandra* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.3* | <0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Carex dioica* | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Carex echinata* | 0.0 | 0.0 | <0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | <0.1 | 0.0 | 0.0 |
| *Carex elata* | 0.1 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Carex flava* | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Carex lasiocarpa* | 0.4 | 1.0* | 0.7 | 0.2 | 0.1 | 0.3 | 0.4 | 0.2 | 0.6 | 0.8 | 0.0 | 0.2 | 0.2 | 0.0 |
| *Carex limosa* | 0.0 | 0.2 | 0.4 | 0.4 | 0.3 | 0.2 | 0.2 | 0.0 | <0.1 | 0.0 | 0.0 | 0.4* | <0.1 | <0.1 |
| *Carex nigra* | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.8* | <0.1 | 0.0 | 0.0 |
| *Carex rostrata* | 1.0* | 0.2 | 0.6 | 0.4 | 0.0 | 0.2 | 0.5 | 0.2 | 0.8 | 0.6 | 0.4 | 0.4 | 1.0 | <0.1 |
| *Carex vesicaria* | <0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.6* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Chamaedaphne calyculata* | 0.0 | 0.3 | 0.1 | 0.6* | 0.2 | <0.1 | <0.1 | 0.0 | 0.0 | 0.2 | 0.0 | 0.1 | 0.3 | 0.6 |
| *Cicuta virosa* | 0.0 | 0.1 | 0.3* | 0.0 | 0.0 | 0.0 | 0.3 | 0.0 | 0.1 | 0.0 | 0.0 | <0.1 | 0.0 | 0.0 |

| Species | Society | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 |
| *Dactylorhiza incarnata* | 0.2* | 0.0 | 0.0 | 0.0 | 0.0 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Drosera anglica* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | < 0.1 | 0.0 | 0.0 |
| *Drosera rotundifolia* | 0.1 | 0.1 | 0.1 | 0.2 | < 0.1 | 0.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.0* | 0.4 | 0.6 |
| *Dryopteris cristata* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | < 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Eleocharis mamillata* | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Empetrum nigrum* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.2* |
| *Equisetum fluviatile* | 0.4 | 0.0 | < 0.1 | 0.1 | 0.4 | 0.2 | 0.1 | 0.4 | 0.0 | 0.2 | 0.0 | 0.0 | 0.2 | 0.0 |
| *Epilobium palustre* | 0.0 | 0.1 | 0.1 | 0.0 | 0.0 | 0.0 | 0.2 | 0.0 | < 0.1 | 0.0 | 0.0 | < 0.1 | 0.0 | 0.0 |
| *Eriophorum angustifolium* | 0.1 | 0.3 | 0.1 | 0.0 | 0.6* | < 0.1 | < 0.1 | 0.0 | < 0.1 | 0.0 | 0.4 | 0.1 | 0.1 | < 0.1 |
| *Eriophorum vaginatum* | 0.0 | 0.0 | 0.0 | 0.5 | 0.1 | 0.0 | 0.0 | <0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.9* |
| *Filipendula ulmaria* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | < 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Galium palustre* | 0.3 | 0.3 | < 0.1 | 0.0 | 0.0 | 0.3 | 0.6* | 0.0 | 0.0 | < 0.1 | 0.0 | < 0.1 | 0.0 | 0.0 |
| *Galium trifidum* | 0.0 | 0.0 | < 0.1 | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.3* | 0.0 | 0.0 | 0.0 | 0.0 |
| *Hydrocharis morsus-ranae* | 0.0 | 0.0 | < 0.1 | 0.0 | 0.0 | 0.0 | < 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Iris pseudacorus* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Juncus effusus* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Juncus filiformis* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.6* | 0.0 | 0.0 | 0.0 |
| *Ledum palustre* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | < 0.1 |
| *Lemna minor* | 0.2* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | < 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Luzula pilosa* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | < 0.1 | 0.0 |
| *Lycopus europaeus* | 0.2 | 0.1 | 0.0 | 0.0 | 0.0 | 0.3 | 0.8* | 0.0 | 0.1 | 0.0 | 0.0 | <0.1 | 0.0 | 0.0 |
| *Lysimachia thyrsiflora* | 0.0 | 0.1 | 0.5 | 0.0 | 0.0 | < 0.1 | < 0.1 | 0.0 | 0.2 | 0.7* | 0.2 | 0.0 | 0.1 | 0.0 |
| *Lysimachia vulgaris* | 0.1 | 0.0 | 0.4 | 0.7* | 0.0 | 0.5 | 0.2 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | <0.1 | 0.0 |
| *Lythrum salicaria* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | < 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Malaxis monophyllos* | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Melampyrum pratense* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | < 0.1 | 0.0 | 0.0 | 0.0 | 0.3* | < 0.1 |
| *Menyanthes trifoliata* | 0.7 | 0.6 | 0.8 | 0.2 | 0.1 | 1.0* | < 0.1 | 0.0 | < 0.1 | < 0.1 | 0.1 | 0.3 | 0.3 | 0.0 |
| *Molinia caerulea* | 0.0 | 0.0 | 0.0 | 0.4 | 0.0 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | 1.0* | 0.0 | 0.0 | 0.0 |

| Species | Society | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 |
| *Myosotis scorpioides* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.2* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Nymphaea alba* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.3* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Nuphar lutea* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | < 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Oxycoccus palustris* | 0.2 | 0.8 | 0.8 | 0.8 | 0.7 | 0.5 | 0.1 | 0.0 | 0.4 | 0.0 | 0.0 | 1.0 | 1.0 | 1.0* |
| *Parnassia palustris* | 0.0 | 0.0 | 0.0 | 0.2* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Peucedanum palustre* | 0.0 | 0.7 | 0.2 | 0.7 | 0.1 | 0.3 | 0.8* | < 0.1 | 0.2 | 0.6 | 0.1 | 0.2 | 0.4 | 0.0 |
| *Phragmites australis* | 0.0 | 0.0 | 0.2 | 0.0 | 0.0 | 0.0 | 0.4 | 0.9* | 0.0 | 0.0 | 0.0 | < 0.1 | 0.0 | 0.0 |
| *Potamogeton natans* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.2 | 0.3* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Potentilla erecta* | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Potentilla palustris* | 1.0* | 1.0 | 0.6 | 0.6 | 0.4 | 0.8 | 0.8 | 0.7 | 0.4 | 0.6 | 0.0 | 0.3 | 0.0 | 0.0 |
| *Ranunculus lingua* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | < 0.1 | 0.0 | < 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Rhynchospora alba* | 0.1 | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.4* | 0.0 | 0.0 |
| *Rumex aquaticus* | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | < 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Scheuchzeria palustris* | 0.2 | 0.0 | 0.4 | 0.2 | 0.1 | 0.3 | < 0.1 | 0.0 | < 0.1 | 0.0 | 0.0 | 0.7 | 1.0* | 0.6 |
| *Scutellaria galericulata* | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | < 0.1 | 0.6* | 0.0 | 0.0 | 0.4 | 0.0 | < 0.1 | 0.0 | 0.0 |
| *Scirpus sylvaticus* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | < 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Stellaria palustris* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.4 | 0.0 | 0.0 | 0.5* | 0.0 | 0.0 | 0.0 | 0.0 |
| *Succisa pratensis* | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Trientalis europaea* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | < 0.1 | 0.0 |
| *Trichophorum alpinum* | 0.0 | 0.0 | 0.0 | 0.2* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Thelypteris palustris* | 0.1 | 0.8 | 0.0 | 0.0 | 0.0 | 0.9* | 0.2 | 0.0 | < 0.1 | < 0.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Typha latifolia* | 0.0 | 0.7* | 0.0 | 0.2 | 0.0 | 0.1 | 0.4 | 0.0 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Utricularia minor* | 0.3* | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.2 | < 0.1 | < 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Vaccinium myrtillus* | 0.0 | 0.0 | 0.0 | < 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | < 0.1 |
| *Vaccinium vitis-idaea* | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | < 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Veronica scutellata* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | < 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Viola palustris* | 0.0 | 0.0 | 0.1 | 0.1 | 0.0 | 0.8* | < 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | < 0.1 | 0.2 | 0.0 |

12) *Drosera rotundifolia - Rhynchospora alba*,
13) *Carex rostrata - Scheuchzeria palustris*,
14) *Oxycoccus palustris - Eriophorum vaginatum*.

We recorded the *Molinia caerulea - Carex nigra* and *Oxycoccus palustris - Eriophorum vaginatum* synusiae (Societies 11 and 14) in microhabitats with the lowest peat-water pH, and the *Carex rostrata - Potentilla palustris, Lycopus europaeus - Peucedanum palustre* and *Phragmites australis - Carex vesicaria* synusiae (Societies 1, 7 and 8) in microhabitats with the highest peat-water pH. According to the ecological indicator values, microhabitat pH (reaction) and nutrient content were lowest in the *Drosera rotundifolia - Rhynchospora alba* and *Oxycoccus palustris - Eriophorum vaginatum* synusiae (Societies 12 and 14) and highest in the *Lycopus europaeus - Peucedanum palustre* and *Phragmites australis - Carex vesicaria* synusiae (Societies 7 and 8) (Table 6).

*Community types*

Cluster analysis of merged shrub, field and moss layer data, averaged at the community level, resulted in eight significantly (MRPP test) distinct community types (Table 7):

1) *Phragmites australis - Potamogeton natans - Calliergonella cuspidata*,
2) *Lysimachia vulgaris - Thelypteris palustris - Sphagnum squarrosum*,
3) *Lycopus europaeus - Lysimachia thyrsiflora - Calliergon stramineum*,
4) *Carex acutiformis - Carex flava - Sphagnum rubellum*,
5) *Carex rostrata - Scheuchzeria palustris - Sphagnum flexuosum*,
6) *Carex rostrata - Carex canescens - Sphagnum fallax*,
7) *Drosera rotundifolia - Oxycoccus palustris - Sphagnum centrale*,
8) *Chamaedaphne calyculata - Eriophorum vaginatum - Sphagnum magellanicum.*

In Table 8 we can follow the decrease of peat-water pH through this sequence of community types from the first, *Phragmites australis - Potamogeton natans - Calliergonella cuspidata* to the last, i.e. *Drosera rotundifolia - Oxycoccus palustris - Sphagnum centrale* and *Chamaedaphne calyculata - Eriophorum vaginatum - Sphagnum magellanicum*. The indicator values for habitat reaction and nutrient content were well correlated with the measured peat-water pH. Total cover of the moss layer, where the main components were *Sphagnum* species, was highest in more acidic habitats; while the field layer was more abundant in habitats where the reaction values and peat-water pH were highest. In general, the average number of species increased with water pH.

Ordination illustrated an obvious gradient in the analysed data associated with increase in peat-water pH, which had a negative effect on the abundance of *Sphagnum* mosses ($r_{\mathrm{Spearman}} = -0.75$; $p < 0.05$) and a positive effect on field layer cover ($r_{\mathrm{Spearman}} = 0.67$; $p < 0.05$; Figure 2). It also demonstrated an apparent syntaxonomic continuum (Paal 1987) between several community types; only Types 8, 7 and 4, i.e. *Chamaedaphne calyculata - Eriophorum vaginatum - Sphagnum magellanicum, Drosera rotundifolia - Oxycoccus palustris - Sphagnum centrale* and *Carex acutiformis - Carex flava - Sphagnum rubellum* were distinctly separated from communities of other types.

Variation was largest in *Lycopus europaeus - Lysimachia thyrsiflora - Calliergon stramineum* (Type 3; Figure 2) communities which included numerous different synusiae of both bryophytes and vascular plants (Tables 9 and 10). Minimal variance was characteristic for the *Phragmites australis - Potamogeton natans - Calliergonella cuspidata* (Type 1), *Lysimachia vulgaris - Thelypteris palustris - Sphagnum squarrosum* (Type 2) and *Carex acutiformis - Carex flava - Sphagnum rubellum* (Type 4) communities (even though the first embraces synusiae of five bryophyte and seven vascular plant societies; Tables 9 and 10).

Cross-tabulation of the community types and bryophyte societies enables an overview, according to which the moss layer was typologically most homogeneous in the *Carex acutiformis - Carex flava - Sphagnum rubellum* and *Drosera rotundifolia - Oxycoccus palustris - Spahgnum centrale* (Types 4 and 7) communities, where only three bryophyte societies were represented (Table 9). The moss layer was most variable in the *Lysimachia vulgaris - Thelypteris palustris - Sphagnum squarrosum* and *Carex rostrata - Scheuchzeria palustris - Sphagnum flexuosum* (Types 2 and 5) communities, both of which included bryophyte synusiae of six societies. At the same time, synusiae of the *Calliergonella cuspidata*, *Sphagnum magellanicum - Sphagnum fuscum, Sphagnum centrale - Sphagnum cuspidatum, Sphagnum angustifolium* and *Sphagnum fallax* societies (Societies 1, 3, 7, 8 and 9) were components of three types of communities, while the *Sphagnum squarrosum* and *Sphagnum flexuosum* synusiae (Societies 4 and 5) were represented in communities of six and seven types, respectively.

Considering the societies of vascular plants, *Drosera rotundifolia - Oxycoccus palustris - Sphagnum centrale* (Type 7) communities were rather homogeneous, comprising only synusiae of three societies, whereas *Lycopus europaeus -*

Table 6. Median values of peat-water pH and average values of other environmental variables of vascular plant societies. Notation: WET = lake water exchange type, AVT = adjacent vegetation type; other notations as in Table 4.

| Society | Statistics | Variables | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | WET | AVT | pH | Temp | L | T | M | R | N | CovF | CovM |
| 1) *Carex rostrata - Potentilla palustris* | Med/Aver | 1 | 1 | $5.8^{g}$ | 21.6 | $7.7^{ef}$ | $4.3^{cde}$ | $9.3^{def}$ | $3.8^{d}$ | $2.7^{ef}$ | $66^{bcd}$ | $65^{bc}$ |
| | Min | | | 3.9 | 17.7 | 6.7 | 4.0 | 8.5 | 3.1 | 1.9 | 30 | 2 |
| | Max | | | 6.9 | 27.7 | 8.6 | 5.6 | 10.0 | 4.7 | 4.6 | 90 | 100 |
| 2) *Carex lasiocarpa - Typha latifolia* | Med/Aver | 2 | 2 | $4.6^{ef}$ | 23.4 | $7.8^{f}$ | $4.5^{def}$ | $9.1^{bcd}$ | $3.9^{d}$ | $2.7^{def}$ | $87^{e}$ | $86^{def}$ |
| | Min | | | 3.7 | 17.5 | 6.9 | 4.1 | 9.0 | 3.1 | 2.0 | 60 | 40 |
| | Max | | | 5.7 | 26.9 | 8.4 | 5.1 | 9.2 | 4.6 | 3.8 | 95 | 100 |
| 3) *Carex canescens - Menyanthes trifoliata* | Med/Aver | 1 | 1 | $4.1^{cde}$ | 24.3 | $7.6^{def}$ | $4.2^{bc}$ | $9.5^{ef}$ | $3.8^{d}$ | $2.8^{ef}$ | $65^{bc}$ | $79^{cde}$ |
| | Min | | | 3.5 | 20.4 | 6.9 | 4.0 | 9.0 | 3.1 | 1.9 | 40 | 0 |
| | Max | | | 5.8 | 29.2 | 8.6 | 4.5 | 9.8 | 4.8 | 4.3 | 100 | 100 |
| 4) *Chamaedaphne calyculata - Lysimachia vulgaris* | Med/Aver | 1 | 1 | $3.8^{cde}$ | 24.0 | $7.4^{abcdef}$ | $4.1^{bc}$ | $9.0^{bc}$ | $3.0^{c}$ | $2.2^{bcd}$ | $62^{bc}$ | $99^{efg}$ |
| | Min | | | 3.5 | 18.1 | 6.6 | 3.6 | 7.6 | 2.2 | 1.5 | 30 | 90 |
| | Max | | | 6.4 | 26.8 | 8.4 | 4.8 | 9.7 | 4.4 | 3.4 | 90 | 100 |
| 5) *Eriophorum angustifolium - Oxycoccus palustris* | Med/Aver | 2 | 2 | $4.8^{def}$ | 22.6 | $7.4^{abcdef}$ | $4.0^{b}$ | $9.2^{cde}$ | $2.8^{bc}$ | $1.9^{bc}$ | $67^{bcd}$ | $97^{efg}$ |
| | Min | | | 3.5 | 19.2 | 7.0 | 3.1 | 9.0 | 1.9 | 1.0 | 5 | 80 |
| | Max | | | 5.3 | 27.1 | 8.0 | 5.0 | 10.0 | 5.0 | 5.0 | 95 | 100 |
| 6) *Menyanthes trifoliata - Thelypteris palustris* | Med/Aver | 2 | 1 | $4.9^{fg}$ | 21.8 | $7.1^{a}$ | $4.6^{fg}$ | $9.3^{de}$ | $4.0^{d}$ | $3.1^{f}$ | $81^{de}$ | $84^{cdef}$ |
| | Min | | | 3.8 | 18.7 | 6.2 | 4.1 | 8.9 | 2.8 | 2.0 | 40 | 20 |
| | Max | | | 6.5 | 26.5 | 8.0 | 5.5 | 9.7 | 5.1 | 4.6 | 100 | 100 |
| 7) *Lycopus europaeus - Peucedanum palustre* | Med/Aver | 1 | 1 | $5.2^{fg}$ | 23.4 | $7.3^{abcd}$ | $4.8^{g}$ | $9.4^{ef}$ | $5.1^{e}$ | $4.2^{g}$ | $82^{e}$ | $24^{a}$ |
| | Min | | | 4.3 | 19.2 | 6.5 | 4.1 | 9.0 | 4.0 | 2.3 | 30 | 0 |
| | Max | | | 6.2 | 30.8 | 8.8 | 5.8 | 10.0 | 6.5 | 6.9 | 100 | 100 |

| Society | Statistics | Variables | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | WET | AVT | pH | Temp | L | T | M | R | N | CovF | CovM |
| 8) *Phragmites australis - Carex vesicaria* | Med/Aver | 1 | 1 | $5.1^{g}$ | 22.2 | $7.4^{abcde}$ | $4.7^{fg}$ | $9.4^{def}$ | $5.5^{e}$ | $4.4^{g}$ | $62^{bc}$ | $46^{b}$ |
| | Min | | | 4.3 | 19.2 | 6.9 | 4.1 | 9.1 | 4.0 | 2.3 | 25 | 0 |
| | Max | | | 6.5 | 24.1 | 8.6 | 5.1 | 9.8 | 6.5 | 5.5 | 90 | 100 |
| 9) *Calla palustris - Carex rostrata* | Med/Aver | 1 | 1 | $3.9^{cde}$ | 22.0 | $7.5^{cdef}$ | $4.4^{cde}$ | $9.6^{f}$ | $4.2^{d}$ | $3.2^{f}$ | $61^{b}$ | $88^{defg}$ |
| | Min | | | 3.4 | 17.2 | 6.2 | 4.0 | 9.1 | 3.4 | 1.9 | 20 | 0 |
| | Max | | | 6.4 | 31.5 | 8.4 | 4.9 | 10.0 | 5.8 | 4.8 | 100 | 100 |
| 10) *Agrostis canina - Lysimachia thyrsiflora* | Med/Aver | 3 | 2 | $4.9^{ef}$ | 21.9 | $7.6^{def}$ | $4.5^{ef}$ | $9.3^{def}$ | $4.2^{d}$ | $3.1^{f}$ | $77^{cde}$ | $73^{cd}$ |
| | Min | | | 3.6 | 16.6 | 6.4 | 4.1 | 9.0 | 3.7 | 2.2 | 40 | 0 |
| | Max | | | 5.4 | 30.9 | 8.5 | 5.3 | 9.8 | 5.5 | 4.4 | 90 | 100 |
| 11) *Carex nigra - Molinia caerulea* | Med/Aver | 2 | 2 | $3.7^{a}$ | 24.4 | $7.1^{abc}$ | $4.6^{efg}$ | $8.2^{a}$ | $3.9^{d}$ | $2.7^{def}$ | $52^{ab}$ | $100^{efg}$ |
| | Min | | | 2.7 | 22.2 | 6.4 | 4.1 | 7.4 | 3.5 | 2.3 | 30 | 98 |
| | Max | | | 3.9 | 26.4 | 7.8 | 5.2 | 9.4 | 4.8 | 3.1 | 70 | 100 |
| 12) *Drosera rotundifolia - Rhynchospora alba* | Med/Aver | 1 | 1 | $4.0^{bcd}$ | 24.1 | $7.7^{f}$ | $4.2^{bcd}$ | $9.3^{de}$ | $2.6^{b}$ | $1.8^{b}$ | $45^{a}$ | $97^{fg}$ |
| | Min | | | 3.4 | 19.8 | 7.0 | 4.0 | 8.8 | 1.3 | 1.1 | 15 | 20 |
| | Max | | | 7.3 | 29.3 | 8.8 | 4.9 | 10.0 | 3.8 | 2.9 | 80 | 100 |
| 13) *Carex rostrata - Scheuchzeria palustris* | Med/Aver | 1 | 1 | $3.9^{abc}$ | 22.0 | $7.4^{bcef}$ | $4.2^{bcd}$ | $9.3^{def}$ | $3.0^{c}$ | $2.4^{cdef}$ | $47^{a}$ | $100^{fg}$ |
| | Min | | | 3.4 | 18.5 | 6.7 | 4.0 | 8.3 | 2.4 | 1.6 | 25 | 100 |
| | Max | | | 4.3 | 24.5 | 8.3 | 5.0 | 9.8 | 4.0 | 3.3 | 80 | 100 |
| 14) *Oxycoccus palustris - Eriophorum vaginatum* | Med/Aver | 1 | 1 | $3.6^{ab}$ | 23.5 | $7.2^{abd}$ | $3.6^{a}$ | $8.9^{b}$ | $2.0^{a}$ | $1.1^{a}$ | $38^{a}$ | $99^{g}$ |
| | Min | | | 2.9 | 18.2 | 6.7 | 3.1 | 8.2 | 1.6 | 1.0 | 10 | 63 |
| | Max | | | 4.8 | 30.5 | 7.7 | 4.0 | 9.5 | 2.7 | 2.0 | 70 | 100 |
| p | | | | $< 0.001$ | 0.072 | $< 0.001$ | $< 0.001$ | $< 0.001$ | $< 0.001$ | $< 0.001$ | $< 0.001$ | $< 0.001$ |

Table 7. Centroids (species frequency) of community types. Aver No = average number of species; significant ($p < 0.05$) indicator species are marked with asterisks (*).

| Species | Community type | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| Aver No shrub layer | 2 | 1 | 0 | 0 | 2 | 0 | 0 | 0 |
| *Alnus glutinosa* | 0.3 | - | - | - | - | - | - | - |
| *Alnus incana* | - | 0.2 | - | - | - | - | - | - |
| *Betula pubescens* | - | 0.4 | 0.2 | - | 0.1 | - | - | - |
| *Frangula alnus* | - | - | - | - | 0.1 | - | - | - |
| *Picea abies* | 0.3 | 0.2 | - | - | 0.1 | 0.1 | - | - |
| *Pinus sylvestris* | - | - | - | - | 0.1 | - | - | - |
| *Salix cinerea* | - | 0.2 | 0.2 | - | - | - | - | - |
| *Salix lapponum* | - | - | - | - | 0.1 | - | - | - |
| *Salix pentandra* | 0.3 | - | - | - | - | - | - | - |
| *Salix phylicifolia* | 0.3 | 0.2 | - | - | - | - | - | - |
| *Salix rosmarinifolia* | 0.3 | 0.2 | - | - | - | - | - | - |
| Field layer cover, % | 75 | 85 | 74 | 70 | 54 | 60 | 34 | 38 |
| Aver No field layer | 10 | 19 | 19 | 10 | 13 | 10 | 8 | 10 |
| *Andromeda polifolia* | - | 0.2 | 0.2 | 0.8 | 0.6 | - | - | 0.6 |
| *Agrostis canina* | - | 0.6 | 0.5 | - | 0.4 | 0.4 | 0.5 | - |
| *Agrostis stolonifera* | - | 0.2 | 0.2 | - | - | - | - | - |
| *Alisma plantago-aquatica* | - | - | - | - | - | 0.1 | - | - |
| *Bidens cernua* | - | - | 0.2 | 0.3 | - | - | - | - |
| *Calamagrostis neglecta* | 0.3 | 0.8* | 0.3 | - | 0.1 | 0.4 | - | - |
| *Calamagrostis purpurea* | - | 0.2 | - | 0.5* | - | - | - | - |
| *Calla palustris* | 1.0 | 0.8 | 1.0* | - | 0.3 | 0.8 | 0.5 | - |
| *Calluna vulgaris* | - | - | - | - | - | 0.1 | - | 0.4 |
| *Cardamine* sp. | - | - | 0.2 | 0.3 | - | - | - | - |
| *Carex acuta* | 0.3 | - | - | 0.5* | - | - | - | - |
| *Carex acutiformis* | - | - | - | 0.8* | - | 0.1 | - | - |
| *Carex canescens* | - | 0.4 | 0.7 | - | - | 0.7 | - | - |
| *Carex disticha* | - | - | 0.2 | - | - | - | - | - |
| *Carex diandra* | - | 0.4 | 0.2 | - | - | - | - | - |
| *Carex dioica* | - | - | - | - | 0.1 | - | - | - |
| *Carex echinata* | - | - | 0.2 | - | 0.1 | - | - | - |
| *Carex elata* | 0.3 | - | 0.3 | - | - | - | - | - |
| *Carex flava* | - | - | - | 0.8* | - | 0.1 | - | - |
| *Carex lasiocarpa* | 0.7 | 0.8 | 0.8 | 0.8 | 0.6 | 0.6 | - | - |
| *Carex limosa* | 0.3 | 0.4 | 0.5 | - | 0.6 | 0.3 | 0.5 | 0.4 |
| *Carex nigra* | - | - | - | - | 0.1 | 0.2 | - | - |
| *Carex rostrata* | 0.7 | 0.8 | 0.8 | - | 1.0* | 0.9 | 0.8 | 0.2 |
| *Carex vesicaria* | 0.7* | - | - | - | - | 0.1 | - | - |

| Species | Community type | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| *Chamaedaphne calyculata* | - | 0.4 | - | - | 0.6 | 0.2 | - | 1.0* |
| *Cicuta virosa* | - | 0.2 | 0.8* | - | 0.3 | - | 0.3 | - |
| *Dactyloriza incarnata* | - | 0.4 | - | - | 0.1 | - | - | - |
| *Drosera anglica* | - | - | - | - | - | - | - | 0.2 |
| *Drosera rotundifolia* | - | 0.4 | 0.5 | - | 0.9 | 0.1 | 1.0 | 1.0* |
| *Dryopteris cristata* | - | - | 0.2 | - | - | - | - | - |
| *Eleocharis mamillata* | - | 0.2 | - | - | - | - | - | - |
| *Empetrum nigrum* | - | - | - | 0.5 | - | - | - | 0.4 |
| *Equisetum fluviatile* | 0.7 | 0.6 | 0.2 | 0.3 | 0.3 | - | 0.3 | - |
| *Epilobium palustre* | - | 1.0* | 0.5 | 0.5 | 0.1 | - | - | - |
| *Eriophorum angustifolium* | 0.3 | 0.2 | 0.5 | 0.3 | 0.8 | 0.2 | 0.5 | 0.4 |
| *Eriophorum vaginatum* | 0.3 | - | - | - | - | 0.3 | 0.3 | 1.0* |
| *Filipendula ulmaria* | - | 0.2 | - | 0.5 | - | - | - | - |
| *Galium palustre* | 0.3 | 1.0* | 0.8 | 0.3 | 0.1 | 0.1 | - | - |
| *Galium trifidum* | - | - | 0.2 | - | - | - | - | - |
| *Hydrocharis morsus-ranae* | - | - | 0.2 | - | - | - | - | - |
| *Iris pseudacorus* | - | 0.2 | - | - | - | - | - | - |
| *Juncus effusus* | - | - | - | - | - | 0.1 | - | - |
| *Juncus filiformis* | - | - | - | - | - | 0.1 | - | - |
| *Ledum palustre* | - | - | - | - | - | - | - | 0.2 |
| *Lemna minor* | 0.3 | - | - | - | - | - | - | - |
| *Luzula pilosa* | - | - | - | - | - | - | 0.3 | - |
| *Lycopus europaeus* | 0.7 | 0.4 | 1.0* | 0.5 | 0.1 | 0.1 | - | - |
| *Lysimachia thyrsiflora* | - | 0.2 | 1.0* | 0.3 | 0.3 | 0.4 | 0.3 | - |
| *Lysimachia vulgaris* | 1.0 | 1.0* | 0.3 | - | 0.4 | 0.1 | - | - |
| *Lythrum salicaria* | - | 0.2 | - | - | - | - | - | - |
| *Malaxis monophyllos* | 0.3 | - | - | - | - | - | - | - |
| *Melampyrum pratense* | - | - | - | 0.8* | - | 0.1 | 0.3 | 0.2 |
| *Menyanthes trifoliata* | 0.3 | 1.0* | 0.5 | - | 1.0 | 0.3 | 0.8 | - |
| *Molinia caerulea* | - | 0.4 | - | - | 0.3 | 0.3 | - | - |
| *Myosotis scorpioides* | - | - | 0.3* | - | - | - | - | - |
| *Nymphaea alba* | 0.7* | - | - | - | - | - | - | - |
| *Nuphar lutea* | - | - | 0.2 | 0.8* | - | - | - | - |
| *Oxycoccus palustris* | 0.3 | 1.0 | 0.5 | - | 1.0 | 0.4 | 1.0 | 1.0 |
| *Parnassia palustris* | - | - | - | 0.5* | 0.1 | - | - | - |
| *Peucedanum palustre* | 0.7 | 1.0* | 1.0 | - | 0.5 | 0.9 | 0.5 | - |
| *Phragmites australis* | 0.7* | - | 0.2 | - | - | 0.1 | - | 0.2 |
| *Potamogeton natans* | 1.0* | - | - | - | - | - | - | - |
| *Potentilla erecta* | - | - | - | 0.8* | 0.1 | - | - | - |
| *Potentilla palustris* | 1.0 | 1.0* | 1.0 | - | 0.9 | 0.8 | 0.3 | - |
| *Ranunculus lingua* | - | - | 0.2 | - | - | - | - | - |
| *Rhynchospora alba* | - | - | - | - | 0.3 | - | 0.3 | 0.2 |

| Species | Community type | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| *Rumex aquaticus* | - | - | 0.2 | 0.5* | - | - | - | - |
| *Scheuchzeria palustris* | - | 0.6 | 0.7 | 0.5 | 1.0* | 0.3 | 0.8 | 0.8 |
| *Scutellaria galericulata* | 0.3 | 0.6 | 0.8* | - | - | - | 0.3 | - |
| *Scirpus sylvaticus* | - | - | 0.2 | 0.3 | - | - | - | - |
| *Stellaria palustris* | 0.3 | 0.8 | 0.7 | - | 0.1 | 0.3 | - | - |
| *Succisa pratensis* | - | - | - | - | 0.1 | - | - | - |
| *Trientalis europaea* | - | - | - | - | - | - | 0.3 | - |
| *Trichophorum alpinum* | - | - | - | - | 0.1 | - | - | - |
| *Thelypteris palustris* | - | 1.0* | 0.3 | - | 0.3 | 0.2 | - | - |
| *Typha latifolia* | 0.7 | 0.8* | 0.5 | - | 0.1 | - | - | - |
| *Utricularia minor* | 0.7* | - | 0.2 | - | - | - | - | - |
| *Vaccinium myrtillus* | - | - | - | - | - | 0.3 | - | - |
| *Vaccinium vitis-idaea* | - | - | - | - | - | 0.2 | - | - |
| *Veronica scutellata* | - | 0.2 | - | - | - | - | - | - |
| *Viola palustris* | - | 1.0* | 0.3 | - | 0.3 | - | 0.5 | - |
| Moss layer cover, % | 18.0 | 82.0 | 57.0 | 95.0 | 97.0 | 87.0 | 10- | 10- |
| Aver No moss layer | 2.0 | 3.0 | 5.0 | 6.0 | 4.0 | 3.0 | 9.0 | 3.0 |
| *Aulacomnium palustre* | - | - | - | 0.5* | - | 0.2 | - | - |
| *Brachythecium oedipodium* | - | - | 0.2 | 0.5 | 0.1 | 0.1 | 1.0* | - |
| *Brachythecium salebrosum* | - | - | 0.2 | - | 0.1 | 0.1 | 1.0* | - |
| *Calliergonella cuspidata* | 1.0* | 0.6 | - | 0.5 | - | 0.2 | - | - |
| *Calliergon cordifolium* | 0.7 | - | 0.5 | 0.8 | - | - | 1.0* | - |
| *Calliergon stramineum* | - | 0.6 | 0.7 | - | 0.6 | 0.2 | 1.0* | - |
| *Calypogia muelleriana* | - | - | 0.2 | - | - | - | - | - |
| *Campylium polygamum* | 0.7* | - | - | - | - | - | - | - |
| *Dicranum polysetum* | - | - | - | - | - | 0.1 | - | - |
| *Plagiomnium elatum* | - | 0.4* | - | - | - | - | - | - |
| *Pleurozium schreberi* | - | - | - | - | - | 0.1 | - | - |
| *Polytrichum strictum* | - | - | - | 0.5 | 0.1 | - | 0.3 | - |
| *Sphagnum angustifolium* | - | 0.2 | - | 0.5 | 0.1 | - | - | - |
| *Sphagnum centrale* | - | - | 0.3 | - | 0.1 | 0.4 | 1.0* | - |
| *Sphagnum cuspidatum* | - | - | - | 0.5 | - | - | 0.3 | 0.2 |
| *Sphagnum fallax* | - | - | 0.8 | 1.0 | 0.3 | 0.8 | 1.0 | 0.8 |
| *Sphagnum flexuosum* | 0.7 | 1.0 | 0.7 | - | 0.9 | 0.4 | 1.0 | 0.4 |
| *Sphagnum fuscum* | - | - | - | - | - | - | - | 0.4* |
| *Sphagnum magellanicum* | - | - | - | - | 0.4 | 0.1 | - | 0.8* |
| *Sphagnum rubellum* | - | - | - | 0.8* | - | - | - | 0.2 |
| *Sphagnum squarrosum* | 0.3 | 1.0* | 0.8 | - | 0.5 | 0.6 | 1.0 | - |
| *Sphagnum subnitens* | - | - | - | - | 0.1 | - | - | - |
| *Warnstorfia exannulatus* | - | - | 0.2 | - | - | - | - | - |

Table 8. Median values of pH, average values of other environmental variables and community characteristics by community type. No spp. = average number of species, other notations as in Table 4.

| Community type | Statistic | Variable | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | pH | Temp | L | T | M | R | N | CovF | CovM | No spp. |
| 1 | Med/Aver | $6.1^{e}$ | 20.8 | 7.6 | $4.5^{bc}$ | 9.6 | $5.0^{d}$ | $3.9^{d}$ | $75^{cd}$ | $18^{a}$ | $20^{bcd}$ |
| | Min | 4.6 | 18.7 | 7.0 | 4.3 | 9.4 | 4.2 | 3.1 | 69 | 2 | 10 |
| | Max | 6.2 | 23.1 | 8.1 | 5.0 | 9.9 | 6.1 | 5.2 | 87 | 41 | 29 |
| 2 | Med/Aver | $5.0^{de}$ | 22.6 | 7.4 | $4.7^{c}$ | 9.2 | $4.2^{cd}$ | $3.3^{cd}$ | $85^{d}$ | $82^{bc}$ | $27^{d}$ |
| | Min | 4.6 | 19.0 | 6.9 | 4.5 | 9.1 | 4.0 | 2.9 | 74 | 45 | 22 |
| | Max | 5.8 | 24.9 | 7.9 | 5.0 | 9.5 | 4.5 | 3.8 | 90 | 99 | 32 |
| 3 | Med/Aver | $4.8^{cd}$ | 23.9 | 7.4 | $4.6^{c}$ | 9.4 | $4.4^{cd}$ | $3.6^{cd}$ | $74^{cd}$ | $57^{b}$ | $25^{cd}$ |
| | Min | 3.8 | 20.2 | 7.0 | 4.0 | 9.2 | 3.3 | 2.2 | 52 | 0 | 16 |
| | Max | 5.4 | 28.4 | 7.8 | 5.1 | 9.7 | 5.4 | 4.9 | 90 | 100 | 30 |
| 4 | Med/Aver | $4.5^{bcd}$ | 21.0 | 7.6 | $4.1^{ab}$ | 9.2 | $2.9^{ab}$ | $1.9^{ab}$ | $70^{bcd}$ | $95^{c}$ | $18^{ab}$ |
| | Min | 3.8 | 18.9 | 7.3 | 3.8 | 9.1 | 2.4 | 1.7 | 44 | 84 | 16 |
| | Max | 4.9 | 23.5 | 8.1 | 4.3 | 9.3 | 3.8 | 2.5 | 86 | 100 | 20 |
| 5 | Med/Aver | $4.1^{bc}$ | 23.5 | 7.5 | $4.2^{ab}$ | 9.2 | $3.0^{b}$ | $2.0^{b}$ | $54^{b}$ | $97^{c}$ | $18^{b}$ |
| | Min | 4.0 | 19.8 | 7.1 | 4.0 | 8.5 | 2.3 | 1.4 | 35 | 84 | 9 |
| | Max | 6.2 | 25.6 | 7.9 | 4.6 | 9.6 | 3.7 | 2.7 | 76 | 100 | 26 |
| 6 | Med/Aver | $4.1^{abc}$ | 23.6 | 7.3 | $4.4^{bc}$ | 9.1 | $4.0^{c}$ | $2.9^{c}$ | $60^{bc}$ | $87^{c}$ | $15^{ab}$ |
| | Min | 3.4 | 18.9 | 6.6 | 3.6 | 7.5 | 2.6 | 1.5 | 43 | 42 | 7 |
| | Max | 5.3 | 30.3 | 7.7 | 4.9 | 9.7 | 4.9 | 3.9 | 80 | 100 | 25 |
| 7 | Med/Aver | $3.7^{ab}$ | 22.8 | 7.4 | $4.0^{ab}$ | 9.2 | $2.7^{ab}$ | $2.0^{ab}$ | $34^{a}$ | $100^{c}$ | $18^{bc}$ |
| | Min | 4.4 | 19.7 | 7.0 | 3.2 | 8.9 | 2.1 | 1.1 | 14 | 100 | 14 |
| | Max | 4.0 | 26.5 | 7.8 | 4.5 | 9.7 | 3.1 | 2.5 | 43 | 100 | 23 |
| 8 | Med/Aver | $3.6^{a}$ | 23.6 | 7.4 | $3.8^{a}$ | 8.9 | $2.0^{a}$ | $1.2^{a}$ | $38^{a}$ | $100^{c}$ | $11^{a}$ |
| | Min | 3.5 | 20.0 | 7.0 | 3.5 | 8.5 | 1.6 | 1.0 | 29 | 100 | 7 |
| | Max | 3.7 | 26.5 | 8.1 | 4.4 | 9.2 | 2.5 | 1.9 | 54 | 100 | 14 |
| p | | $< 0.001$ | 0.643 | 0.891 | 0.003 | 0.348 | $< 0.001$ | $< 0.001$ | $< 0.001$ | $< 0.001$ | $< 0.001$ |

*Lysimachia thyrsiflora* - *Calliergon stramineum* (Type 3) communities included synusiae of 13 societies of a total of 14 vascular plant societies (Table 10). The *Carex rostrata* - *Potentilla palustris*, *Menyanthes trifoliata* - *Thelypteris palustris*, *Lycopus europaeus* - *Peucedanum palustre* and *Phragmites australis* - *Carex vesicaria* synusiae (Societies 1, 6, 7 and 8) were confined to communities of only two types, wheras synusiae of *Carex lasiocarpa* - *Typha latifolia*, *Agrostis canina* - *Lysimachia thyrsiflora* and *Drosera rotundifolia* - *Rhynchospora alba* (Societies 2, 10 and 12) were represented in six community types, and the *Chamaedaphne calyculata* - *Lysimachia vulgaris* synusiae (Society 4) participated in communities of seven types.

Three types of communities were represented at oligotrophic Lake Saarjärv, semidystrophic Lake Palojärv and eutrophic Lake Rooni; but around dystrophic Lake Väike-Virna, semidystrophic Lake Vaskna, eutrophic Lake Räimi and acidotrophic Lake Saareküla, communities of no more than one type were recorded, all different. The *Lycopus europaea* - *Lysimachia thyrsiflora* - *Calliergon stramineum* and *Carex rostrata* - *Scheuchzeria palustris* - *Sphagnum flexuosum* (Types 3 and 5) communities had the largest ecological amplitudes as they occurred around lakes belonging to four limnological types (Table 11), whilst *Carex acutiformis* - *Carex flava* - *Sphagnum rubellum* (Type 4) communities occurred only around oligotrophic Lakes Saarjärv and Kise. Thus, it is difficult to find any regular correspondence between the limnological lake types and the numbers of different communities encountered around them.

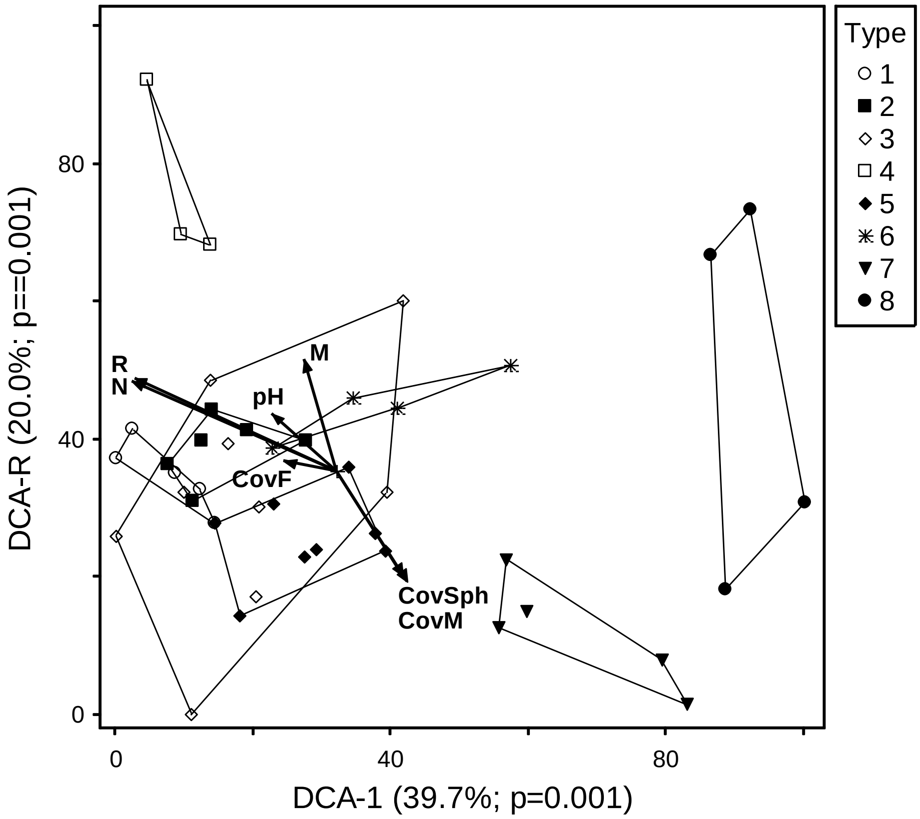

Figure 2. DCA biplot of quagmire communities and environmental variables. Notation: pH = peat-water pH; L, T, M, R, N = Ellenberg indicator values for habitat light, temperature, moisture, reaction and nutrients, respectively; CovF = field layer (dwarf shrubs + forbs + grasses + sedges) total projective cover (%); CovM = moss layer total projective cover (%); CovSph = *Sphagnum* species total cover (%); Area = lake area (ha); Y = latitude coordinates.

## DISCUSSION

The formation of quagmires by terrestrialisation can take place by several ecological pathways (Laasimer 1965, Sjörs 1983, Yelina *et al*. 1984, Joosten & Clarke 2002) and, therefore, their diversity is remarkably high (Succow & Jescke 1986, Succow 2001). Nevertheless, several authors (e.g. Moore & Bellamy 1974, Kollist 1988, Van Wirdum 1990) have argued that rather distinct vegetation zones can often be identified in quagmires around shallow lakes or pools. Starting from open water, they are dominated by (i) mainly *Phragmites australis*, (ii) small/short sedges, (iii) tall sedges and, (iv) *Eriophorum angustifolium* and/or ericoid dwarf shrubs such as *Chamaedaphne calyculata* and *Calluna vulgaris*, with *Sphagnum* species in the moss layer.

This kind of zonation was not discovered in the current study. Although reed-dominated *Phragmites australis* - *Potamogeton natans* - *Calliergon cuspidatum* communities occurred around four of the lakes, they did not always form a distinct belt but instead alternated with other communities. *Carex vesicaria* and *Carex acuta* grew locally between *Phragmites australis*; although *Carex lasiocarpa* and *Carex rostrata* were recorded in communities of most types, these tall sedges were relatively sparse and did not usually determine the community's physiognomy. From the sedge-rich communities, *Carex rostrata* - *Scheuchzeria palustris* - *Sphagnum flexuosum* was identified around seven lakes and covered comparatively large areas locally, but adjoined reed communities at only two lakes. Communities of *Carex rostrata* - *Carex canescens* - *Sphagnum fallax* (Type 6) did not occur with reed communities. A narrow belt of the *Carex acutiformis* - *Carex flava* - *Sphagnum rubellum* (Type 4) communities was present on the landward side of the reed-rich community only at oligotrophic Lake Saarjärv. Consequently, our results are more in conformity with the assertions of Sjörs (1983) and Yelina *et al*. (1984) that, despite some common trends, the successional replacement of plant communities in quagmires is predominantly multidirectional.

Table 9. Cross-tabulation of community types and bryophyte societies (number and percentage of their occurrence).

| Bryophyte society | Community type | | | | | | | | Total number |
|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | |
| 1) *Calliergonella cuspidata* | 4<br>16 % | | 1<br>3 % | 6<br>67 % | | | | | 11 |
| 2) *Calliergon cordifolium* | | 5<br>19 % | | 1<br>11 % | 1<br>3 % | | | 2<br>11 % | 9 |
| 3) *Sphagnum magellanicum* - *Sphagnum fuscum* | | | | 2<br>22 % | 3<br>9 % | | 10<br>40 % | | 15 |
| 4) *Sphagnum squarrosum* | 9<br>36 % | 8<br>31 % | 14<br>35 % | | 6<br>17 % | 4<br>20 % | | 2<br>11 % | 42 |
| 5) *Sphagnum flexuosum* | 3<br>12 % | 6<br>23 % | 4<br>10 % | | 19<br>54 % | 10<br>50 % | 3<br>11 % | 7<br>37 % | 52 |
| 6) *Calliergon stramineum* | 5<br>20 % | 3<br>10 % | | | 5<br>14 % | 1<br>5 % | | 1<br>5 % | 15 |
| 7) *Sphagnum centrale* - *Sphagnum cuspidatum* | | 2<br>8 % | 7<br>18 % | | | 5<br>25 % | | | 14 |
| 8) *Sphagnum angustifolium* | 4<br>16 % | | | | 1<br>3 % | | | 7<br>37 % | 14 |
| 9) *Sphagnum fallax* | | 2<br>8 % | 14<br>35 % | | | | 12<br>48 % | | 28 |
| Total number | 25 | 26 | 40 | 9 | 35 | 20 | 25 | 19 | 200 |

The results of this study do not confirm the assertions of several authors (e.g. Laasimer 1965, Ilomets *et al*. 1995, Ott & Kõiv 1999) that the development of quagmires depends on lake limnological type (mainly trophicity). Although *Carex rostrata* - *Scheuchzeria palustris* - *Sphagnum flexuosum* communities were discovered around four semidystrophic lakes, the adjacent communities were of different types. The same was demonstrated by the *Carex acutiformis* - *Carex flava* - *Sphagnum rubellum* communities recorded around oligotrophic Lakes Kise and Saarjärv, and by *Lysimachia vulgaris* - *Thelypteris palustris* - *Sphagnum squarrosum* communities discovered around mixotrophic Lakes Suur-Apja and Mustjärv (Table 11). Communities of *Lysimachia vulgaris* - *Thelypteris palustris* - *Sphagnum squarrosum* and *Lycopus europaeus* - *Lysimachia thyrsiflora* - *Calliergon stramineum* occurred side by side around four lakes all belonging to different limnological types. Lack of concordance between the limnological types of lakes and the types of quagmire communities developed around them may be conditioned by the fact_that the quagmires around these lakes were not at the same successional stage. Also, a stronger relationship between lake trophicity and quagmire types might have emerged if we had considered a wider geographical region and/or a larger selection of lakes.

The thickness of the peat layer in mires, including quagmires, will increase gradually over time but, so long as alkaline water can move freely underneath the floating mat, the peat layer will not become acidified. It is only when the surface water becomes disconnected from alkaline groundwater that the depletion of bases in infiltrating rainwater is no longer compensated (Van Diggelen *et al*. 1996). The alkaline water from surrounding mineral soils also turns acidic because its content of electrolytes will decrease in the course of filtering through a thicker acidic peat layer (Succow 2001). Consequently, mire succession may cause and, at the same time, be the result of decreasing supplies of mineral nutrients. The mineral soil water supplying minerotrophic mire sites becomes acidified and leached, leading to meiotrophication (Sjörs 1983, Zobel 1988).

In the current study, quagmire communities that almost lacked *Sphagnum* species were recorded only around eutrophic Lake Nauska and acidotrophic Lake Saareküla, while on the shores of seven lakes we discovered only quagmires with considerable *Sphagnum* cover (Table 11). According to the statements above, the quagmires connected with

Table 10. Cross-tabulation of community types and vascular plant societies (number and percentage of their occurrence).

| Vascular plant society | Community type | | | | | | | | Total number |
|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | |
| 1) *Carex rostrata - Potentilla palustris* | 8<br>32 % | | 2<br>4 % | | | | | | 10 |
| 2) *Carex lasiocarpa - Typha latifolia* | 3<br>12 % | 4<br>13 % | 2<br>4 % | 1<br>7 % | 6<br>15 % | 1<br>5 % | | | 17 |
| 3) *Carex canescens - Menyanthes trifoliata* | 3<br>12 % | 6<br>20 % | 3<br>7 % | | 2<br>5 % | | | 1<br>5 % | 15 |
| 4) *Chamaedaphne calyculata - Lysimachia vulgaris-* | 3<br>12 % | 4<br>13 % | 2<br>4 % | 1<br>7 % | 1<br>2 % | 2<br>10 % | | 1<br>5 % | 14 |
| 5) *Eriophorum vaginatum - Oxycoccus palustris* | | 3<br>10 % | 4<br>9 % | 1<br>7 % | | | | | 8 |
| 6) *Menyanthes trifoliata - Thelypteris palustris* | | 1<br>3 % | 7<br>16 % | | | | | | 8 |
| 7) *Lycopus europaeus - Peucedanum palustre* | | | 6<br>13 % | | 1<br>2 % | | | | 7 |
| 8) *Phragmites australis - Carex vesicaria* | | | 1<br>2 % | 5<br>33 % | | | | | 6 |
| 9) *Calla palustris - Carex rostrata* | 1<br>4 % | | 2<br>4 % | | 8<br>20 % | 3<br>15 % | 4<br>17 % | | 18 |
| 10) *Agrostis canina - Lysimachia thysrsiflora* | 6<br>24 % | 5<br>17 % | 4<br>9 % | 4<br>27 % | 6<br>15 % | | | 6<br>30 % | 31 |
| 11) *Carex nigra - Molinia caerulea* | | | | | 1<br>2 % | 7<br>35 % | 12<br>50 % | 7<br>35 % | 27 |
| 12) *Drosera rotundifolia - Rhynchospora alba* | 1<br>4 % | 2<br>7 % | 1<br>2 % | | 15<br>37 % | 1<br>5 % | | 4<br>20 % | 24 |
| 13) *Carex rostrata - Scheuchzeria palustris* | | | 5<br>11 % | | 1<br>2 % | 4<br>20 % | 8<br>33 % | | 18 |
| 14) *Oxycoccus palustris - Eriophorum vaginatum* | | 5<br>17 % | 6<br>13 % | 3<br>20 % | | 2<br>10 % | | 1<br>5 % | 17 |
| Total number | 25 | 30 | 45 | 15 | 41 | 20 | 24 | 20 | 220 |

Lakes Nauska and Saareküla are minerotrophic and represent a late stage of incipient terrestrialisation, whereas the quagmires related to the second group of lakes are mixotrophic and presumably successionally older. However, around most of these lakes, microcoenoses with and without *Sphagnum* species occurred side by side or intermixed. Therefore, we can conclude that terrestrialisation of these lakes is proceeding in mosaic-like patches according to lake water depth and bottom characteristics, groundwater supply and mobility, topography of adjacent mineral land and plant communities on these areas. Indeed, Laasimer (1965) has observed that, in the terrestrialisation of dystrophic lakes, the floating mat may initially be formed by *Sphagnum* mosses, *Carex limosa* and other bog species so that paludification will already commence with the oligotrophic phase. The examples we studied included only one dystrophic lake (Väike-Virna), where only the mixotrophic quagmire community, *Chamaedaphne calyculata* - *Eriophorum vaginatum* - *Sphagnum magellanicum* type, was recorded. The successional stage to which it belongs cannot be judged without a detailed analysis of the peat layer; the same holds for all other quagmire communities in which the vascular plant and *Sphagnum* species are typical for raised bogs.

Comparison of the results of cluster analyses carried out at both synusia and community levels

Table 11. Distribution of plant communities in quagmires around the studied lakes. Notation for limnological types as in Table 1.

| Lake | Limnological type | Community type | | | | | | | | Total number |
|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | |
| Kise | OL | | | | x | | | x | | 2 |
| Saarjärv (Misso) | OL | x | | | x | x | | | | 3 |
| Väike-Virna | DY | | | | | | | | x | 1 |
| Alasjärv | SD | x | | | | x | | | | 2 |
| Kirikumäe | SD | | | x | | | | x | | 2 |
| Palojärv (Ihamaru) | SD | | x | x | | x | | | | 3 |
| Põrste | SD | | | | | x | | x | | 2 |
| Vaskna | SD | | | | | x | | | | 1 |
| Suur-Apja | SM | | x | | | | x | | | 2 |
| Mustjärv (Orava) | SM | | x | x | | | | | | 2 |
| Punso | SM | | | | | x | | x | | 2 |
| Nauska | SE | x | | x | | | | | | 2 |
| Rooni | SE | | x | x | | x | | | | 3 |
| Räimi | SE | | | | | | x | | | 1 |
| Meelva | AT | | x | x | | | | | | 2 |
| Saareküla | AT | | | x | | | | | | 1 |
| Viroste | AT | x | | | | | | | x | 2 |
| Total number | | 4 | 5 | 7 | 2 | 7 | 2 | 4 | 2 | 33 |

enabled a detailed synopsis of the syntaxonomical structure of the quagmire communities. Our results distinctly show a relative independency of synusiae; similar moss synusiae can associate with synusiae of various vascular plant societies and *vice versa* (Van Wirdum 1990, Dierβen 1996).

So far, little attention has been paid to the typology and detailed structure of quaking mire plant communities in the boreal zone. Amongst fen vegetation types in western Estonia, Trass (1955, 1958) described six quaking mire community types: (i) *Phragmitetum communis* (= *australis*), (ii) *Caricetum limosae scorpidiosum*, (iii) *Caricetum lasiocarpae scorpidiosum*, (iv) *Caricetum inflatae* (= *rostratae*) *drepanocladiosum*, (v) *Caricetum diandrae* and (vi) *Schoenetum ferruginei scorpidiosum*. Due to calcareous bedrock and calcium-rich groundwater, the conditions for mire development in western Estonia are not comparable to those for the quagmires included in the present study, which was restricted to lakes with water hardness less than 80 mg $HCO_3$ $L^{-1}$. Only our reed-dominated *Phragmites australis* - *Potamogeton natans* - *Calliergonella cuspidata* communities are somewhat similar to the *Phragmitetum communis* in western Estonia. Quaking bogs are not amongst the transitional mires mentioned by Trass (1955, 1958).

Transitional or mixotrophic quaking bogs are also not considered in the overviews compiled by Laasimer (1965) and Masing (1975, 1988). According to Laasimer (1965), two groups of quaking mires can be distinguished. The first group includes eutrophic communities of the *Schoenus ferrugineus* - *Scorpidium scorpioides* association (peat-water pH 6–7); the other group embraces more mesotrophic quagmires of the *Carex lasiocarpa* - *Carex inflata* (= *rostrata*) association (peat-water pH 4.4–5.5) which has several variants. Laasimer (1965) pointed out that there is no fundamental difference between ‘true’ and quaking fens; peculiarities are conditioned mainly by the high water-level in quaking mires reaching or covering the peat surface and/or different electrolyte concentrations in groundwater. Masing (1975) recognised two associations of floating fen communities in limnogeneous mire sites: (i) *Schoenus* quagmire (rich floating fen) and (ii) *Carex* quagmire ~ *Carex lasiocarpa* - *C. rostrata* association (poor floating fen).

In the classification published by Paal (1997), three community types were identified in the minerotrophic quagmire site type: (i) *Scorpidio* -

*Schoenetum*, *Phragmitetum australis* and (iii) *Equisetetum fluviatilis*. The mixotrophic quagmire site type was also represented by three community types: (i) *Scorpidio* - *Caricetum lasiocarpae*, (ii) *Caricetum diandrae* and (iii) *Cariceto limosae* - *Menyanthemum*. However, more specific criteria for differentiation of minerotrophic and mixotrophic quagmires were not discussed.

A distinct and easily recognisable indicator of peat-water acidification and mire meiotrophication is the appearance and increasing abundance of *Sphagnum* species in the moss layer (Valk 1988, Botch & Smagin 1993, Succow & Stegmann 2001). Therefore, in the Estonian mire inventory of 1997–2011 (Paal *et. al*. 1998, Paal & Leibak 2011, 2013) a conditional criterion was adopted: if the total cover of *Sphagnum* species in a mire community exceeded 10 %, it was defined as mixotrophic bog. However, in the current study, instead of projective cover of every bryophyte species, only their frequency was estimated. Using additional data about the Estonian distribution and autecology of both vascular plants (Krall *et al*. 2010) and *Sphagnum* species (Vellak *et al*. 2013), as well as measured peat-water pH, we can identify the communites *Phragmites australis* - *Potamogeton natans* - *Calliergonella cuspidata*, *Lysimachia vulgaris* - *Thelypteris palustris* - *Sphagnum squarrosum*, *Lycopus europaeus* - *Lysimachia thyrsiflora* - *Calliergon stramineum*, *Carex acutiformis* - *Carex flava* - *Sphagnum rubellum*, *Carex rostrata* - *Scheuchzeria palustris* - *Sphagnum flexuosum* and *Carex rostrata* - *Carex canescens* - *Sphagnum fallax* (Communities 1–6) as types of minerotrophic quaking fen, while communities of *Drosera rotundifolia* - *Oxycoccus palustris* - *Sphagnum centrale* and *Chamaedaphne calyculata* - *Eriophorum vaginatum* - *Sphagnum magellanicum* (Communities 7 and 8) represent mixotrophic quaking bog.

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