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The biocenotic value of Slītere National Park, Latvia, with special reference to inter-dune mires

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SUMMARY

Inter-dune wetlands in Europe harbour many Red List species because they are very nutrient-poor ecosystems. Most of these wetlands are geologically very young and no or little peat formation has occurred. In Slītere National Park the numerous inter-dune wetlands are relatively old, up to 4500 years old, and most mire communities are peat forming and they are well preserved. However, the hydrological systems that have conserved the mires are largely unknown. In the present study we analysed 128 vegetation relevés of dune mires in order to assess the variation in ecological mire types. We also carried out several short-time studies to get an insight into the peat development and hydrological conditions that sustain the mires. We describe peat profiles and measured temperature profiles and electrical conductivity in 26 dune valleys. We distinguished three main vegetation units and ten sub-units, representing various stages in peat formation. Based on electrical conductivity and temperature profiles we hypothesised that the mires were sustained by both local and more regional groundwater flows, of which the latter were possibly disturbed by anthropogenic influences, mainly outside the National Park. The importance of the Park was evaluated by comparing it to species lists of wetlands from all countries bordering the Baltic Sea. On the European scale the inter-dune wetlands of Slītere National Park are very important because they represent well-developed examples of mire formation on a landscape scale, which elsewhere in most of Europe are rare or have become extinct due to intensive land use.

KEY WORDS: Baltic Sea, bog, fen, hydrology, Littorina Sea stage, Natura 2000

INTRODUCTION

Slītere National Park is situated in the north-western part of Latvia in the coastal area located between the Baltic Sea and the Gulf of Riga (Figure 1). The first form of protection was introduced to the area already in 1922 and eventually in 2000 the National Park was established, its terrestrial part covering an area of over 162 km². The natural values of the Park constitute an important element of the European system of nature protection. This seems especially true for ecosystems of accumulative coasts and their associated natural mires, occurring here in different successional stages. These values can be evaluated based upon the diversity of endangered, rare and protected species as well as the diversity, extent and naturalness of the ecosystems. In total, 55 species from the European Union's (EU's) Habitats Directive 92/43/EEC, 57 species from the Birds Directive 79/409/EEC, and 170 species from the Bern

Convention are known in the Park (Slītere National Park Management Plan 2010).

The outstanding value of intact mires (and especially of different types of fen) for supporting biodiversity are frequently stressed in the literature. However, the situation differs greatly in this respect across Europe. The best-preserved mires occur in Fennoscandia and the Baltic countries (Pakalne & Aleksāns 2017) and in mountainous regions of central Europe, while in the lowlands of western and central Europe they are disappearing with increasing speed (Wheeler *et al.* 1995, Hajkova *et al.* 2015, Kotowski *et al.* 2016, Grootjans *et al.* 2017).

Inter-dune wetlands along the Atlantic coast in NW Europe also harbour a large number of Red List species, like *Schoenus nigricans*, *Liparis loeselii*, *Dactylorhiza incarnata*, and *Epipactis palustris*, but they occur almost exclusively on mineral soils in dune slacks influenced by calcareous groundwater originating from relatively small hydrological



Figure 1. Map of the study area.

systems (Grootjans *et al.* 2017). In contrast to the Latvian inter-dune mires, where Red List species may have survived several thousands of years, the above-mentioned species in the very young dune slacks of NW Europe are pioneer species (Lammerts & Grootjans 1998) with a life span of less than 30 years (Kooijman *et al.* 2016), after which natural succession shifts the vegetation into forests. Such pioneer habitats in dune slack of the Atlantic coast are considered to be analogous to glacial habitats by Dickson (1973) and Weeda (1996). For Central Europe Hajek *et al.* (2011) confirmed that rare relict fen species in the western Carpathians were confined to ancient fens whose origin is dated back to the Late Glacial or Early Holocene. Later Hajkova *et al.* (2015) analysed mire development and occurrence of present-day Red Lists species in inter-dune mires in south-west Slovakia (Borská lowland), and their palynological research showed that Boreal fen species were found in abundance at the beginning of the interstadial period. (*ca.* 14,000–13,500 cal BP). Nowadays the dune slacks in this area are dominated by eutrophic reed beds (with *Phragmites australis* and *Glyceria maxima*). Little of the original mire forming communities has remained due to drainage, peat extraction and planting of pine trees on the surrounding dunes.

Biocenotic values of the inter-dune mires in the Slītere National Park

Inter-dune mires in the Slītere National Park are well-developed and harbour many vascular and bryophyte species that are endangered in most of NW and Central Europe (Pakalne 1994, 1995, Pakalne & Kalnina 2005, Strazdiņa *et al.* 2011). Many of them are considered very valuable and endangered in the countries of the Baltic Sea catchment (Ingelög *et al.* 1993). Because of the geographic location of the Slītere National Park area – in the coastal zone at the interface between the countries of the Central European Lowlands and Fennoscandia – it seems appropriate to relate the status of the flora to this regional context. For that reason, in this paper we consider the vascular plants and bryophytes found in the mires of the Park, according to the threat categories established for vascular plants in the countries bordering the Baltic Sea (Ingelög *et al.* 1993). The highly natural mire and forest ecosystems of the Slītere National Park offer a valuable reference for studies on the biology, dynamics and habitat requirements of these species.

The rationale to select the inter-dune mires of Slītere National Park for more detailed ecohydrological study is that it is one of the few little-disturbed mire complexes in NW and Central Europe that can serve as a reference for restoration activities throughout this region.

In the present paper we aim to: (i) present an overview of mire types and communities in the inter-dune depressions, (ii) evaluate the importance of the Slītere National Park for conserving diversity of endangered, rare and protected mire species on an international level and (iii) present a hypothesis for further hydrological research on the possible functioning of the hydrological systems that sustain the mires. For this we present and discuss measurements of electrical conductivity (EC) and temperature in peat profiles in a transect across a series of inter-dune mires.

STUDY AREA

Geological history

The Littorina Sea period represents a stage in the development of the Baltic Sea that started *ca.* 9500 years BP, and has continued to the present (Borzenkova *et al.* 2015). During that period several changes in sea and coastal land level occurred as the result of the interplay of the glacio-isostatic adjustment, climate change and morpho-dynamic coastal processes (Harff *et al.* 2017, Häusler *et al.* 2017). One of the consequences of the erosive

activity of the Littorina Sea is a high inactive sea cliff situated 2-4 km from the present sea front.

The present day landscape consists of numerous sand dune ridges, interspaced with mires. This landscape originated *ca.* 4700 years BP as a marine accumulation plane situated between the inactive cliff and the shoreline. The interdune mires started to develop between *ca.* 4,500 and 3,000 years BP (Pakalne & Kalnina 2005, Borzenkova *et al.* 2015, Kalnina 2017). In some areas, like in the present raised bog area (Bažu Mire), peat formation was so active that small dune ridges were overgrown with peat.

The dune ridges are probably decalcified over a depth of more than 20 metres. This estimation is based on findings of Stuyfzand (1993) and Sival *et al.* (1997) who calculated that the decalcification rate in NW-European dune soils would be about 1 metre per century, given an initial lime content of 1% and an infiltration flux of 0.75 mm day⁻¹.

Geologically, the area consists of unconfined Quaternary sand sediments underlain by loam and moraine clay lenses, which act as semi-confining layers for the sandstone aquifer (Virbulis *et al.* 2013, LEGMC 2018). The sandstone aquifer occurs at a

depth of about 20 m below the surface in the wetlands area and about 50 m below the surface in the cliff area (LEGMC 2018).

Wetlands in the Slītere National Park

Wetlands in the Slītere National Park comprise open-water lakes in the inter-dune depressions, ranging from recently- formed floating mats to well-developed poor and rich fens (Figure 2). Different types of swamp and bog woods occur throughout the area.

The rich flora and fauna of the park harbours 292 species red-listed in Latvia and 268 protected by law in Latvia (Slītere National Park Management Plan 2010). The Park is also very rich in bryophytes, reaching about 65% of all species found in Latvia (Āboliņa *et al.* 2016). The total number of bryophytes and liverworts is 366 species (275 mosses and 91 liverworts; Strazdiņa *et al.* 2011). Nearly 20 percent are protected under law or red-listed in Latvia, including 37 mosses and 30 liverworts. From them, *Buxbaumia viridis*, *Dicranum viride*, *Hamatocaulis vernicosus*, *Leucobryum glaucum* and *Sphagnum imbricatum* are listed in the European Union Habitats Directive. Limiting the species composition to



Figure 2. Overview of the calcareous spring fen (top left), Pēterezera lake with a sequence of rich fen to bog (top right), Kukšupe inter-dune rich fen (bottom left) and Imanta inter-dune poor fen (bottom right).

wetlands (referring to fens, bogs, swamps, and springs), the bryodiversity of Slītere National Park maintains at least 151 moss and 46 liverwort species (Strazdiņa *et al.* 2011).

The main study area consists of *ca.* 3.8 km² and is situated in the central part of the Park. It stretches from the coastal village of Saunags to the Bažu Mire expanse (Figure 3) and contains a system of inter-dune wetlands locally known as “Kukšupes” and “Imanta” inter-dune mires.

In order to the study the ecohydrological relationships of the inter-dune mires, a 1750 m long transect was set out and studied in July 2009 by the participants of the International Peatland Course in Latvia and Finland. The transect started in a bog, Bažu Mire, and crossed inter-dune mires (Kukšupes and Imanta inter-dune mires) perpendicularly to the present sea coast (Figure 3). For botanical synthesis and description of mire vegetation types additional data have been used, obtained from two other mires studied in the Park: the Pēterezera inter-dune mire and the Slītere spring mire, situated next to the ancient Littorina Sea coast near the Slītere Lighthouse (Figure 3).

Although the inter-dune mires of the National Park appear to be almost untouched, former

hydrological disturbances can still be seen. For instance, shallow drainage ditches still exist in the area with the calcareous spring mires near the Lighthouse. Some of these (forestry) drainage ditches have been dug through the dune ridges in order to transport the water directly to the sea (see Figure 7). Agricultural drainage systems occur between the old Littorina coastline and Bažu Mire, and are still in use (Elshehawi 2019).

METHODS

Vegetation of the inter-dune mires

Vegetation composition of inter-dune fens and bogs was studied in the years 2009, 2016 and 2017. The vegetation relevés were taken in each of the transect's points, following the Braun-Blanquet approach (Braun-Blanquet 1965). Additional relevés were obtained from the study of Pakalne (1994). In total 128 vegetation relevés were used for further analyses. Coverage of species was estimated using an ordinal scale (from 1 to 9).

The collected data were analysed with the software CANOCO version 4.5, using Detrended Correspondence Analysis (DCA) (Hill & Gauch

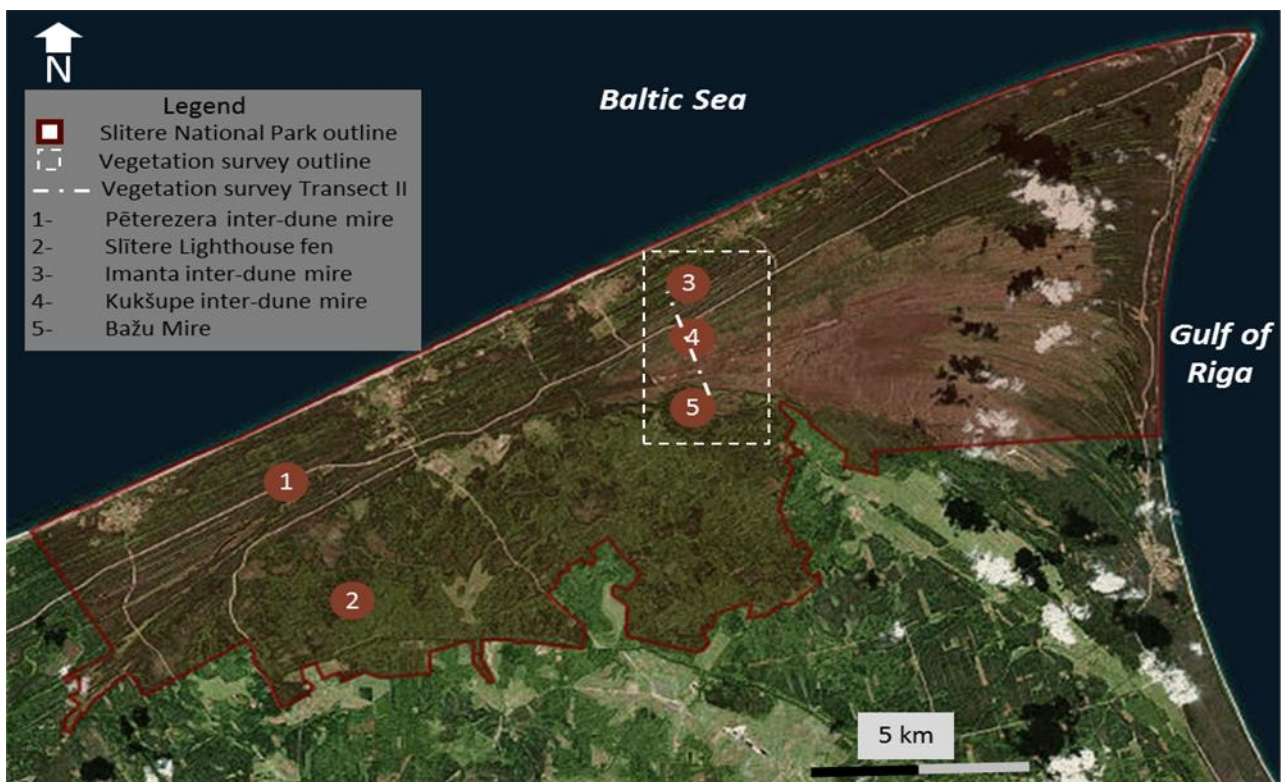


Figure 3. Distribution of mires in Slītere National Park. Study sites: 1 = Pēterezera inter-dune mire (PM); 2 = fen near Slītere Lighthouse (FEN); 3 = Imanta inter-dune mire (IM); 4 = Kukšupe inter-dune mire (KM); 5 = Bažu Mire (BM).

1980). The arch effect was removed by detrending by segments. The ordination was performed without transformation of cover values and without downweighting of rare species. Characteristic species of mire vegetation units (of the rank of classes, orders and alliances) were used to further group species. The diagnostic value of the species followed Ratyńska *et al.* (2010). For fen classification we followed the recent publication on European fens of Peterka *et al.* (2017). The nomenclature of vascular plants follows Flora Europea (Tutin *et al.* 1968–1993), that of mosses follows Hodgetts (2015).

The importance of the vascular plant species for international wetland protection was illustrated by considering the endangerment classes attributed to each species in eleven countries and regions bordering the Baltic Sea (Ingelög *et al.* 1993). For endangered and rare bryophytes, the information concerning threat categories for each country of the Baltic Sea Basin has been obtained from the publication of Hodgetts (2015).

Natura 2000 habitat types and occurrence of rare species

The classification of Natura 2000 habitats follows the Latvian manual (Auniņš 2013), while the list of wetland species of the Slītere National Park was compiled based on available data concerning vascular plants (Pakalne & Aleksāns 2017) and bryophytes (Strazdiņa *et al.* 2011) and our own observations. For comparison with other countries around the Baltic Sea a subset of mire flora, containing only vascular plants and mosses (*Bryales* and *Sphagnales*) has been used.

The floristic data from our study areas within the Park were collected by us, including the relevant earlier records by Pakalne (1994). In the current paper the evaluation of wetland habitats on the local and international scale is based upon our own research as well as on current inventories of Natura-2000 habitats in the Slītere National Park (Pakalne & Aleksāns 2017).

Peat development

In order to get an impression of the vegetation development during peat formation, 23 peat cores, collected with a Russian peat corer with a chamber length of 50 cm, were described in the field. Bog peat was recognised by the presence of dominant *Sphagnum* remnants, which could not be identified as separate species. The bog peat was often accompanied with *Eriophorum vaginatum* and *Scheuchzeria* remnants. Sedge peat was recognised by the presence of dense small root remnants, sometimes in combination with a small share of large

sedge or reed (*Phragmites australis*) roots. Gytja was recognised as completely decomposed sediment with often small shell remains.

Measurements of electrical conductivity (EC) and temperature

Temperature profiles and measurement of EC in the soil may provide information on the origin of water flows. Soil profiles directly fed by precipitation water or influenced by local hydrological systems will reflect temperature conditions relating to the most recent weather conditions (day and night regimes or hot or cold periods in recent time frames). Groundwater from regional systems has a very constant temperature, since temperatures are not influenced by daily or even annual fluctuation in temperatures (Rose 1966, Van Wirdum 1991). EC measurements directly in the peat soils measures bulk EC of the soil. In peat soils with a high content of organic matter the EC measurements indicate primarily the concentration of the total amount of dissolved solids; infiltrated precipitation water gives low values; calcareous groundwater gives relatively high values. Mineral deposits such as sand layers influence the measurements significantly, which makes it necessary to ignore measurements taken in shallow sand layers or close to the mineral border of the peat profile. EC profiles in peat deposits can indicate if the profile is influenced by infiltrating precipitation water or discharging groundwater from surrounding areas. In areas with dominant calcareous soils, this method is not very useful, because calcareous groundwater can originate from both local and regional hydrological systems.

EC and temperature profiles were measured on 17th of July 2009 in 34 sites (257 measurements of EC/Temp). The measurements were done directly in the peat every 20 cm, using a 2 m metal probe with sensors at the bottom (Van Wirdum 1991). The mean air temperature on 17th July was 24.4 °C with temperatures during the day exceeding 36 °C (weather station Kolka). The mean daily air and soil temperature during the preceding two weeks was 21.3 and 14.9 °C, respectively. The mean annual air temperature was 5.9 °C (weather station Riga).

RESULTS

Vegetation of the inter-dune mires

Numerical vegetation analysis resulted in the identification of ten main vegetation units. The main species groups represented are: fens (class *Scheuchzerio-Caricetea fuscae*) and raised bogs (class *Oxycocco-Sphagneteta*). The latter group also

includes woodland sites with a high coverage of “bog-woodland” species in the tree and shrub layers. The DCA ordination (Figure 4) shows a clear separation between extremely rich fen and rich fen vegetation along the *x*-axis. This is due to the presence of species preferring calcium-rich and mesotrophic conditions. Examples are: *Schoenus ferrugineus*, *Carex hostiana*, *Juncus subnodulosus*, *Sesleria caerulea* and *Primula farinosa*. Most of these species belong to the *Caricion davallianae* alliance. Plots representing rich fens occupy the central part of the graph. Their vegetation reflects mesotrophic fen conditions with characteristic species, such as *Carex panicea*, *Campylium stellatum*, *Juncus alpino-articulatus*, *Drepanocladus revolvens*, and *Liparis loeselii*. Small rhizomatous sedges, such as *Carex diandra*, *C. chordorrhiza*, *C. limosa* and *C. heleonastes*, as well as several brown moss species, are also present and may gain a high coverage. The relative spread of rich fen sites along the *y*-axis in Figure 4 can be attributed to the variation in their wetness and pH. The drier sites occupy the upper part of the *y*-axis. The wetter types consist of floating mats with a prevalence of sedges, such as *Carex lasiocarpa* and *C. rostrata*. In the moss layer *Sphagnum* species dominate (mainly *S. cuspidatum* and *S. flexuosum*). The right side of the *x*-axis is occupied by poor fen and bog vegetation. These plots are dominated by true bog mosses such as *Sphagnum magellanicum* and other characteristic species of the class *Oxycocco-Sphagnetea*. A group of characteristic species in the bog forest vegetation besides typical bog species consists of several ericaceous shrubs and some forest mosses. The tree layer is formed, almost exclusively, of *Pinus sylvestris* and *Betula pubescens*.

The various mire types are presented in more detail in the Appendix. The extremely rich fens can be divided in two sub types: one dominated by *Schoenus ferrugineus* (a) and the other dominated by *Juncus subnodulosus* (b). Both subtypes are almost exclusively located within the spring fen situated below the ancient sea coast, next to Slītere Lighthouse.

The inter-dune mires (including the Kukšupe and Pēterezera mires), represent rich fen vegetation (alliance *Saxifrago-Tomentypnion* Lapshina 2010). Four subgroups have been distinguished (c, d, e, f,) in which *Saxifrago-Tomentypnion* elements and the characteristic species of higher syntaxa dominate.

The mire vegetation distinguished as groups g and h displays features of transitional character between the rich and the intermediate fens. *Saxifrago-Tomentypnion* elements are still abundant, but it misses completely the floral elements of *Caricion*

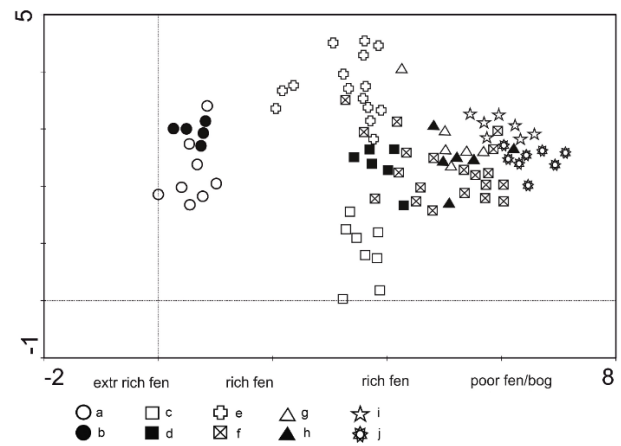


Figure 4. Results of Detrended Correspondence Analysis (DCA) of 128 relevés of mire vegetation in Slītere National Park, Latvia. Codes of species groups refer to the synoptic table (Appendix).

davallianae (= extremely rich fen). Instead, species that are most common in bogs become more pronounced (species of the *Oxycocco-Sphagnetea* class, combined with fen species of the *Scheuchzerio-Caricetea fuscae* class). According to the dominant bog-moss species, two plant communities can be distinguished: the *Sphagnum cuspidatum* community (g) and the *Sphagnum flexuosum* community (h). Two subtypes have been distinguished: a more open vegetation (i) dominated by bog mosses (mainly *Sphagnum magellanicum* and *S. flexuosum*) and ericaceous dwarf shrubs, and (ii) a subtype with much *Sphagnum fallax* (j) and with a high frequency of tree species.

Peat development in relation to hydrological conditions

Figure 5a shows the distribution of peat types in the 23 peat cores along the 1750 m long transect from south to north that crosses 22 dune valleys (Figure 3). We have only distinguished two main peat types; bog peat (yellow), sedge peat (brown) and one lake deposit: gytija (grey). Going from south to north most inter-dune mires show occurrence of sedge peat, particularly in the earliest stages of peat formation. Only in the centre of the transect is bog peat found throughout the profile. The deepest valleys also show gytija deposits in the deepest parts, indicating that lakes have been more common in the early stages of peat formation. The central part of the transect shows that sedge peat occurs throughout the depth of the peat and most valleys had a shallow water layer on the surface. Most other valleys first deposited sedge peat, sometimes with wood peat, but *Sphagnum* peat was deposited in later stages. Not all of these mires

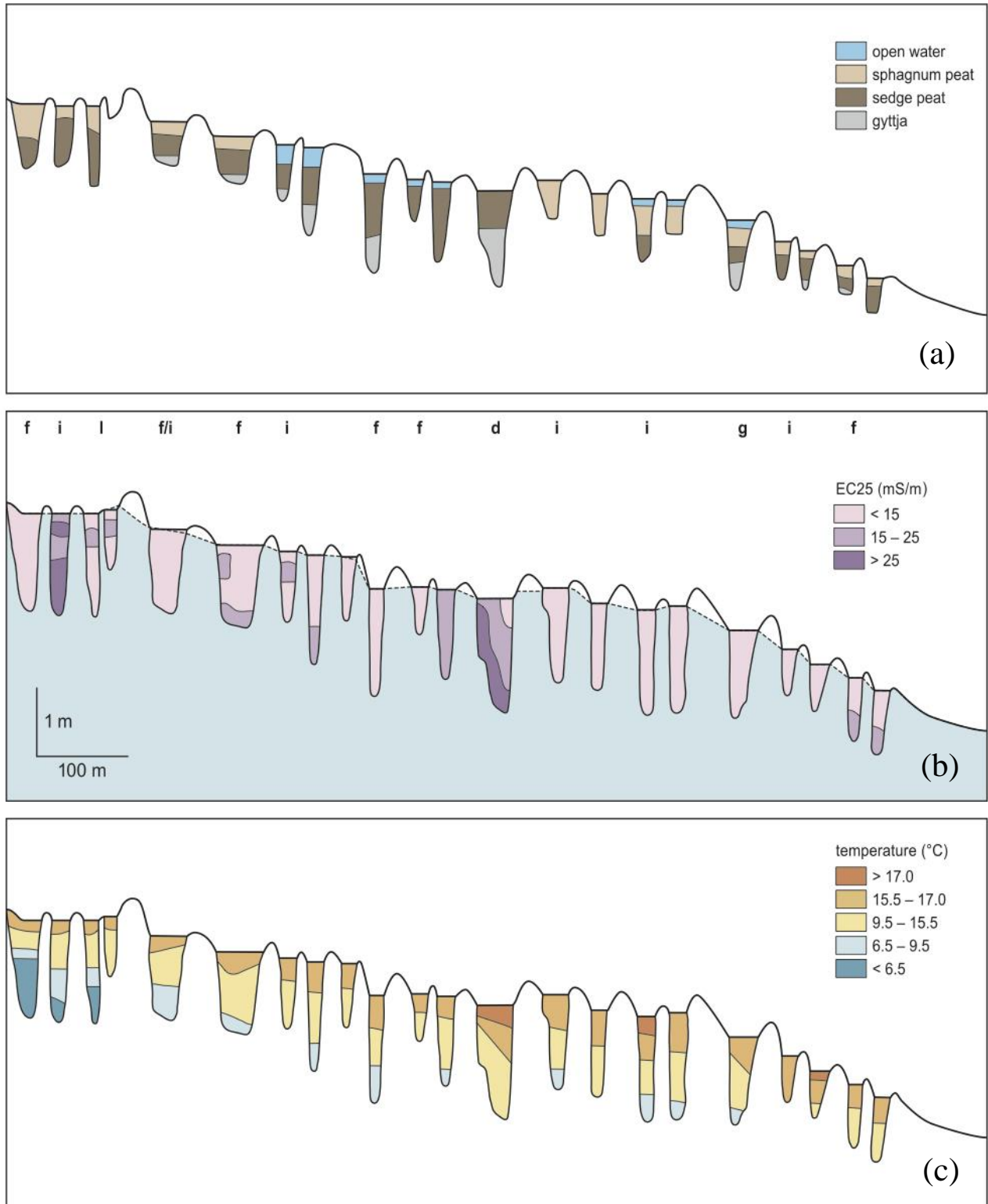


Figure 5. Showing a) peat profiles along the transect (codes at the uppermost line **(c-i)** relate to the vegetation types distinguished in the present study (Appendix), b) results of electrical conductivity measurements in all peat profiles along the transect measured in July 2009 and c) results of temperature measurements measured in July 2009.

are open bogs. Most of them now support shrub and tree vegetation with a layer of *Sphagnum* at the surface.

Electrical conductivity (EC) and temperature profiles

The EC measurements (Figure 5b) show that most valley mires have groundwater with a low electrical conductivity (< 15 mS/m). Out of the 22 valleys two have distinctly higher values (> 25 mS/m), indicating that they are influenced by relatively mineral-rich groundwater. The most central valley shows high values in deeper layers and also at the south side of the valley. The opposite side of this valley has much lower values in the upper 50-60 cm. The two valleys at the most northern end of the transect only have high values in deeper layers.

The temperature profiles show that in general the southern mires are colder in deeper layers than the central valleys and the northern ones (Figure 5c). The most southern mire has cold water (< 6.5 °C) in most of the profile, while most other valleys only have relatively cold water (6.5-8 °C) in the deepest part of the profile. The warmest water is found in the top layers of the treeless mires in the centre and to the north. The most central valley with a living sedge (fen) vegetation also shows that the south side of the valley is much colder than the north side. This is most evident in the layers of 20-100 cm below the surface.

Natura 2000 habitat types and occurrence of rare species

The GIS analysis of the land cover of the area depicted in Figure 6, shows that almost the entire landscape segment, containing the studied bog and interdune mires, has been covered by a variety of Natura 2000 protected habitats. Most of them (marked with an asterisk) are priority habitats, demanding special attention within the EU. Almost all habitat types mentioned in Figure 6 (*ca.* 90%) represent natural wetlands, wetland forests and dune forests. The forest types mentioned are considered to be local climax communities, existing now without any conscious influence of humans.

The list of wetland flora of the Slītere National Park contains 249 vascular plant species (Slītere National Park Management Plan 2010). Of these, 168 species (67.5 %) are Red List species in the countries surrounding the Baltic Sea. Out of this group we have analysed in detail the status of 195 vascular plant and bryophyte species found in the studied mires.

Their conservational status (presented in column “LAT” of Table 1) is compared with the status of the same group of species in the countries and regions constituting the Baltic Sea catchment. There is a clear

difference in the percentage of endangered species. The lowest number of endangered mire species is found in Fennoscandia and in the Baltic republics, an intermediate number in countries of central and eastern Europe, and the highest number in the two German Federal States. A similar pattern is visible when the numbers of extinct species are compared. The numbers presented in the “not occurring” line are a reflection of the floristic dissimilarity between the Latvian mire floras and those of the other regions.

DISCUSSION

Mires in the Slītere National Park

Mire communities and ecological mire types

Based on the analysis of 128 vegetation relevés from the inter-dune wetlands in the Slītere National Park, we distinguished three main units and ten subunits (for more details see the Appendix). The main units represent only three out of 13 characteristic fen species groups distinguished in Europe by Peterka *et al.* (2017): (i) the *Caricion davallianae* Klika 1934, (ii) the *Saxifrago-Tomentypnion* Lapshina 2010 and (iii) the *Stygio-Caricion limosae* Nordhagen 1943, which consist of so-called “dystrophic hollows communities” – *Scheuchzerion palustris* Nordhagen ex Tx. 1937, which in our study area show the highest similarity to poor fens with bog elements.

The inter-dune mires of Slītere represent the full range of European mire types, recognised originally in Fennoscandia (see discussion in Økland *et al.*, 2001) and adapted for Central Europe by Bragazza & Gerdol (1999), Hajek *et al.*, (2006) (see overview in Joosten *et al.* (2017)). The DCA shows that the main axis of variation (*x*-axis) is related to the occurrence of calciphilous species (in extremely rich fens) on the one hand and acidophilous species (in bogs) on the other hand.

Extremely rich fens only occur at the Slītere lighthouse underneath the steep Littorina Sea cliff. Rich fen vegetation occurs at various places in the inter-dune mires. The best examples are in Kukšupe Mire and in Pēterezera mire. The poor fen vegetation regularly occurs in many inter-dune mires, while Bažu Mire represents the real bogs in our study area. Apart from such well-developed near-natural mire types, many successional stages and degeneration stages can be found in the inter-dune wetlands. Most of these sub types belong to acidophilous alder and birch communities.

Such a large variation of near-natural ecological mire types concentrated in a rather small area is nowadays very rare in Europe and the preservation of

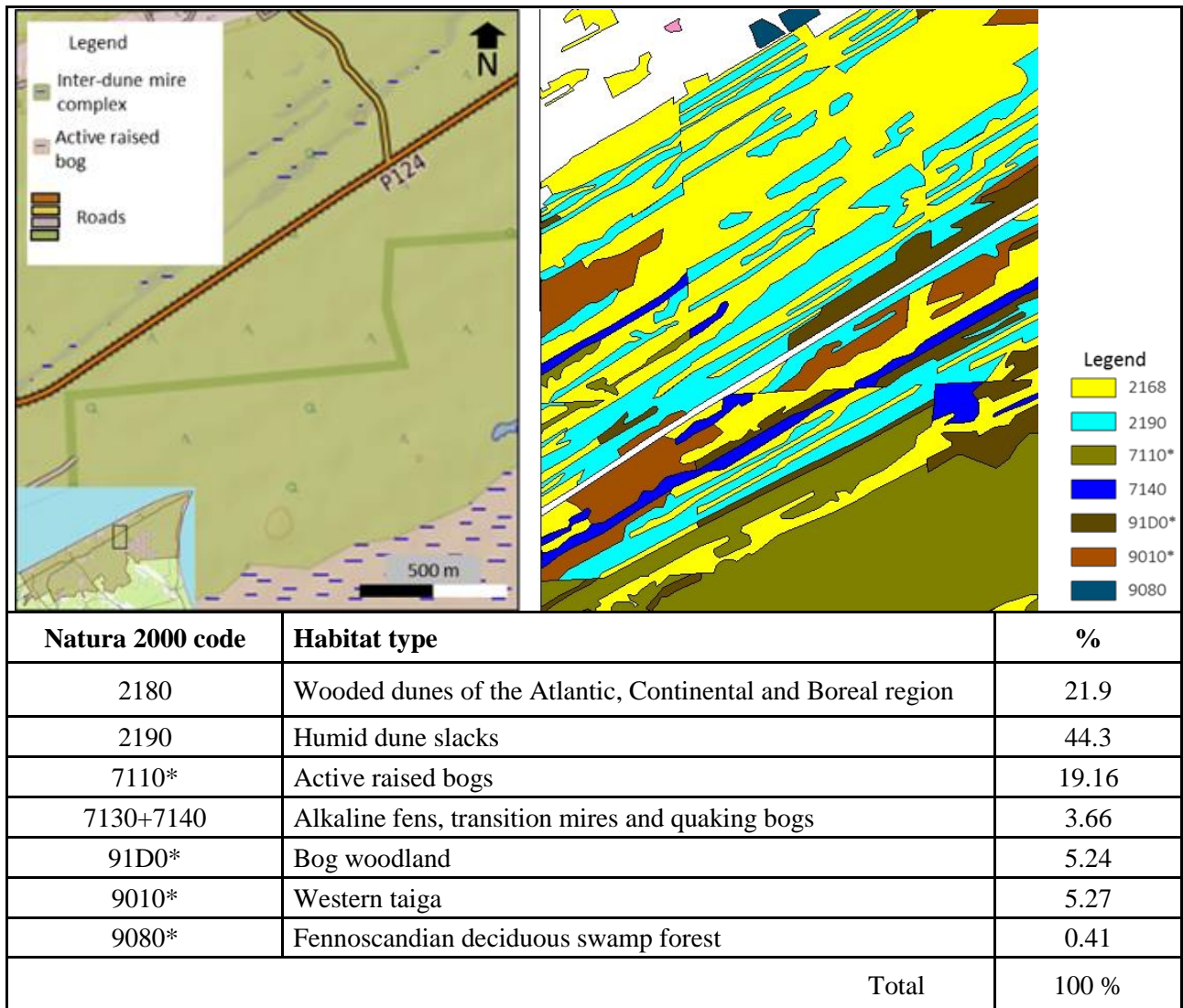


Figure 6. Occurrence of Natura 2000 habitat types and their percentage distribution in the study area.

Table 1. Vascular plant and bryophyte flora of the Slītere National Park mires in relation to their Red List status in the countries of the Baltic catchment area. Country codes: SWE – Sweden; FIN – Finland; EST – Estonia; LAT – Latvia; LIT – Lithuania; RUS – North-western Russia; POL – Poland; MEC – Mecklenburg-Vorpommern (Germany); SCH – Schleswig-Holstein (Germany); DEN – Denmark.

Country/Region	SWE	FIN	EST	LAT	LIT	RUS	POL	MEC	SCH	DEN
No of Red List species	3	12	9	23	15	26	28	87	83	21
Extinct	-	1	-	-	1	-	1	4	11	1
Red List species %	1.6	6.4	4.6	11.8	7.8	13.6	14.4	46.0	44.2	11.2
Not occurring	1	6	-	-	2	4	-	6	7	8

this complex of inter-dune mires is very important for understanding natural peat development on the landscape scale.

Peat development in the inter-dune mires

The descriptions of recognisable remnants of higher plants and/or mosses in the peat layers in the transect through the inter-dune wetlands shows that the deep valleys started as lakes, but some valleys appear to always have been groundwater fed fens or rainwater fed bogs. We found that groundwater fed fens were much more abundant in the past, but most of the mires shifted toward bogs or *Sphagnum* dominated poor fens or even to bogs. These findings are in line with detailed palynological research of Kalnina (2017), who studied the mire development of the adjoining Bažu Mire (see also Pakalne & Kalnina 2005). But further palynological research in the inter-dune mires is recommended.

Different groundwater flows?

The high variety of ecological mire types, and associated successional stages of mire development in the Slītere National Park, probably reflects the hydrological position of mires in the landscape.

Although little or no hydrological data were available in the Slītere National Park, our temperature and electrical conductivity measurements in the peat profiles point to the presence of different groundwater flows that

influence the mires. The EC-measurements indicate that in some fens mineral-rich groundwater is entering the mires and, on some occasions, even reaches the surface of the mire. Some mires appear to be isolated from these groundwater flows and are only fed by very local groundwater or precipitation water. And this is not a recent phenomenon. Some of the valleys have always been bog-like systems with dominance of *Sphagnum* species. Most of the inter-dune mires have been lakes or fens influenced by relatively base-rich groundwater and in a later stage turned to poor fens. The temperature profiles show that the most southern mires receive the coldest groundwater. Considering the fact that the measurements were done in a very warm period (July 2009) this points to rather deep groundwater flows that are hardly influenced by seasonal changes in temperature. Figure 7 shows a simple conceptual model of possible groundwater flows. Based on the measured patterns in EC and temperature in the peat profile we hypothesise that most of the groundwater that is feeding the inter-dune mires does not have a very local origin (the neighbouring dunes), but originates from the old coast area, which is now a high plateau capable of recharging large amounts of groundwater. An alternative explanation of the occurrence of mineral-rich groundwater in several mires is that the groundwater originates from more local dune systems. This groundwater may have passed through sand layers that have not yet been

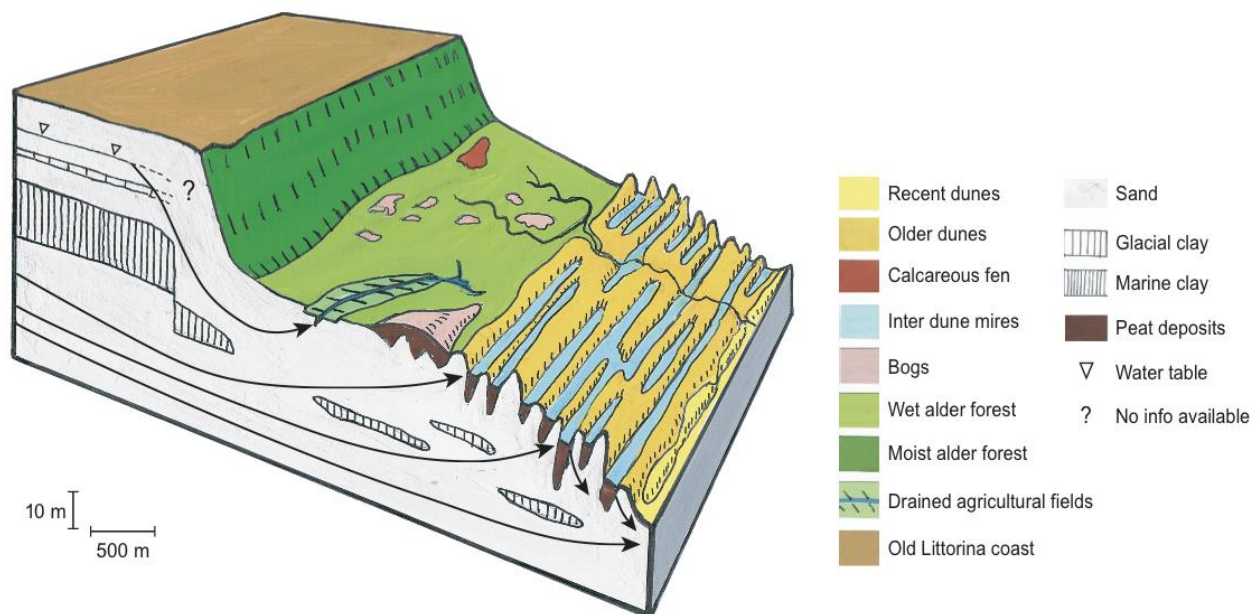


Figure 7. Conceptual model of possible groundwater flow patterns in the transects through Bažu Mire, Kukšupe and Imanta inter-dune mires.

leached at depths of more than 20 meters below the surface. More information is needed on decalcification depth in the dune areas.

The deep valley with a well-developed rich fen vegetation in the centre of the transect shows a remarkable phenomenon. Both the temperatures and the electrical conductivity on the southern side of the mire differ considerably from the northern side. The southern side appears to receive mineral-rich cold groundwater, while the opposite side has mineral-poor and warm groundwater in the upper layers. So, apparently, this mire is a flow-through mire, where groundwater discharges on one side and infiltrates again at the other side, as was described in coastal dune slacks in the Netherlands (Stuyfzand 1993, Sival *et al.* 1997), in England (Davy *et al.*, 2006) and in calcareous fens in Slovakia (Grootjans *et al.* 2006).

Future hydrological research needs

The question is now: is the landscape structure of the Slītere National Park still almost natural, as could be judged from the abundance of Natura 2000 habitat types? Or are there still disturbances that should be dealt with to prevent further deterioration of the inter-dune mires? Some hydrological disturbances in the Park are being eliminated by the current EC LIFE “Wetlands” project aimed at restoring the large bog (Bažu Mire). But we found also remnants of former forest-drainage systems north of Pēterezera mire, which are still releasing groundwater and surface water to the coast. Also, outside the boundaries of the Park we found erosive streams that drain large amounts of water. And deeply drained agricultural enclaves may also have an influence on the hydrological system that is supplying the studied inter-dune mires with groundwater. So, there is a need for hydrological monitoring and modelling of the whole area in order to assess possible hydrological impacts and to simulate past and present groundwater flow paths.

In such a hydrological model the recent influence of postglacial land uplift (Rehell & Virtanen 2015) and estimated sea level rise (Groh *et al.* 2017) should be incorporated. Postglacial land uplift may increase groundwater losses from the hydrological system because of an increase in the hydraulic gradient, while sea level rise may reduce groundwater losses. Although the effect of land uplift is probably small (2-4 mm/yr; <http://neogeo.lv/?p=15436>), it is not negligible. Even small structural changes in the hydrological system can trigger relatively strong changes in vegetation succession and this will increase the need for more restoration management and can eventually lead to loss of characteristic species of natural mires (Pakalne 1994).

Importance of Slītere National Park for Natura 2000 network

In the Slītere National Park a very high proportion of the landscape consists of protected (Natura 2000) habitat types, representing Europe’s most valuable dune forests and mires, which is an indication that the landscape structure still has a high naturalness, thus rendering its importance as a reference area on the international scale.

The number of endangered and protected species varies strongly between countries around the Baltic Sea. In Sweden, Finland, Estonia, and Lithuania, the proportions of Red List species in the total list of wetland species is relatively low – between 2–8 % – indicating that most of the wetland species are not considered threatened in those countries. In Latvia, Poland, Denmark and north-west Russia this percentage is higher (11–14%), while in Germany (Mecklenburg and Schleswig-Holstein) a very high proportion of the wetland species list is considered endangered and threatened (46 and 44 respectively). This reflects the high pressure from land-use practices on the conservation status of mires and wetlands in Germany. In countries like Latvia, Poland, and north-west Russia, groundwater-fed mires belong to the relatively well-preserved ecosystems on the country scale (Wolejko 2002, Pakalne & Kalnina 2005). A similar pattern emerges when only the numbers of species that have become extinct in particular countries are compared; the German numbers are the highest. So, this analysis of endangered and protected species shows that the Slītere National Park is not only of great importance for Latvia, but also for the whole region around the Baltic Sea because here one may still find an almost complete sequence of peat forming mire types next to each other under very different hydrological conditions.

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Appendix

Synoptic table of plant communities of Slītere National Park mires.

Code	a	b	c	d	e	f	g	h	i	j
Dominant vegetation type	Schoenus ferrugineus	Juncus subnodulosus	Hydrocotyle vulgaris	Carex diandra	Small sedges	Carex lasiocarpa	Sphagnum cuspidatum	Sphagnum flexuosum	Sphagnum magellanicum	Ledo-Pinetum
Mire type	Extr. rich fen	Extr. rich fen	Rich fen	Rich fen	Rich fen	Rich fen	Rich fen / Dystrophic hollows	Rich fen / Dystrophic hollows	Poor fen / bog	Bog wood
Number of records	12	8	10	7	27	24	8	6	13	13
<i>Caricion davallianae</i>										
<i>Schoenus ferrugineus</i>	V									
<i>Carex hostiana</i>	V	I								
<i>Succisa pratensis</i>	III									
<i>Dactylorhiza incarnata</i>	II				II					
<i>Pinguicula vulgaris</i>	II									
<i>Juncus subnodulosus</i>		V								
<i>Carex lepidocarpa</i>		V		I	I	I				
<i>Dactylorhiza fuchsii</i>		II								
<i>Sesleria caerulea</i>	V	V								
<i>Fissidens adianthoides</i>	III	IV	I							
<i>Potentilla erecta</i>	V	V				IV				
<i>Carex flacca</i>	II	II								
<i>Primula farinosa</i>	III	III								
<i>Carex panicea</i>	II	V	V	IV		I				
<i>Campylium stellatum</i>	III	V	II	I	I	I		I		
<i>Juncus alpino-articulatus</i>			III	III	I	I				
<i>Drepanocladus revolvens</i>	II		II	I	III	I				
<i>Liparis loeselii</i>				I	II					
<i>Riccardia pinguis</i>						IV				

Code	a	b	c	d	e	f	g	h	i	j
Dominant vegetation type	Schoenus ferrugineus	Juncus subnodulosus	Hydrocotyle vulgaris	Carex diandra	Small sedges	Carex lasiocarpa	Sphagnum cuspidatum	Sphagnum flexuosum	Sphagnum magellanicum	Ledo-Pinetum
Mire type	Extr. rich fen	Extr. rich fen	Rich fen	Rich fen	Rich fen	Rich fen	Rich fen / Dystrophic hollows	Rich fen / Dystrophic hollows	Poor fen / bog	Bog wood
Number of records	12	8	10	7	27	24	8	6	13	13
Saxifrago-Tomentypnion										
<i>Carex diandra</i>	II		II	V	III	I	I	I		
<i>Carex chordorrhiza</i>				V	III	I	IV	I		
<i>Carex limosa</i>			III	V	V	I	II	I	II	I
<i>Carex heleonastes</i>					IV	I				
<i>Carex lasiocarpa</i>	I	II	V	IV	II	IV	IV	IV	III	I
<i>Menyanthes trifoliata</i>	III	III		V	V	IV	V	V		
<i>Bryum pseudotriquetrum</i>		I		III	V	I		I		
<i>Galium palustre</i>			V	I	I	III		II		I
<i>Cardamine pratensis</i>		I	II	I	II	I				
<i>Eriophorum gracile</i>	I			IV	I	II				
<i>Epipactis palustris</i>	III	II		I	I					
Previous Ch. Caricion lasiocarpae										
<i>Potentilla palustris</i>			V	V	IV	IV	II	III		
<i>Peucedanum palustre</i>			V	V	IV	III	I	III		
<i>Carex rostrata</i>			V	I	IV	II	V	I		
<i>Calliergon giganteum</i>			V	III	II	I				
<i>Ranunculus lingua</i>			I	I	IV	I				
<i>Cinclidium stygium</i>				IV		I				
Rhynchosporion albae										
<i>Sphagnum cuspidatum</i>							V		III	I
<i>Sphagnum flexuosum</i>						I	I	V	V	II
<i>Aulacomnium palustre</i>	I					I		II	V	II
<i>Scheuchzeria palustris</i>				I	III	I	II		III	

Code	a	b	c	d	e	f	g	h	i	j
Dominant vegetation type	Schoenus ferrugineus	Juncus subnodulosus	Hydrocotyle vulgaris	Carex diandra	Small sedges	Carex lasiocarpa	Sphagnum cuspidatum	Sphagnum flexuosum	Sphagnum magellanicum	Ledo-Pinetum
Mire type	Extr. rich fen	Extr. rich fen	Rich fen	Rich fen	Rich fen	Rich fen	Rich fen / Dystrophic hollows	Rich fen / Dystrophic hollows	Poor fen / bog	Bog wood
Number of records	12	8	10	7	27	24	8	6	13	13
<i>Rhynchospora alba</i>					I	I	I		I	
<i>Drosera intermedia</i>					III	I	I			
<i>Juncus stygius</i>					III					
<i>Scheuchzerietalia palustris</i>										
<i>Scorpidium scorpioides</i>			I	V	V	II	I			
<i>Scirpus hudsonianus</i> = <i>Trichophorum alpinum</i>	I			I	IV	I	I			
<i>Equisetum fluviatile</i>			V	V	I	III		I		I
<i>Stellaria palustris</i>					III	I		I	I	
<i>Drosera anglica</i>					II	I	I			
<i>Sphagnum fallax</i>						I			I	IV
<i>Scheuchzerio-Caricetea fuscae</i>										
<i>Hydrocotyle vulgaris</i>			V							
<i>Veronica scutellata</i>			III							
<i>Pedicularis palustris</i>			IV	IV		I				
<i>Calliergonella cuspidata</i>	III	V	V	I	III	II				
<i>Carex dioica</i>	III	III	I	I		II				
<i>Carex serotina</i>	I		I	I	IV	I				
<i>Carex nigra</i>	I	II	I		I	II	IV	IV	III	IV
<i>Eriophorum angustifolium</i>	III	I	II	I	III	II	II	II	III	
<i>Carex echinata</i>	I					II	II	III	I	IV
<i>Polytrichum commune</i>						I	II	III	I	IV
<i>Agrostis canina</i>		I					II	III		I
<i>Carex curta</i>						II	II	II		I
<i>Straminergon stramineum</i>							I	II	I	I

Code	a	b	c	d	e	f	g	h	i	j
Dominant vegetation type	Schoenus ferrugineus	Juncus subnodulosus	Hydrocotyle vulgaris	Carex diandra	Small sedges	Carex lasiocarpa	Sphagnum cuspidatum	Sphagnum flexuosum	Sphagnum magellanicum	Ledo-Pinetum
Mire type	Extr. rich fen	Extr. rich fen	Rich fen	Rich fen	Rich fen	Rich fen	Rich fen / Dystrophic hollows	Rich fen / Dystrophic hollows	Poor fen / bog	Bog wood
Number of records	12	8	10	7	27	24	8	6	13	13
<i>Sphagnetalia magellanici</i>										
<i>Andromeda polifolia</i>				I		I	II	II	V	III
<i>Eriophorum vaginatum</i>						I	I	I	V	V
<i>Sphagnum magellanicum</i>				I					V	IV
<i>Rubus chamaemorus</i>						I			II	IV
<i>Oxycocco-Sphagnetea</i>										
<i>Vaccinium oxycoccus</i>	II	IV	II		IV	IV	V	V	V	V
<i>Drosera rotundifolia</i>	I			I	II	I	I	I	V	I
<i>Sphagnum angustifolium</i>						I		I	I	I
Bog forest										
<i>Pinus sylvestris</i>	II	II	IV	I	I	II	III	III	V	V
<i>Betula pubescens</i>	I			I	III	III		III	II	IV
<i>Ledum palustre</i>						III	II	II	III	V
<i>Vaccinium uliginosum</i>						I			I	II
<i>Piceetalia excelsae</i>										
<i>Empetrum nigrum</i>		II		I		II			III	V
<i>Vaccinium vitis-idaea</i>		II				II		I	I	IV
<i>Vaccinium myrtillus</i>						II		I	I	III
<i>Pleurozium schreberi</i>						I		I	I	II
<i>Hylocomium splendens</i>						I				II
<i>Molinio-Arrhenatheretea</i>										
<i>Molinia caerulea</i>	IV	V								
<i>Angelica sylvestris</i>		II								
<i>Lysimachia vulgaris</i>		IV	I			II		I		

Code	a	b	c	d	e	f	g	h	i	j
Dominant vegetation type	Schoenus ferrugineus	Juncus subnodulosus	Hydrocotyle vulgaris	Carex diandra	Small sedges	Carex lasiocarpa	Sphagnum cuspidatum	Sphagnum flexuosum	Sphagnum magellanicum	Ledo-Pinetum
Mire type	Extr. rich fen	Extr. rich fen	Rich fen	Rich fen	Rich fen	Rich fen	Rich fen / Dystrophic hollows	Rich fen / Dystrophic hollows	Poor fen / bog	Bog wood
Number of records	12	8	10	7	27	24	8	6	13	13
<i>Caltha palustris</i>			III	III	I	I				
<i>Juncus effusus</i>						I	IV		I	I
<i>Alnetea glutinosae</i>										
<i>Salix aurita</i>			II	I	II	III	II	IV		III
<i>Alnus glutinosa</i>			I	III	I	II		III	I	
<i>Thelypteris palustris</i>			II	I		II		II		I
<i>Salix pentandra</i>			II	I	I	I				
<i>Calamagrostis canescens</i>						I		I	I	I
<i>Salix rosmarinifolia</i>	I	II			I	I				
<i>Myrica gale</i>						I	I	II		
Other species										
<i>Phragmites australis</i>	II	V			I					
<i>Carex disticha</i>		IV								
<i>Utricularia intermedia</i>			V	V	IV	III	II	I	I	I
<i>Calluna vulgaris</i>		I		I		I		I	III	II
<i>Betula pendula</i>	I					I		I	III	IV
<i>Dactylorhiza maculata</i>	II	II					I	I		I
<i>Sphagnum palustre</i> d						II	I	I	II	I
<i>Utricularia minor</i>				I		I	I	I		
<i>Carex elata</i>	I		II			I		I		
<i>Polytrichum juniperinum</i> d									III	I