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Gradients, species richness and communities in eastern Finnish sloping fens

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In Scandinavia, three gradients (poor–rich, water table, margin–expanse) are considered in vegetation classification of mires. We re-analysed the data of Paavo Havas from 1961 on sloping fens in eastern Finland using NMDS ordination analysis, which also revealed a three-dimensional structure of the classic gradients, with the poor–rich gradient associated with pH. Water table level, and the unstable–stable water regime gradient were also of importance. Our analysis confirmed the interpretation by Havas but further stressed the role of the poor–rich gradient as the main direction of variation in sloping fens. Species richness increased with pH, and from mire expanse to margin vegetation, but decreased towards too wet or seasonally too dry conditions. Eastern Finnish sloping-fen plant communities resemble those in sloping fens elsewhere in Scandinavia, but also those in montane-subalpine-alpine fens in central and south-eastern Europe.

Introduction

In recent years, studies to quantify both environmental gradients and vegetation types across large areas have been undertaken, as knowledge of the distributions of vegetation types is particularly important for conservation and management (Jiménez-Alfaro *et al.* 2013, Douda *et al.* 2015, Peterka *et al*. 2017 Laitinen *et al*. 2019). Results obtained at the regional level often serve as references and are used to validate those from continental-scale studies developing classifications and surveying of larger-scale distribution patterns of vegetation types. To date, however, studies on the links between environmental gradients and mire vegetation types recognized in different parts of Europe are few (*see* Laitinen *et al*. 2017).

Recently, the focus of traditional mire vegetation surveys in Europe has clearly turned from Scandinavia to central Europe (*see* e.g. Hájek *et al*. 2006, Pawlikovski *et al*. 2013). Peterka *et al.* (2017) made the first attempt to create a classification system for European fen communities (minerotrophic mires of the *Scheuchzerio palustris–Caricetea fuscae* class) at the alliance level. The system used in their study followed the Braun-Blanquet approach, and was consistent with the synopsis of nomenclaturally valid high-rank syntaxa in Europe (Mucina *et al*. 2016).

In Finland, vegetation surveys (Cajander 1913) begun long before adoption of classification schemes with the three following gradients: poor–rich gradient (Sjörs 1952, Sjörs & Gunnarsson 2002, Tahvanainen 2004), mire surface-level gradient (hummock level–lawn–flark level including carpet and mud-bottom; Sjörs 1948, Laitinen *et al*. 2008a), and mire margin–expanse complex gradient (Sjörs 1948, Joosten *et al.* 2017). These gradients served as a basis for vegetation classification (Ruuhijärvi 1960, Persson 1962), and were later analysed with modern methods of data analysis (Pakarinen & Ruuhijärvi 1978, Moen 1990, Moen *et al*. 2011).

A physiognomic mire margin–expanse concept (*see* Økland *et al.* 2001) discriminates between mire margin and expanse communities based on the occurrence of trees. However, many Finnish studies (Ruuhijärvi 1960, Eurola & Kaakinen 1978, Eurola *et al.* 1984, 1995, 2015, Ruuhijärvi & Lindholm 2006) provided a complex ecohydrological interpretation of the original mire margin–expanse gradient of Sjörs (1948) (but *see* Rehell *et al*. 2019), according to which, mire-margin vegetation receives supplementary nutrients directly from mineral soil through a shallow peat layer in swamp forests (*Bruchmoorigkeit*; Tuomikoski 1942, Ruuhijärvi 1960, Eurola 1962), through flooding or surface water from snowmelt (*Sumpfigkeit*; Brandt 1948, Tuomikoski 1955, Ruuhijärvi 1960) and/or through rising of groundwater in spring fens (*Quelligkeit*; Ruuhijärvi 1960). Mire expanse vegetation is thus nutritionally self-sufficient, and supports *Pinus sylvestris* mires (*Reisermoore*; Ruuhijärvi 1960, Eurola 1962), treeless poor fens and bogs (*Weissmoore*; Ruuhijärvi 1960, Eurola 1962), as well as rich fens (*Braunmoore*; Ruuhijärvi 1960).

According to Havas (1961), sloping fens are fens (peatland) situated on sloping ground but he did not define the slope-angle range. His data reveal, however, that this range should be from 1° to 12°. In more oceanic areas of Scandinavia slopes may exceed 20° (Moen 1990, 1999, Joosten *et al.* 2017). Ruuhijärvi (1960), Havas (1961) and Eurola *et al*. (1984, 1995, 2015) regarded sloping fens as a topographic variant of aapa mires. Generally, sloping fens occur in mountainous areas with cool climate associated with hygric oceanity (Eurola & Kaakinen 1982, Eurola *et al*. 1982, 1991). In central Europe, such fens are found only in areas with high precipitation in montane, subalpine and low alpine belts (Grünig 1994, Steiner 2005, Cubizolle & Thebaud 2014, Dítě *et al*. 2015). In Scandinavia, they are common in mid-boreal to northern boreal zones and in low-alpine belts (Moen 1990, 1999, Rydin *et al*. 1999, Gunnarsson & Löfroth 2014). In Finland, they occur in eastern (Havas 1961) and north-eastern parts of the country (Paasovaara 1986), while their occurrence further north in Lapland is largely unknown (but *see* Laitinen *et al*. 2011, Kaakinen *et al*. 2018). The southernmost sloping fens (North Karelia, southeastern Finland) have largely lost their natural state due to human activity (Kaakinen *et al*. 2018).

Havas (1961) was the first to include measurements of environmental variables in a vegetation survey of eastern Finnish sloping fens. He found that in sloping fens, temporal variation in water conditions affected the vegetation of lawns, and included the mire surface level and the poor–rich gradient, as well as the effects of mowing and grazing (*Wiesenartigkeit*) in his interpretation (*see* Moen *et al*. 2011). He however did not much consider differences among different parts of a single mire.

We re-analysed the data of Havas (1961) using NMDS ordination to reveal (1) gradients in plant community composition, and (2) their dependence on environmental variables and plant diversity. We also defined vegetation types using indicator species assemblages based on the gradient structure. Finally, we compared the classic mire-gradient interpretation with the approach in central Europe, and scrutinize similarities of plant communities between Scandi-

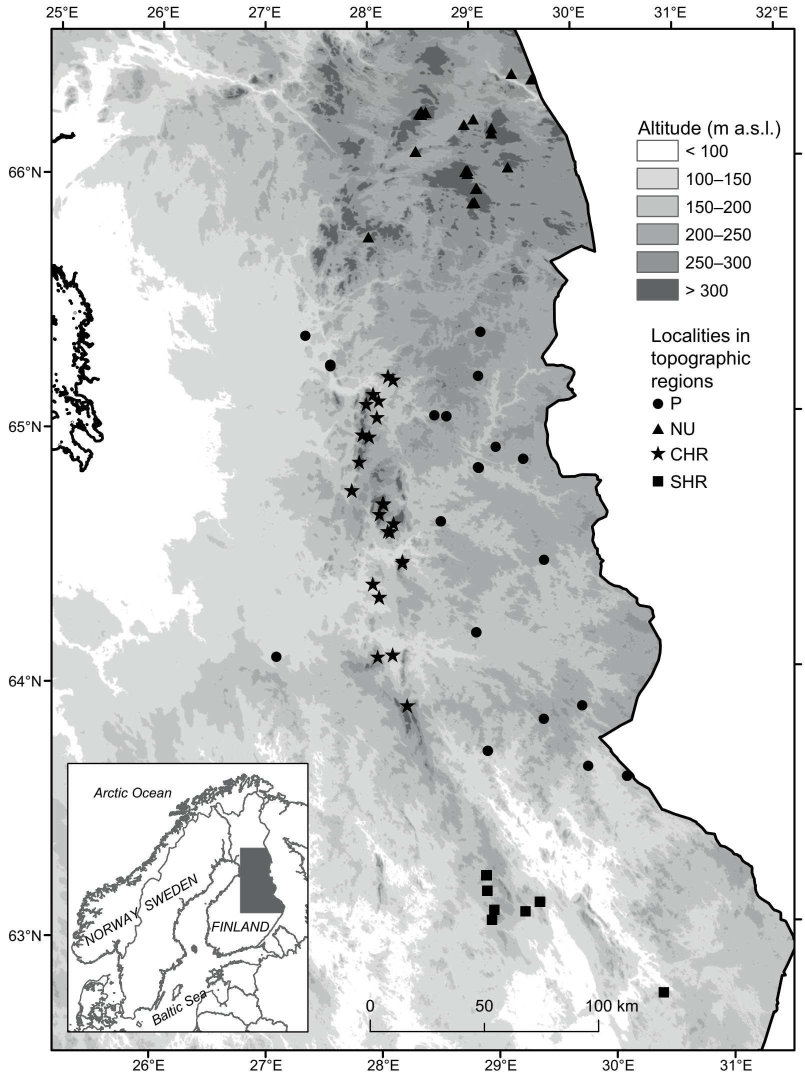

Fig. 1. Studied area in eastern Finland with study localities classified *a priori* into the following topographic regions: P = peripheral region, NU = northern uplands, CHR = central hill range, SHR = southern hill range (*see* Appendix 1). Most of the localities in SHR, CHR and P are in the mid-boreal zone, and those in NU are in the northern boreal zone.

navian sloping fens and central European montane–subalpine–alpine fens.

Study area, material and methods

Study area

The studied area (Fig. 1 and Appendix 1) lies within the Fennosarmatian Precambrian bedrock block (Alalammi 1990) covered to different degrees by glacial deposits. It stretches from the mid-boreal to the north-boreal zone. In 1921–1960, the annual mean temperatures ranged from ca. +2.5 to 0 °C and the effective temperature sum of the growing season from 750 to 1000 °C (Alalammi 1987). In the same period, annual precipitation and maximum snow depth in the forests were 600–750 mm (Alalammi 1987) and 65–90 cm, respectively. Climate conditions can be defined as thermally continental, but with hygric oceanity increasing towards higher elevations, where *Picea abies* forests with extensive snow damage almost exclusively prevail, and where sloping fens are also found (Eurola & Kaakinen 1982, Eurola *et al*. 1982, 1991). Between 1847 and 2013, the mean annual temperature rose by ca. 2 °C, and warming has accelerated after the 1960s (Mikkonen *et al.* 2015).

Material

Nomenclature of plants and vegetation

Nomenclature for vascular plants follows Hämet-Ahti *et al.* (1998), for bryophytes Ulvinen *et al.* (2002), and for lichens Stenroos *et al.* (2011). In the analyses, *Scorpidium cossonii* and *S. revolvens* were treated together, because the taxon *Drepanocladus revolvens* recognized by Havas (1962) includes these two species.

Our treatment of vegetation (species composition, ecology and climatic ranges) focused on the community level. The community names of the eastern Finnish sloping fens follow Havas (1961), and those of the Finnish mire site types follow Ruuhijärvi (1960: original names in German) and Eurola *et al.* (2015: names in English). The nomenclature of Scandinavian plant communities follows Sjörs (1946), Persson (1962) and Moen *et al.* (2011); that of central European communities, associations and alliances follows Hájek *et al.* (2005, 2006, 2008), Hájková *et al.* (2006), Sekulová *et al.* (2011), Conradi and Friedman (2013), and Peterka *et al.* (2014).

Vegetation data

We used all vegetation data of Havas (1961) except for site PP4 (*rimpi* vegetation), the location of which could not be confirmed. One vegetation sample generally included five 1-m^2 vegetation plots. Havas (1961) used the following cover scale (%-cover): 1, 3, 5, 7, 10, 20, 30, 40, …, 100. In his tables, cover estimates were given as medians. Species frequencies were estimated on the scale from 1 to 5, standing for the number of plots in which the species was found. In sites with trees, Havas (1961) estimated the cover in 100-m^2 (10 × 10 m) squares. We used the median cover values as well as the additional species occurrences to include as much compositional information as possible. Additionally, he included the species that were found just outside the plots indicating them with ‘+’. We included those with the cover value of 0.25%.

Geospatial and environmental data

We determined approximate geographical coordinates and elevations above sea level of the sampling sites using the site descriptions given in Havas (1961). We first located each mire on a map, and then assigned the coordinates and elevation of its central point to all vegetation samples from this mire (Fig. 1). Thus, although the location data for all the samples within the site are the same, we considered it sufficient for regional-scale comparisons.

Water pH values for sample plots were taken from Havas (1961). The values for hummock-level sites (*Calluna vulgaris–Molinia caerulea–Sphagnum fuscum* community), and few other site types were lacking. Slope angle was first included but we decided to omit it, as it did not reveal any interpretable pattern.

The temperature and precipitation data were obtained from the Finnish Meteorological Institute. Using R package *gstat* (Gräler *et al.* 2016), we interpolated the averages of monthly precipitation and temperature to a 1 × 1-km grid using kriging, with covariates for lake density and elevation. Although elevation was included in the interpolation, the data for high elevations — above 200 m a.s.l. and 300 m a.s.l. in the southern and northern parts of the study area, respectively — were not available, hence the precipitation values may be underestimated.

In our analyses, we used mean annual temperature, mean annual temperature range, and annual precipitation sum.

Methods

Sloping fen occurrence

To establish a regional sub-division for the vegetation analysis, we used topographic regions (Fig. 1 and Appendix 1) instead of ordinary climate-phytogeographical zones of mire or forest vegetation. This was done because topography and elevation are significant factors for the vegetation of poor fens and mesic heath forests in mid-boreal hilly areas (Eurola & Kaakinen 1982, Eurola *et al*. 1991). The high-elevation areas were classified as the core regions of sloping fens, and the low-elevation areas around the core regions as the peripheral regions (*see* Appendix 1). Rough limits between the peripheral and core regions were at about 150 m a.s.l. and about 200 m a.s.l. in the southern and northern parts of the study area. The core and peripheral regions, however, were not defined by following exact contour lines but by grouping the mires studied by Havas (1960) into those on large forested hill-areas and those around such areas.

Ecological species groups

We used ecological species groups based on the groups in Havas (1961) to aid the vegetation analysis interpretation (Appendix 2). We, however, added some species of contact habitats of boreal mires, occurring in the material, to describe the continuum from mires to other habitats. These species groups were representative for (1) flark–lawn–hummock-level gradient, (2) gradient along the unstable–stable water regime, (3) the poor–rich gradient, and the transitions to (4) forest vegetation (groups Hum-Pinus, Hum-Picea, Herb-Picea), (5) spring vegetation, and (6) meadow vegetation (*see* Appendix 1).

Species richness

The species richness for each vegetation sample was based on the data of Havas (1961). Although he included all species, he did not account for the area effect, thus species richness is informative of the communities only.

Non-metric multidimensional scaling ordination (NMDS) analysis

We used the NMDS ordination (Kruskal 1964, Faith *et al*. 1987) to reveal gradients in the plant communities. NMDS is an unconstrained ordination that condenses *n*-dimensional information of species matrix to *k*-dimensional ordination based on dissimilarities between samples. Thus, the ordination represents variation in composition of plant communities that can be compared to other measurements and attributes of the samples. For the measure of dissimilarity/distance in plant communities, we used the Bray-Curtis dissimilarity (Minchin *et al.* 1987). The NMDS axes are not uniquely defined, and any rotation of the solution will retain the same distances among the points in ordination. Thus, the solution can be so that the first axis covers most of the variation (Kruskal 1964), or the solution can be rotated so that the axes are optimally interpretable in ecological terms. We rotated the solution according to the most strongly correlated environmental variable (pH) describing the main environmental gradient. Correlation of each measured environmental variable was assessed by fitting a first-degree trend surface which is uniquely defined by its gradient, or the direction of the steepest change in the surface. In the ordination space this is shown by an arrow whose length indicates goodness of fit. For certain variables, we chose to use non-linear trend surfaces as isocline curves to better illustrate the relationship with ordination. These were obtained by fitting an isometric thin-plate spline for the environmental variable on ordination space (*see* https://cran.r-project.org/package=vegan). As the axes are not uniquely defined in NMDS, no correlations with the axes were calculated, but the fitted vector gives a rotation-invariant way of describing the goodness of solution in predicting the environmental variable.

The analyses were performed with R package *vegan* (https://cran.r-project.org/package=vegan).

Formation and description of communities

After several trial runs, we decided to use the original communities (*Siedlungsgruppe*) that were based on floristic similarities and differences (Havas 1961; Appendix 3). There were two reasons for that: (1) they appeared as distinct groups in the NMDS ordination, and (2) they compare to botanical Finnish mire site types (Ruuhijärvi 1960, Eurola 1962, Eurola & Kaakinen 1978, Eurola *et al*. 1984, 1995, 2015) and to sloping-fen communities of the Central Scandes in Sweden (Sjörs 1946).

In the results, we present communities with the indicator species for gradients (based on NMDS). We used the mire species that Eurola *et al*. (2015) grouped regarding gradients as follows: (I) four classes of the poor–rich gradient (ombro-, oligo-, meso- and eutrophic), (II) three classes of mire surface levels (hummock level, intermediate level, flark level), and (III) six classes of the mire margin–expanse gradient. The mire margin categories included species indicating effects of (1) groundwater from springs, (2) surface water, and (3) mineral soil and forest. Mire-expanse categories included groups of species typical for (1) *Pinus sylvestris* forest and hummock-level bogs, (2) poor fens and hollow to lawn level bogs, and (3) rich fens.

For the oligotrophic–eutrophic gradient of Eurola *et al*. (2015), we used the poor–rich classification of Sjörs (1948, 1952), Persson (1962), and Sjörs and Gunnarsson (2002):

- extremely poor fens had at least one indicator of weak minerotrophy (oligotrophy or oligo–mesotrophy); moderately poor fens had at least one indicator of stronger minerotrophy (mesotrophy and often additionally meso-eutrophy);
- intermediate fens had several indicators of mesotrophy and meso-eutrophy (*see* Ruuhijärvi 1960 for the description of *Molinia Braunmoore-Weissmoore*), with rich-fen species (eutrophic) occasionally present;
- rich fens were dominated either by minerotrophic *Sphagnum* spp. (mainly *S. warnstorfii* with the rich-fen proper indicator *Tomentypnum nitens*), or by rich-fen brown-mosses of various mire surface levels and various margin–expanse status.

We based our mire surface-level classification (flark, lawn, and hummock levels) on dominating (indicator) species. Regarding the water regime, we applied the following classification: unstable water regime evidenced by the *Molinia* species group of Havas (1861), and disturbance indicators (*Störzeiger*) of Dierssen (1982) (*Carex nigra*, *Agrostis canina*, etc.); and stable water regime evidenced by *Eriophorum vaginatum* species group of Havas (1961), the bulk of species in the *Menyanthes* species group, the hummock-level species, and the species indicating groundwater effect (our *Paludella* group and *Sphagnum warnstorfii*). The stable water regime indicator species do not tolerate severe seasonal drying of the peat surface (Laitinen 2008).

Mire margin–expanse vegetation classification was based on the presence/absence of mire-margin indicator species, reflecting either mineral-soil effect (spruce-mire effect according to Eurola *et al*. 2015; *Bruchmoorigkeit* in Ruuhijärvi 1960, Eurola 1962), surface-water effect (*Sumpfigkeit*; Brandt 1948, Tuomikoski 1955, Ruuhijärvi 1960), and/or groundwater effect (*Quelligkeit*; Ruuhijärvi 1960).

Results

NMDS analysis

Environmental gradients

Water pH (NMDS 1) was the most significant variable, explaining 69% of the vegetation variation presented by the ordination (Fig. 2). It ranged from 4.0 (community 7) to > 6.4 (subcommunity 5.2). Of the climatic variables (NMDS 2), mean annual precipitation was the most significant explaining 24% of the vegetation variation presented in the ordination, followed by mean annual temperature (9%), and annual average temperature range (8%). Slope angle (exposition) effect was negligible (not shown).

Gradients by indicator species groups and communities

NMDS 1, NMDS 2 and NMDS 3 divided indicator species groups (Appendix 2) in the ordinations (Figs. 3 and 4). The poor–rich gradient (L-Rich, *Campylium stellatum* group) approximately followed the pH gradient along NMDS 1 (Fig. 3).

NMDS 2 separated hummock-level species (Hum-Pinus, *Empetrum* group) and flark-level species (Flark, *Menyanthes* group) (Fig. 3), as

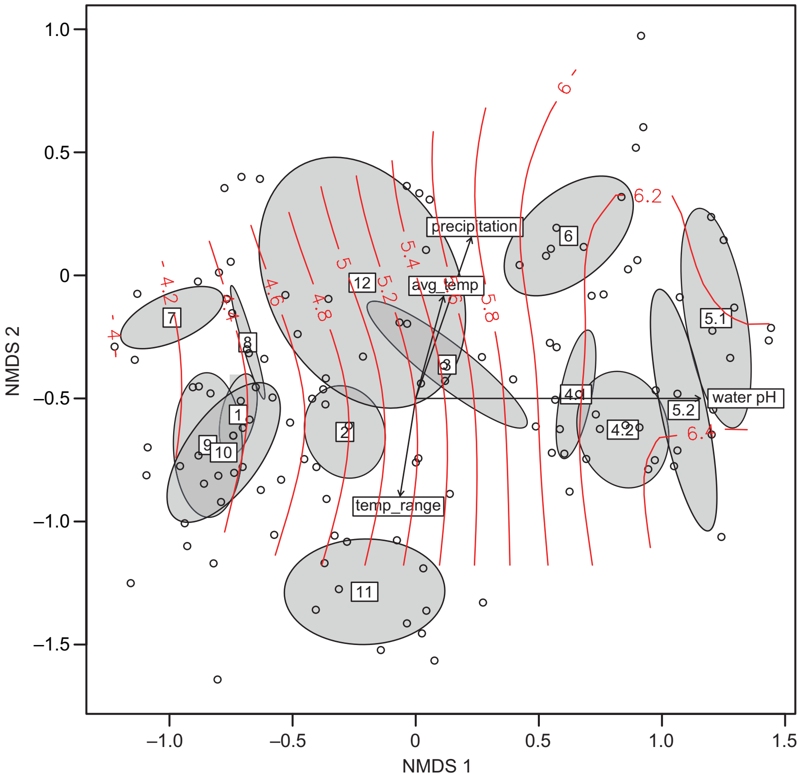

Fig. 2. NMDS ordination; circles = sample plots, numbers = communities (*see* Appendix 3), vectors = pH, precipitation, average temperature, temperature range. Ellipses show standard deviations for the communities. The result was rotated to align pH with axis (NMDS) 1.

well as the hummock-level communities (11, 10, 9), lawn communities (7, 8, 1, 2, 3, 4, 5; except 6 separated along NMDS 3, *see* Fig. 4), and flark community (12).

NMDS 3 separated species in the L-Unstable group (*Molinia* group), as well as in Hum-Picea (*Carex globularis* group) and Herb-Picea (*Filipendula* group) groups (Fig. 4). There was an indication of the gradient from unstable (bottom part of Fig. 4) to stable (top part of Fig. 4) water regimes along NMDS 3. NMDS 2 and NMDS 3 best separated the species groups Spring (*Paludella* group) and Meadow (*Festuca* group) (Appendix 2).

Extremely poor fen communities (7, 8, 1, 9, 10) formed a loose cluster related to low pH (Figs. 2, 3 and 4). They also were very clearly positioned along NMDS 3, representing unstable–stable gradient. Moderately poor fen communities (12, 2, 11) were positioned along NMDS 2 (mire surface level gradient), while the only intermediate fen community (3) had a central position in the ordination. Rich mire margin fen community (6) was separated from the other communities in all dimensions.

Sub-communities 4.1, 4.2, 5.1 and 5.2 formed a tight cluster along NMDS 1, with some separation along NMDS 3: mire margin–expanse gradient was evident, while the stable–unstable gradient was less so (Fig. 4). They also slightly differed along NMDS 1 (poor–rich gradient; Figs. 2 and 3)

Gradient structure by topographic regions

Vegetation sample plots, grouped according to the four topographic regions, largely overlapped in the NMDS ordination (Fig. 5). The centres of regional groups, however, formed a series nearly along the poor–rich gradient (NMDS 1). They formed a continuum from the peripheral region (P) — largest proportion of poor-fen vegetation — to northern uplands (NU), to central hill range (CHR), and to the southern hill range (SHR) —

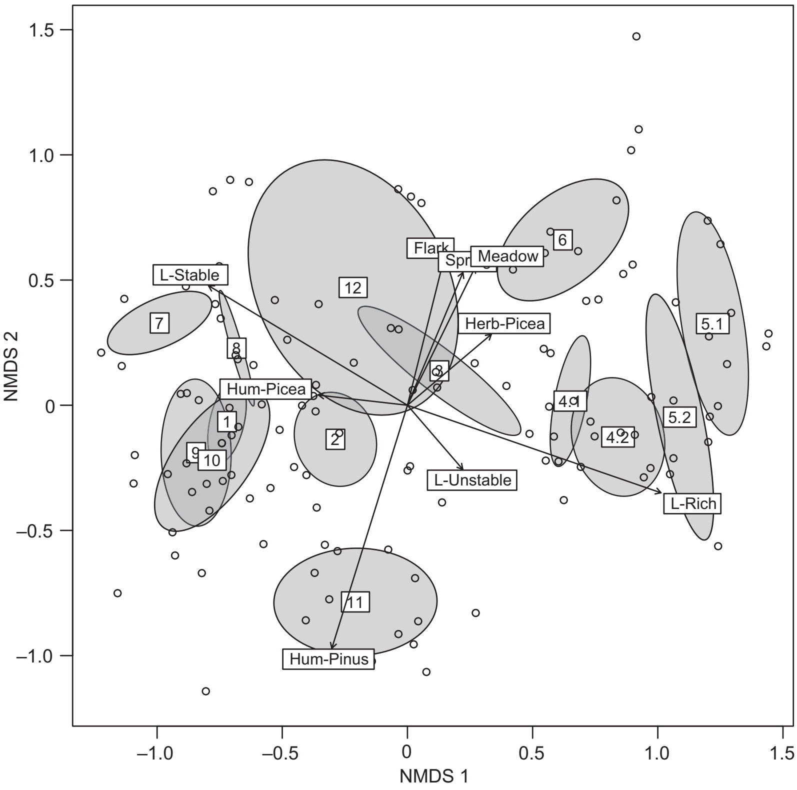

Fig. 3. NMDS ordination; circles = sample plots, numbers = communities (*see* Appendix 3), vectors = indicator species groups (*see* Appendix 2). Ellipses show standard deviations for the communities. The result was rotated to align pH with axis (NMDS) 1.

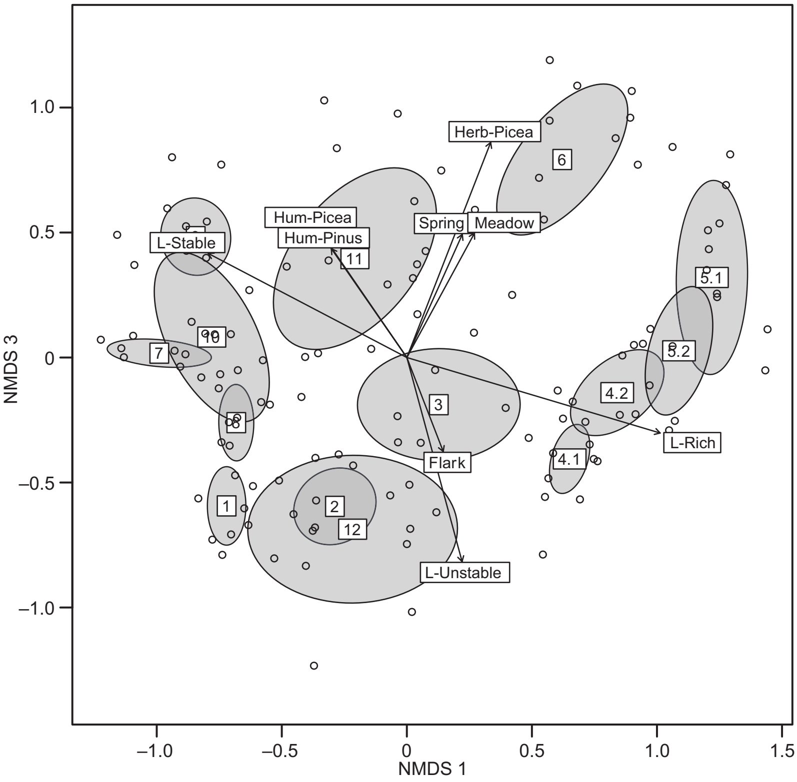

Fig. 4. NMDS ordination; circles = sample plots, numbers = communities (*see* Appendix 3), vectors = indicator species groups (*see* Appendix 2). Ellipses show standard deviations for the communities. The result was rotated to align pH with axis (NMDS) 1.

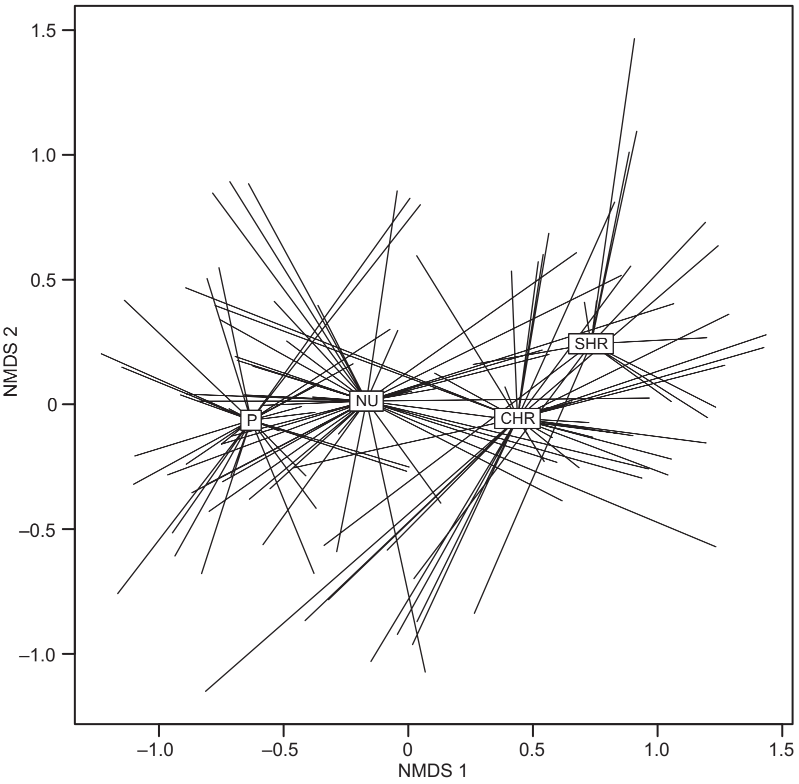

Fig. 5. Plots grouped according to topographic regions; P = peripheral region, NU = northern uplands, CHR = central hill range, SHR = southern hill range. For topographic regions, *see* Appendix 1.

smallest proportion of poor-fen vegetation. The three high-elevation topographic regions were arranged from north to south as follows: NU, CHR, and SHR, reflecting climatic variation.

Species richness

Species richness varied from ~10 to > 45 species per vegetation sample plot, largely increasing along NMDS 1, and the poor-rich gradient. The lowest species richness was in community 7 with the lowest pH (Fig. 6). The maximum species richness, however, was recorded not in plots with maximum pH but in the mire margin communities of rich lawn fens (sub-communities 5.1 and 5.2), and in the weakly rich mire margin community 6 (Fig. 7). Community 1 was one with the lowest species richness (Fig. 7). Also the wettest habitats (community 12) included plots with very low species richness (Fig. 7).

Species richness was also associated with the topographic regions, as it clearly increased from the peripheral region (P) towards the core areas of high elevation, and towards the south (from NU to CHR to SHR) (Fig. 5).

Plant community types

In this chapter, the fens are described in the following order: extremely poor fens (communities 7, 8, 1, 9, 10), moderately poor fens (communities 12, 2, 11), intermediate fens (community 3), rich fens (communities 6, 4 (4.1, 4.2), 5 (5.1, 5.2)).

Extremely poor lawn fens

Carex pauciflora was the most frequent extremely poor-fen indicator in all communities. Lawn indicators were the dominants *Trichophorum cespitosum*, *Eriophorum vaginatum*, *Sphagnum compactum* or *S. angustifolium* (the latter two at different sample plots), and *S. papillosum.* Mire margin indicators were lacking.

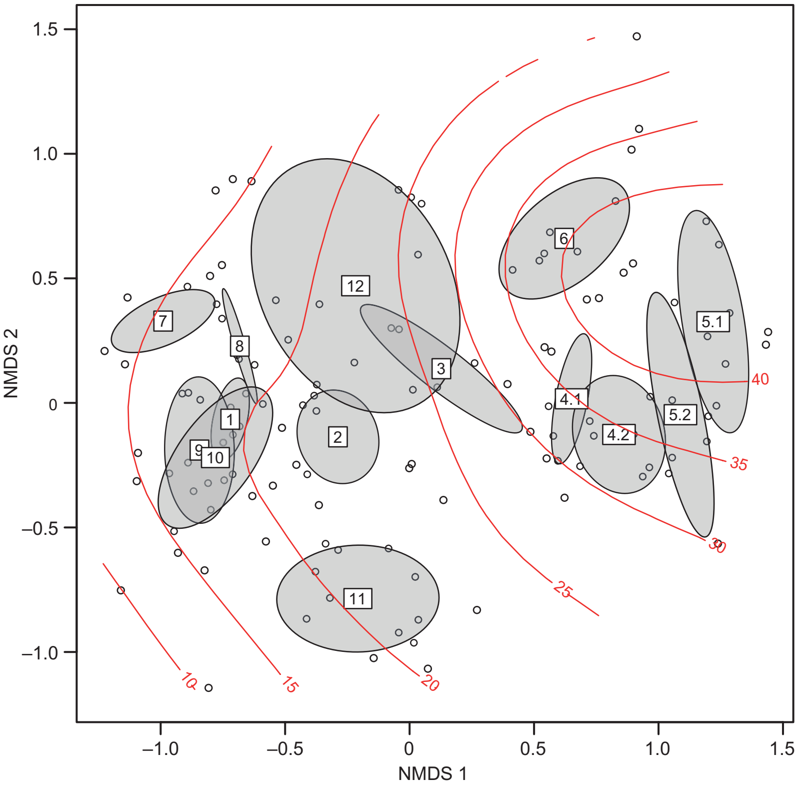

Fig. 6. Grouping of plots (circles), communities (numbers), and average species richness. The ellipses show the standard deviations for the communities. For community names, *see* Appendix 3.

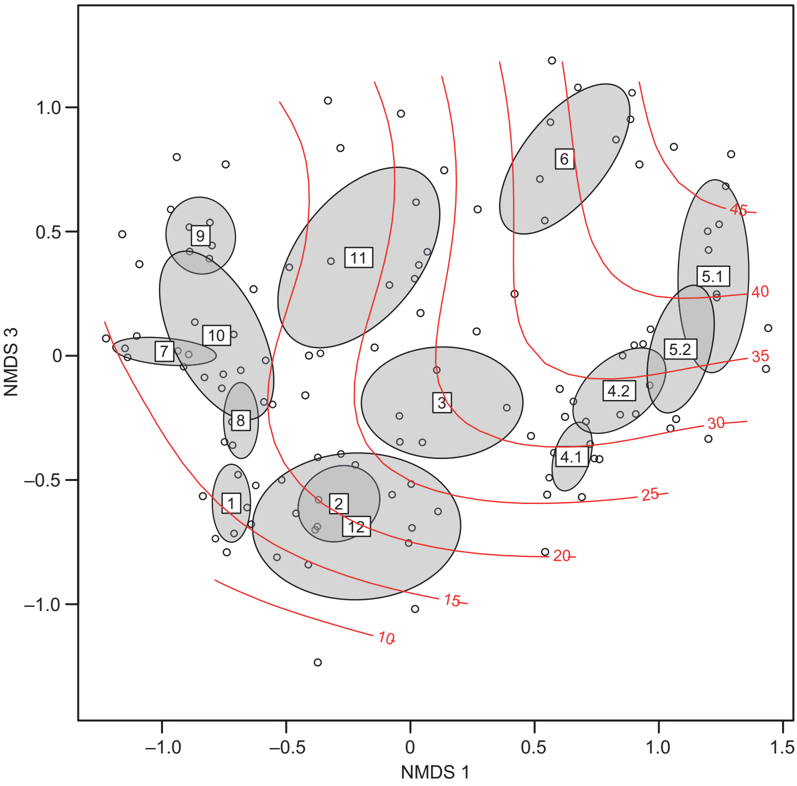

Fig. 7. Grouping of plots (circles), communities (numbers), and average species richness. The ellipses show standard deviations for the communities. For community names, *see* Appendix 3.

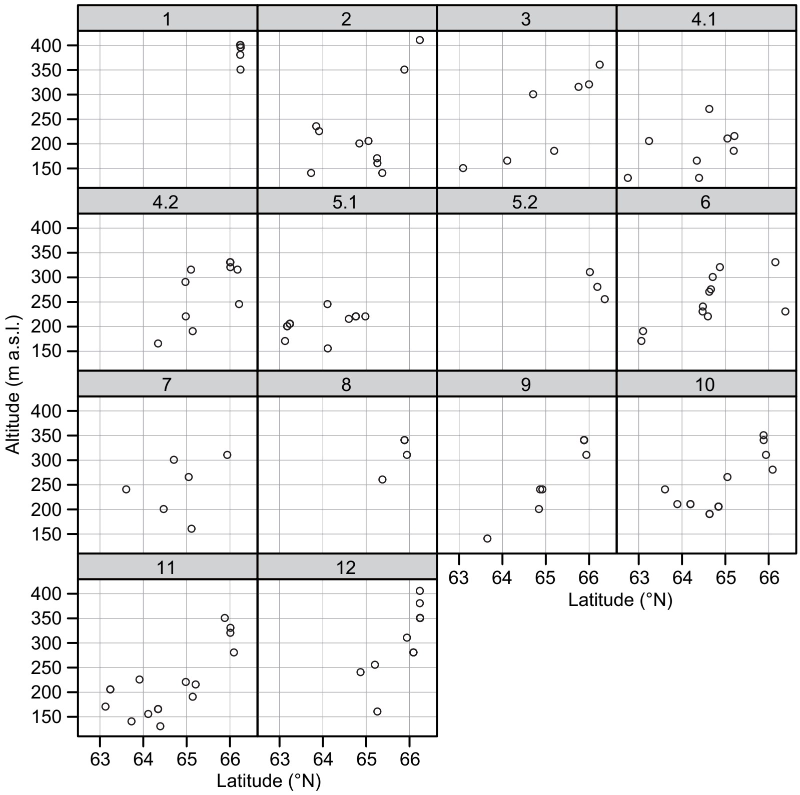

Fig. 8. Latitude–elevation ranges of communities. For community names, *see* Appendix 3.

Community 7 (*Betula nana–Eriophorum vaginatum–Sphagnum angustifolium* community; Figs. 3 and 4): widespread in the study area within an elevation range of 150–300 m a.s.l. (Fig. 8). Additional extremely poor-fen indicators were *Menyanthes trifoliata* (ST water regime) and *Carex rostrata*. Lawn indicators were the dominants *Eriophorum vaginatum* and *Sphagnum angustifolium*. *Betula nana* was most abundant in this community among lawn fens. Central indicators of unstable water regime (*Trichophorum cespitosum*, *Sphagnum compactum*) were lacking.

Community 8 (*Eriophorum vaginatum–Sphagnum lindbergii–S. russowii* community; Fig. 8): northern, occurring at high elevations (250–350 m a.s.l.). Extremely poor-fen indicators were *Sphagnum papillosum*, *S. fallax* and *Carex lasiocarpa*. Lawn indicators *Trichophorum cespitosum*, *Eriophorum vaginatum*, and *Sphagnum papillosum* were constant as were *Andromeda polifolia* and *Betula nana*. *Menyanthes trifoliata* (stable water regime) was absent.

Community 1 (*Trichophorum cespitosum–Sphagnum compactum–Ptilidium ciliare* community; Fig. 8): it represented northern vegetation of high elevations (350–400 m a.s.l.). Extremely poor-fen indicators were *Eriophorum angustifolium*, *Carex rostrata* and *C. lasiocarpa*; their frequencies, however, were low. Lawn indicators were the dominants *Trichophorum cespitosum* and *Sphagnum compactum. Sphagnum tenellum was frequent*, and *Ptilidium ciliare* and some dwarf shrubs were constant (*Andromeda polifolia*, *Betula nana*, *Empetrum nigrum s. lato*, *Vaccinium oxycoccos*, *V. uliginosum*). All abundant species were unstable-water-regime indicators, while stable-water-regime indicators were almost lacking.

Mire margin and expanse vegetation of extremely poor hummock-level mires

Minerotrophic hummock-level vegetation was dominated by *Carex globularis* or dwarf shrubs and sparse stands of trees (*Pinus sylvestris* or *Picea abies*). Dominants in the moss layer were primarily hummock-level species (*Sphagnum fuscum*, *S. russowii*, *S. angustifolium*).

Community 9 (*Carex globularis–Sphagnum fuscum–S. russowii* community; Figs. 3 and 4): represented mire margin vegetation, as it included at least small amounts of mire margin indicators of mineral-soil effect (*Picea abies*, *Carex globularis*, *Equisetum sylvaticum*, *Polytrichum commune*). *Carex globularis*, *Sphagnum fuscum* and *S. angustifolium* were dominants. Wide latitudinal distribution, elevation range 130–350 m a.s.l. (Fig. 8).

Community 10 (*Vaccinium uliginosum–Sphagnum fuscum–S. angustifolium* community): represented mire expanse vegetation with no mire-margin indicators. It included small amounts of indicators of extremely poor fens (*Carex lasiocarpa*, *C. pauciflora*, *C. rostrata*). Dominant species were *Vaccinium uliginosum*, *Sphagnum fuscum*, *S. angustifolium* and *Empetrum nigrum s. lato*. Additional dominants were *Chamaedaphne calyculata* (not in the northernmost parts), *Trichophorum cespitosum*, and occasionally *Sphagnum magellanicum* or *S. balticum.* Wide latitudinal distribution, elevation range 180–350 m a.s.l. (Fig. 8).

Flark fens (moderately poor fens)

Community 12 (flark community): represented mire expanse vegetation with varying poor–rich status and variation from carpet to mud-bottom (Figs. 3 and 4). The elevation range was the greatest among all communities (150–400 m a.s.l.) (Fig. 8). *Carex rostrata–Sphagnum lindbergii* carpet represented northern extremely poor fen. In rich flark fens, e.g. *Eriophorum latifolium*, *Scorpidium revolvens*, and *Aneura pinquis* were present.

Moderately poor lawn fens

Community 2 (*Molinia caerulea–Trichophorum cespitosum–Sphagnum compactum–S papillosum* community): *Molinia caerulea* was the only constant moderately poor fen indicator (Figs. 3 and 4). *Trientalis europaea* occurred in almost half of the plots. There were no or only few intermediate fen indicators per plot, most frequent was *Loeskpynum badium*, while the others were *Selaginella selaginoides*, *Pinguicula vulgaris*, *Sphagnum subfulvum*, *S. warnstorfii* and *Tofieldia pusilla.* Lawn indicators were the dominants *Trichophorum cespitosum*, *Sphagnum papillosum*, and *S. compactum*. Specific mire-margin indicators were lacking. The dominants belonged to the indicators of unstable water regime (*Molinia* group) but also a central indicator of stable water regime (*Sphagnum fuscum*) was infrequently present. Wide distribution, elevation range 150–400 m a.s.l. (Fig. 8).

Fen hummocks (moderately poor fens)

Community 11 (*Calluna vulgaris–Molinia caerulea–Sphagnum fuscum* community): occurred on hummocks of sloping fens (Figs. 3 and 4). The poor–rich status varied markedly according to the presence or absence of moderately poor fen indicators (*Molinia caerulea*, *Solidago virgaurea*, *Trientalis europaea*), intermediate fen indicators (*Carex vaginata*, *Trichophorum alpinum*, *Potentilla erecta*, *Selaginella selaginoides*, *Tofieldia pusilla*, *Bartsia alpina*), and the exceptional presence of rich fen indicators (*Carex flava*, *Salix myrsi-nites*, *Eriophorum latifolium*, *Carex panicea*, *Equisetum variegatum*, *Cinclidium stygium*). The indicators of hummock level included the dominants *Juniperus communis*, *Calluna vulgaris*, *Empetrum nigrum s. lato*, *Sphagnum fuscum*, *Pleurozium schreberi*, *Hylocomium splendens* and *Cladonia rangife-rina*. There was additionally minor variation according to the presence or absence of mire margin species (*Angelica sylvestris*, *Geranium sylvaticum*, *Convallaria majalis*, *Rubus saxatilis*, *Helodium blandowii*). Wide distribution, elevation range 120–350 m a.s.l. (Fig. 8).

Intermediate fens

Community 3 (*Molinia caerulea–Trichophorum cespitosum–Sphagnum warnstorfii* community): represented intermediate lawn fens. Moderately poor fen indicator *Molinia caeurulea* was constant, *Carex echinata* was nearly constant, and *Viola epipsila* occurred several times. In most plots several intermediate fen indicators were present. *Sphagnum warnstorfii*, *Selaginella selaginoides* and *Paludella squarrosa* were nearly constant. Other frequent intermediate fen indicators were *Trichophorum alpinum*, *Sphagnum subfulvum* and *S. subsecundum*. Also *Tofieldia pusilla* was relatively frequent. *Carex dioica*, *Potentilla erecta*, *Parnassia palustris*, *Bartsia alpina*, *Loeskypnum badium* and *Sphagnum teres* were relatively rare. Exceptionally, some of the plots had some rich fen species with a low cover value (*Carex flava*, *Eriophorum latifolium*, *Carex panicea*, *Campylium stellatum* or *Scorpidium scorpioides*). Mire expanse species (*Molinia*, *Trichophorum cespitosum*, *Sphagnum subfulvum*, *S. papillosum*) mostly dominated. Mire margin species were less common (*Sphagnum teres*), apart from *Sphagnum warnstorfii*. Lawn indicators present as dominants were *Trichophorum cespitosum*, variably *Sphagnum subfulvum*, *S. papillosum* and *S. angustifolium*. The higher-lawn indicator *Sphagnum warnstorfii* was also present. The community represented heterogeneous mire expanse vegetation, as ecologically different *Sphagnum* species (*Sphagnum angustifolium*, *S. papillosum*, *S. subfulvum*, *S. subsecundum*, *S. warnstorfii*). Species of stable water regime (*Sphagnum warnstorfii*) dominated in plots. Also *Trichophorum cespitosum* indicating unstable water regime was found among the dominants. Wide distribution, elevation range 150–350 m a.s.l. (Fig. 8).

Mire margin vegetation of rich lawn fens

Community 6 (*Carex magellanica–Filipendula ulmaria–Sphagnum warnstorfii* community) represented higher lawn vegetation (cf. communities 5 and 4 below). Extremely poor fen species *Carex magellanica* and moderately poor fen species *Carex echinata*, *Solidago virgaurea* and *Trientalis europea* were frequent. Intermediate fen indicator *Selaginella selaginoides* was constant. Few rich fen indicators were present, most frequent among them were *Eriophorum latifolium* and *Tomentypnum nitens*. The dominant *Sphagnum warnstorfii* was a prominent indicator of higher lawn, while less frequent and subordinate *Tomentypnun nitens* and *Sphagnum angustifolium* indicated the same surface level. Contrary to the intermediate lawn fen community 3, typical mire expanse vascular plants of lawns (*Trichophorum cespitosum*, *Molinia caerulea*) were rare and typical mire-expanse *Sphagnum* species of lawns (*S. subfulvum, S. papillosum*) were lacking. Mire margin species, especially indicating groundwater and mineral-soil effects, were numerous. They included *Salix phylicifolia*, *Luzula sudetica*, *Angelica sylvestris*, *Crepis paludosa*, *Filipendula ulmaria*, *Geranium sylvaticum*, *Bistorta vivipara*, *Phleum alpinum*, *Bryum pseudotriquetrum*, *Plagiomnium ellipticum*, and *Paludella squarrosa.* Dominant species indicated stable water regime (*Sphagnum warnstorfii*). Wide distribution, elevation range 170–330 m a.s.l. (Fig. 8).

Community 5 (*Carex flava–Filipendula ulmaria–Campylium stellatum* community; (Figs. 3 and 4) represented slightly lower lawn related to community 6 and mire margin vegetation with *Trichophorum cespitosum* almost absent and with abundant mire margin species. *Molinia caerulea* was frequent.

Sub-community 5.1 (*C. nigra* sub-community): represented southern mire margin vegetation occurring at low elevations (150–250 m a.s.l.) (Fig. 8). Constant rich-fen indicators included *Carex flava*, *Eriophorum latifolium*, *Campylium stellatum* and *Scorpidium revolvens s. lato.* Lawn indicators included the dominant moss species (*Campylium stellatum*, *Scorpidium revolvens s. lato*). Frequent mire margin species indicating surface-water, groundwater and mineral-soil effects were numerous. They included *Carex nigra*, *C. canescens*, *Equisetum palustre*, *Angelica* *sylvestris*, *Crepis paludosa*, *Filipendula ulmaria*, *Geranium sylvaticum*, *Pedicularis palustris*, *Bistorta vivipara*, *Rubus arcticus*, and *Bryum pseudotriquetrum*. *Carex nigra* appeared as an indicator of the unstable water regime.

Sub-community 5.2 (*Saussurea alpina* sub-community): represented clearly northern mire margin vegetation at intermediate elevations (250–300 m a.s.l.) (Fig. 8) in the Kuusamo area. Constant rich-fen indicators were *Pinguicula alpina*, *Cinclidium stygium*, *Scorpidium revolvens s. lato* and *Aneura pinguis*. Lawn indicators were the dominants *Campylium stellatum* and *Scorpidium revolvens s. lato*. Frequent mire margin species (including *Pinguicula alpina*, *Saussurea alpina*, *Equisetum fluviatile*, *Angelica sylvestris*, *Crepis paludosa*) were primarily indicators of groundwater and mineral-soil effects. Based on the dominants, stable water regime was evident.

Mire expanse vegetation of rich lawn fens

Community 4 (*Carex flava–Trichophorum cespitosum–Campylium stellatum* community): represented lower lawn mire expanse vegetation with *Trichophorum cespitosum* as a dominant, while mire margin species were scarce. *Molinia caerulea* was constant. The dominants were indicators of unstable water regime, while some indicators of stable water regime also occurred (*Menyanthes trifoliata*, *Sphagnum warnstorfii*).

Sub-community 4.1 (*Loeskypnum badium* sub-community): represented slightly southern mire expanse vegetation and occurred at relatively low elevations (120–270 m a.s.l.) (Fig. 8). Intermediate-fen species *Loeskypnum badium* was constant, as well as rich-fen indicators *Carex flava*, *Eriophorum latifolium* and *Campylium stellatum*. Lawn indicators were the dominants *Trichophorum cespitosum* and *Campylium stellatum*.

Sub-community 4.2 (*Pseudocalliergon trifarium* sub-community): represented slightly northern mire expanse vegetation occurring at slightly higher elevations (170–330 m a.s.l.) (Fig. 8). Constant rich-fen indicators were the same as in sub-community 4.1., but additionally *Pseudocalliergon trifarium* was frequent. Intermediate fen species *Loeskypnum badium* was nearly absent. Extremely rich fen indicator *Catoscopium nigritum* was abundant in one plot.

Discussion

Gradient structure and gradients of different scale and significance

A three-dimensional vegetation gradient structure in eastern Finnish sloping fens revealed in this study resembles the three-gradient structures of Sjörs (1948), Ruuhijärvi (1960) and Persson (1962). Environmental variables (pH, temperature, precipitation), however, supported separation along only two dimensions in the ordination, and only few species groups were separated along the third dimension. The poor–rich gradient associated with pH formed the first dimension in the NMDS ordination. Increasing evidence shows that this gradient, related to pH (Tahvanainen 2004), or to pH and base cations (Sjörs & Gunnarsson 2002, Hajek *et al*. 2006), is the main gradient in fens (Sjörs 1948, 1952, Hájek *et al*. 2006, Peterka *et al*. 2017). In our study the poor–rich gradient was also associated with the topographic regions that formed a continuum in the ordination, with differences in the abundance of poor and rich fen vegetation among regions differing in bedrock. Thus, it seems that the type of bedrock affects variation in water chemistry and vegetation in the sloping fens of eastern Finland (*see* Tahvanainen 2004). A considerable proportion of rich fens (*Braunmoore*; Ruuhijärvi 1960) in eastern Finland (Havas 1961), may be due to the prevalence of mafic and calcareous bedrock in hill ranges in northwestern part of Northern Karelia, western part of Kainuu and northeastern part of Kuusamo uplands (Simonen 1987). Sjörs (1946) recorded a greater proportion of poor to intermediate fens on siliceous bedrock in the Central Scandes in Sweden.

A gradient along mire surface levels was associated with NMDS , although it was not particularly distinct, as there is less flark-level (wet surfaces) vegetation in sloping fens (Sjörs 1946, Persson 1962, Havas 1961) than in aapa mires (Ruuhijärvi 1960). The surface levels in boreal aapa mires are visible in aerial photos as dark flarks with open water, and lighter (mostly lawn level) belts where lawn and hummock levels mostly prevail (Laitinen *et al*. 2005, 2008a). Ruuhijärvi (1960) found a relationship between large-scale topographic patterns and compositional gradient of mire surface levels. In boreal areas, the surface level gradient is not associated with pH or fertility (*see* the discussion and references in Hájek *et al*. 2006). Hájková *et al*. (2004) found that water level is an important factor explaining within-site (small-scale) vegetation heterogeneity in the Carpathian fens. Small-scale variation in surface levels is also true for boreal mires (Tahvanainen & Tuomaala 2003), but it reflects the larger-scale surface patterns, which justifies its use in vegetation classification (Sjörs 1948, Ruuhijärvi 1960, Persson 1962, Eurola 1962). It should, however, be pointed out that sample plot sizes in studies carried out in Finland and in Scandinavia were too small (1 m^2 and 0.25 m^2, respectively) (Pakarinen 1995), just in order to capture small-scale differences in mire surface levels. However, also using larger phytosociological relevés, Hájek *et al*. (2005) interpreted the ‘succession-related moisture gradient’ as the major compositional gradient in subalpine-spring fens in the Vitosha Mountains in Bulgaria. Thus the mire surface level, as we call it here, is one of the important compositional gradients in fens across Europe (Moen 1990, Økland *et al.* 2001, Vanderpuye *et al.* 2002).

In the NMDS ordination, water regime stability formed the third dimension. Although Sjörs (1946) did not recognize this gradient in his sloping fen study in the oceanic Central Scandes, he found that sloping fens generally have certain features (high decomposition rate of the surface peat) that are associated with greater water level fluctuations (Sjörs 1948). Auer (1922), Havas (1961), Laitinen (2008) and Laitinen *et al*. (2008a, 2008b) emphasised the effect of seasonal peat-surface drying on peat humification, while Havas (1961) first specifically stressed the two extremes in the stability gradient although his interpretation rests on water-table measurements made at six different sites during one growing season (*see* Havas 1961: fig. 112). The prevalently unstable water regime of sloping fens (Sjörs 1946, Havas 1961, Moen 1990) sets them apart from peatlands that more commonly have a stable water regime (Zoltai & Vitt 1995). In our analysis the stable-to-unstable and the mire-margin-to-expanse gradients were connected and partly associated with the same ordination dimension (NMDS 3). Unstable water regime was mainly associated with mire expanse vegetation, while stable water regime was mainly associated with mire margin vegetation. Hydrological patterns in sloping fens partly explain the association between mire margin vegetation and stable water regime. In upper marginal parts of sloping fens, rising groundwater (*Quelligkeit*; Ruuhijärvi 1960) may mitigate seasonal drought (Havas 1961), while in the central parts of sloping fens with mire expanse vegetation, there is no such effect. Since runoff threshold is generally low due to existing slope, the central parts tend to dry out. In the much larger central parts of aapa mires, however, mire expanse vegetation under normal stable water regime largely prevails, as their flark-string system retains water and maintains high runoff threshold (Laitinen *et al*. 2005, 2008a). In sloping fens, the hummock *Sphagnum* species, especially *S. fuscum*, retain water and maintain a stable peat-moisture level (Rydin 1985), and because of that, in our study the hummock-level communities (9, 10, 11) dominated by *S. fuscum* had stable water regime.

Mire margin to expanse gradient (inflow of nutrients *vs*. self-sufficiency; Eurola *et al.* 1984, Eurola & Huttunen 2006, etc.) at least partly seems to correspond to the fertility gradient of Hájek *et al.* (2006) which is based on the abundance of nutrient-demanding herbs and grasses (Hájek *et al.* 2006). In addition to the *Filipendula* (Herb-Picea) species group (mire margin species of moist herb-rich forests), in our analysis we also used the *Festuca* (Meadow) species group to reveal historical anthropogenic effects. After the cessation of haymaking and grazing in the 1950s, a large number of meadow species was a special feature in eastern Finnish sloping fens, as the cessation paradoxically increased the number of those species (Moen 1990, Moen *et al.* 2011, Hajek *et al.* 2006). Meadow species are typical of the fens of the nemoral zone in mountainous areas, where the gradient is clearly different from the poor–rich one (Hájek *et al.* 2006, Jiménez-Alfaro *et al.* 2013). This was also true in the boreal eastern Finnish sloping fens, although the meadow species (*Wiesenartigkeit*; Havas 1961) formed only a minor gradient among mire margin communities of rich fens. Fertility or meadow gradient seems to be of minor importance in boreal Fennoscandian mires, as classified by Økland *et al*. (2001).

Temperature and precipitation, varying from south to north, were associated with NMDS 2, separating mire surface levels. Flark fens (community 12) represent northern vegetation among the communities of eastern Finnish sloping fens (Havas 1961) (Fig. 8). Northerly location of flark fens is associated with Finnish aapa mires, and with the effect of spring floods from melting of snow in those areas (Ruuhijärvi 1960, Laitinen *et al.* 2017). Additionally in sloping fens, poor fens tended to be less common towards the south (Fig. 5), as in the south where elevations are generally lower, the climate is not oceanic enough for the formation of sloping fens (*see* Eurola & Kaakinen 1982), except at sites with groundwater discharge and thus higher poor-rich status.

Species richness and environmental constraints

In the eastern Finnish sloping fens, species richness was positively related to the poor–rich and mire-expanse-to-margin gradient, and negatively to mire surface level. In other words, an increase in wetness resulted in a decrease in species richness, as was also found by Laitinen *et al*. (2017) for northern Finnish boreal wetland habitats, and by Hájek *et al*. (2005) for subalpine fens in the Vitosha Mountains, Bulgaria. Additionally, species richness was negatively related to stable-to-unstable water-regime gradient (water regime instability decreased species richness). It is remarkable that the maximum richness in the eastern Finnish sloping fens did not coincide with the highest pH but was found in communities with meadow species (*Festuca* group), spring-fen species (*Paludella* group), and species of herb-rich forests and herb-rich *Picea abies* mires (*Filipendula* group). In central Norwegian fens, the species richness was similarly highest (> 50 species) in a shrub-dominated fen margin of *Sphagno–Tomentypnion* (Moen *et al*. 2011), as it was in rich fens in central Europe (Hájek *et al.* 2006). Hájková and Hájek (2003) reported that in the flysch zone in the West Carpathians, communities transitional between fens and grasslands belong to the most species-rich vegetation types. We found that the increase in pH (to some degree), as well as in nutrient level (fertility) increased species richness, while extreme water conditions (constantly too wet/ seasonally too dry) reduced it.

Communities in different regions and climates

Eastern Finland and Scandinavia

Most communities in the eastern Finnish sloping fens were widely distributed within the area (Fig. 8). However, the two sub-communities (5.1 and 5.2) in the *Carex flava–Filipendula ulmaria–Campylium stellatum* community were clearly arranged in the south–north direction. The *Carex nigra* sub-community (5.1) represented southern (mid-boreal) vegetation of lower elevations, not occurring in the northern boreal area, while the *Saussurea alpina* sub-community (5.2) represented northern boreal mid-elevation vegetation of the Kuusamo area (Ruuhijärvi 1960, Söyrinki *et al*. 1977), not occurring in the mid-boreal area.

The *Trichophorum cespitosum–Sphagnum compactum–Ptilidium ciliare* community (1) was restricted to the highest elevations (350–400 m a.s.l.), and it may be viewed as indicating the highest possible hygric oceanity (but thermal continentality) among the eastern Finnish sloping-fen communities (*see* Eurola & Kaakinen 1982, Eurola *et al*. 1982, 1991, Paasovaara 1986). *Sphagnum compactum* Weissmoore (Ruuhijärvi 1960) were less oceanic, found in slightly sloping fens at lower elevations. The *Trichophorum cespitosum–Sphagnum compactum* community was found even in flat lowland aapa-mire peripheries. The latter two communities differed from the community of oceanic highlands (community 1) at least in lacking *Ptilidium ciliare*, an indicator of hygric oceanity in lawn fen vegetation (Eurola & Kaakinen 1982). Additionally, the *Eriophorum vaginatum–Sphagnum lindbergii–S. russowii* community (community 8) occurred at relatively high elevations (> 250 m a.s.l.) in sloping fens. This is exactly the elevation above which certain common treed-mire vegetation features of hygric oceanity (lack of *Chamaedaphne calyculata* and scarcity of *Ledum palustre*) appear in the mid-boreal part of our study area. The *Saussurea alpina* subcommunity (5.2) occurred above 250 m a.s.l. It, however, was found only in the Kuusamo area, most of which is located above 250 m a.s.l. Eurola and Kaakinen (1982) discussed the effect of increasing elevation and hygric oceanity only on the vegetation of poor rather than rich fens.

Boreal and alpine zones of the Central Scandes with an oceanic climate, form climatically and topographically optimal range for sloping fens (Sjörs 1946, Moen 1990, 1999, Joosten *et al*. 2017). Vegetation described by Sjörs (1946) (at 600 m a.s.l., Sweden) highlight the poor–rich gradient that included close counterparts to lawn-fen communities of extremely poor to rich fens described by Havas (1961). Additionally, Sjörs (1946: 12) described small areas of sloping fens with flarks. *Ptilidium ciliare* was more frequent in *Trichophorum* lawn communities of the Central Scandes than in communities of E Finland, and oceanic *Narthecium ossifragum* as well as slightly oceanic *Sphagnum pulchrum* were dominants. Using TWINSPAN, Moen *et al*. (2011) classified the vegetation of sloping rich-fen lawns in an area in central Norway close to the one studied by Sjörs (1948). They identified two communities — both having southern *Carex hostiana* and *Succisa pratensis* and alpine *Thalictrum alpinum* — not occuring in eastern Finnish sloping fens (Havas 1961). One of those communities identified by TWINSPAN was in the oceanic area at the elevation of 380–490 m a.s.l. (precipitation 1583 mm) and included oceanic *Erica tetralix*, and that at the less oceanic area at 700–800 m a.s.l. (precipitation 637 mm) included the alpine species *Kobresia simpliciuscula*, *Saxifraga aizoides*, *Pedicularis oederi*, and *Juncus triglumis* that were not found by Havas (1961).

The subalpine northern Scandinavian sloping fens described by Persson (1962) from northern Sweden (350–650 m a.s.l.) lacked *Molinia caerulea* which is frequent in sloping fens in milder and more oceanic parts of Fennoscandia (Auer 1922, Sjörs 1946, Havas 1961, Laitinen *et al*. 2011, Moen *et al*. 2011). Persson (1962: fig. 19) arranged communities two-dimensionally, i.e. along the bog–poor-fen–rich-fen gradient and along the mire surface levels, and studied mire margin communities outside those gradients. He described an *Trichophorum cespitosum–Calliergon sarmentosum–Drepanocladus badius* association of intermediate fens, which Havas (1961) did not consider, but for which Ruuhijärvi (1960) and Laitinen *et al*. (2011) found resembling types with *Molinia* from sloping fens in the Finnish aapa mire area. Intermediate fens are characterized by certain mid- to northern boreal mosses, such as *Loeskypnum badium*, *Sphagnum subfulvum* and *Warnstorfia sarmentosa* (*Braumoore-Weissmoore*; Ruuhijärvi 1960). Rydin *et al*. (1999) regarded intermediate fens as specifically boreal vegetation. Their assumed restricted distribution perhaps is partly due to unclear terminology or definitions, as noted by Hájek *et al*. (2006), who regarded ‘intermediate fen’ as a rarely recognized category. According to Havas (1961), however, intermediate fens (community 3) are a heterogeneous group with ecologically varying dominants, mostly with widely distributed *S. warnstorfii* (*see* Mikulášková *et al*. 2014, Laine *et al*. 2018).

Comparable vegetation in central and southeastern Europe

Sekulová *et al*. (2011) reported the *Trichophoro cespitosi–Sphagnetum compacti* association (Waren 1926) — analogous to community 1 of Havas (1961) — from the West Carpathians, in a subalpine–alpine belt in the nemoral zone in Slovakia and Poland (1500–2100 m a.s.l., precipitation > 1200 mm, mean annual temperature is ~0 °C). We found this boreal community at the highest elevations (350–400 m a.s.l.) among the communities of sloping fens but it had no true alpine species. Similarly, among Bulgarian high-mountain fen communities, *Sphagnum compactum* was most frequently present at the highest elevations (2100–2500 m a.s.l.) (Hájková *et al*. 2006). The Carpathian *Trichophoro cespitosi–Sphagnetum compacti* association includes alpine species (*Homogyne alpina*, *Campanula alpina* and *Soldanella carpatica*), while the boreal *Betula nana*, *Rubus chamaemorus*, and *Sphagnum lindbergii* are lacking. Sekulová *et al*. (2011) classified the Carpathian community into *Oxycocco–Sphagnetea* class (mainly bogs).

The *Molinia caerulea–Trichophorum cespitosum–Sphagnum compactum–S. papillosum* community 2 of Havas (1961) had no analogous vegetation in the West Carpathians (Sekulová *et al*. 2011) or in the Bulgarian mountains (Hájková *et al*. 2006).

Peterka *et al*. (2014) reported a *Sphagno warnstorfii–Tomentypnion* alliance from the Bohemian–Moravian highlands in the Czech Republic at the elevation between 450–730 m a.s.l., in the nemoral zone in (annual precipitation 600–900 m, mean annual temperature 5.0–6.5 °C). This is a major phytosociological vegetation type restricted to protected areas and annually mown sites having numerous threatened or regionally rare species (*Trichophorum alpinum*, *Carex dioica*, *C. chordorrhiza*, *C. limosa*, e.g.). The community resembled community 6 (*Carex magellanica–Filipendula ulmaria–Sphagnum warnstorfii* community) of Havas (1961), corresponding to boreal mire site type *Sphagnum warnstorfianum* rich fens (*Braunmoore*; Ruuhijärvi 1960). This rich-fen habitat (rich *Sphagnum* fen, Hájek *et al*. 2006) hosted boreal brown mosses (*Tomentypnum nitens*, *Paludella squarrosa*), which are considered glacial relicts in central Europe (Rybníček 1966).

Conradi and Fiedmann (2013) reported a small-sedge rich fen *Amblystegio stellate–Caricetum dioicae* community (Osvald 1925) from the Northern Limestone Alps in the montane belt of the nemoral zone in Germany (elevation 1100 m a.s.l., annual prepicitation 1750 mm, mean annual temperature 5 °C). This community can be considered analogous to rich-fen sub-communities 4.1 and 4.2 of Havas (1961), which correspond to a generally recognized boreal (Finnish) mire site type *Campylium stellatum* rich fens (*Braunmoore*; Ruuhijärvi 1960). *Trichophorum cespitosum* was frequent and partly dominant in the montane community as in boreal communities of Havas (1961) (but *see* Dítě *et al*. 2007: 404). In our study area, small cover of *Sphagnum subsecundum* and *S. warnstorfii* was a common feature with that in corresponding boreal rich lawn fens. Conradi and Friedmann (2013) placed the *Amblystegio stellate–Cari-cetum dioicae* community of the Alps in a rich-fen alliance *Caricion davallianae* (*Sheuchzerio palustris–Caricetea fuscae* class). However, they paid attention also to the presence of *Oxycocco–Sphagnetea* species (*Drosera rotundifolia*, *Vaccinium oxycoccos*), which is a feature common to mid- to northern boreal rich fens (Ruuhijärvi 1960, Havas 1961, Heikkilä 1987, Moen 1990, Moen *et al*. 2011).

The Bulgarian high-mountain fen communities (Hájek *et al*. 2005, Hájková *et al*. 2006) in southeastearn Europe clearly deviate from those of the eastern Finnish sloping fens by having species typical for the Balkan region. However, the most common fen-community in the Vitosha Mountains (*Cirsio heterotrichi–Caricetum nigrae*) includes the group of '*Molinion* species' (*Molinia caerulea*, *Succisa pratensis*, *Sanquisorba officinalis*, *Potentilla erecta*; Hájek *et al*. 2005) and *Trichophorum cespitosum* (belonging to *Molinia* species groups of Havas 1961). As Hájková *et al*. (2006) stated that *Molinion* species occur at temporarily wet sites, one may regard that species group as a southern ecological equivalent of the boreal *Molinia* group of Havas (1961), indicating unstable water regime. Thus, a peculiar vegetation-ecological feature characteristic of boreal oceanic sloping fens is present in a community of high-mountain alpine fens in southeastern Europe. On the other hand, the species representing the *Molinion* group of Hájek *et al*. (2005) are less frequent and much more dispersed across different communities within the sub-mountain mire associations of Bulgaria (Hájek *et al*. 2008). This fact further highlights certain ecological similarities among boreal sloping fens and montane–subalpine–alpine fens of more southern vegetation zones.

Conclusion

We suggest that the approach of Sjörs (1948) with three mire gradients, and that of Hájek *et* *al*. (2006) with two main gradients based on pH and calcium (poor–rich gradient), and fertility are basically similar, with differences between them resulting from different study scales (size of surface-level patterns, sample-plot sizes and extent of the study area), study methods, research approaches and terminologies. To us, it seems that the poor–rich gradient, related to pH and base cations, is the general (common) primary gradient in fen vegetation across all regions. The other gradients are associated with wetness (mire surface level), amounts of nutrients (fertility, mire margin–expanse) (Jiménez-Alfaro *et al*. 2013), or geographic-macroclimatic variation evident in continental scale vegetation surveys (Peterka *et al*. 2017). The gradient from stable to unstable water regimes plays a role in exceptional peat-forming conditions as in the boreal sloping fens (Auer 1922, Sjörs 1946, Havas 1961), in flat aapamire parts on water-permeable sand (Laitinen *et al*. 2005, 2008a, 2008b), and it shares some similarities with fen vegetation in subalpine–alpine belts of more southern vegetation zones.

The sloping fens in eastern Finland are diverse mires in the boreal zone, in a climate characterized by thermal continentality and hygric oceanity. They are structured along the poor–rich gradient and two vegetation-composition gradients. In general terms the vegetation gradients were complex and not directly comparable to those found elsewhere in Europe. Instead, we found some communities or vegetation types analogous across Europe, suggesting that European-wide classification schemes are feasible, while local variation deserves attention as well.

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Appendix 1. Description of the study area.

Topographic regions	Peripheral (P)	Northern uplands (NU)	Central hill range (CHR)	Southern hill range (SHR)
Location	E Kainuu, NE part of North Karelia, E part of Northern Ostrobothnia	Koillismaa	W Kainuu	NW to middle part of North Karelia
Hilltop elevation (m a.s.l.)	< 300	400–500	300–380	Mainly 200–300
Vegetation on hilltops	*Pinus sylvestris* and *Picea abies* forests	*Picea abies* forests, exceptionally treeless *Calluna* heath resembling fjelds	*Picea abies* forests, site types common at > 300 m a.s.l.	*Picea abies* and *Pinus sylvestris* forests
Prevailing elevations (m a.s.l.)	120–220	~250	150–250	120–200
Sloping fens	Rare	Frequent	Relatively frequent	Rare
Bedrock area	Mainly siliceous (granitic veins in basement gneiss)	Mainly siliceous (granitic veins in basement gneiss), partly calcareous	Partly calcareous	Siliceous (granitic veins in basement gneiss), partly calcareous
Forest zone*	Mid-boreal forest	Northern boreal forest	Mid-boreal forest	Southern margin of mid-boreal forest
Mire zone	Southern aapa mire	Mainly main aapa mire, partly southern aapa mire	Southern aapa mire	Southern aapa mire, partly eccentric bog
Mowing and grazing in sloping fens before the1950s	Rare	Rare	Common	Common
Vulnerability of sloping fens	Vulnerable	Not threatened	Vulnerable	Largely threatened

* sensu Kalela (1961)

Appendix 2. Indicator species groups. The groups are based mainly on the species groups in Havas (1961). Some species of contact habitats of boreal mires, occurring in the material, were added to show the continuum from mires into habitats other than mires.

L-Unstable = lawn species tolerant to unstable water regime (*Molinia* group)
Molinia caerulea
Trichophorum alpinum
Trichophorum cespitosum
Tofieldia pusilla
Selaginella selaginoides
Sphagnum compactum
S. papillosum
S. subfulvum
Sphagnum tenellum
Campylium stellatum (also L-Rich)
Ptilidium ciliare

L-Stable = lawn species of extremely poor fens with stabile water regime (*Eriophorum vaginatum* group)
Andromeda polifolia
Vaccinium oxycoccos
Carex pauciflora
Eriophorum vaginatum
Drosera rotundifolia
Sphagnum magellanicum
S. angustifolium

L-Rich = rich-fen indicators of lawn fens (*Campylium stellatum* group)
Carex flava
C. panicea
Eriophorum latifolium
Campylium stellatum (also L-Unstable)
Scorpidium revolvens
Catoscopium nigritum
Cinclidium stygium
Pseudocalliergon trifarium
Leiocolea rutheana (L. schulzii)
Aneura pinquis (Riccardia pinquis)

Flark = flark species (*Menyanthes* group)
Carex chordorrhiza
C. limosa
C. rostrata
Drosera longifolia
Menyanthes trifoliata
Rhynchospora alba
Utricularia minor
Sphagnum subsecundum
Scorpidium scorpioides

Hum-Pinus = hummock-level species of *Pinus sylvestris* mires (*Empetrum group*)
Pinus sylvestris
Calluna vulgaris
Chamaedaphne calyculata
Empetrum nigrum s. lato
Vaccinium microcarpum
Sphagnum fuscum
Cladonia rangiferina
C. arbuscula (C. sylvatica)

Hum-Picea = hummock-level species of poor *Picea abies* mires (*Carex globularis* group)
Picea abies
Vaccinium myrtillus
Carex globularis
Equisetum sylvaticum
Polytrichum commune

Herb-Picea = species of herb-rich forests/*Picea abies* mires (*Filipendula* group)
Filipendula ulmaria
Geranium sylvaticum
Angelica sylvestris
Convallaria majalis
Paris quadrifolia
Rubus saxatilis
Carex vaginata

Spring = spring fen species (*Paludella* group)
Paludella squarrosa
Warnstorfia sarmentosa
Rhizomnium pseudopunctatum
Plagiomnium elatum
Philonotis fontana
P. calcarea
P. sp.
Bryum pseudotriquetrum
Meesia uliginosa
Carex capillaris

Meadow = meadow species (*Festuca* group)
Agrostis canina
A. capillaris
Anthoxanthum odoratum
Festuca ovina
F. rubra
Hierochloe hirta ssp. *arctica*
Nardus stricta
Carex nigra
C. pallescens
Achillea millefolium
Cirsium palustre
Galium palustre
Prunella vulgaris
Ranunculus acris
Rhinanthus minor
Leucanthemum vulgare
Trifolium pratense
T. repens
Cerastium fontanum ssp. *vulgare*
Climacium dendroides
Fissidens adianthoides
Calliergonella lindbergii

Appendix 3. Havas (1961) stand groups (*Siedlungsgruppe*), based on floristic similarities and differences, with sub-communities.

Lawn groups
1 *Trichophorum cespitosum–Sphagnum compactum–Ptilidium ciliare* stand group
2 *Molinia caerulea–Trichophorum cespitosum–Sphagnum compactum–S. papillosum* stand group
3 *Molinia caerulea–Trichophorum cespitosum–Sphagnum warnstorfii* stand group
4.1 *Carex flava–Trichophorum cespitosum–Campylium stellatum* stand group, *Loeskypnum badium* sub-community
4.2 *Care flava–Trichophorum cespitosum–Campylium stellatum* stand group, *Pseudocalliergon trifarium* sub-community
5.1 *Carex flava–Filipendula ulmaria–Campylium stellatum* stand group, *Carex nigra* sub-community.
5.2 *Carex flava–Filipendula ulmaria–Campylium stellatum* stand group, *Saussurea alpina* sub-community
6 *Carex magellanica–Filipendula ulmaria–Sphagnum warnstorfii* stand group
7 *Betula nana–Eriophorum vaginatum–Sphagnum angustifolium* stand group
8 *Eriophorum vaginatum–Sphagnum lindbergii–S. russowii* stand group
Hummock-level groups
9 *Carex globularis–Sphagnum fuscum–S. russowii* stand group
10 *Vaccinium uliginosum–Sphagnum fuscum–S. angustifolium* stand group
11 *Calluna vulgaris–Molinia caerulea–Sphagnum fuscum* stand group
Flark vegetation
12 Flark (*rimpi*) vegetation