

# Regional and vegetation-ecological patterns in northern boreal flark fens of Finnish Lapland: analysis from a classic material

Jarmo Laitinen<sup>1</sup>, Jari Oksanen<sup>2</sup>, Eero Kaakinen<sup>3</sup>, Miia Parviainen<sup>4</sup>,  
Martin Küttim<sup>5</sup> & Rauno Ruuhijärvi<sup>6</sup>

<sup>1</sup> Ecology & genetics, Botanical Museum, P.O. Box 3000, FI-90014 University of Oulu, Finland

<sup>2</sup> Ecology & genetics, P.O. Box 3000, FI-90014 University of Oulu, Finland

<sup>3</sup> Kurkelantie 1 D 38, FI-90230 Oulu, Finland

<sup>4</sup> Natural Resources Institute Finland (Luke), P.O. Box 413, FI-90014 University of Oulu, Finland

<sup>5</sup> Institute of Ecology, School of Natural Sciences and Health, Tallinn University, Uus-Sadama 5, EE-10120 Tallinn, Estonia

<sup>6</sup> Pyytie 3, 01450 Vantaa, Finland

Received 21 Feb. 2017, final version received 20 Mar. 2017, accepted 27 Mar. 2017

Laitinen J., Oksanen J., Kaakinen E., Parviainen M., Küttim M. & Ruuhijärvi R. 2017: Regional and vegetation-ecological patterns in northern boreal flark fens of Finnish Lapland: analysis from a classic material. — *Ann. Bot. Fennici* 54: 179–195.

We analysed and interpreted ecologically a part of classic peatland vegetation material of prof. Rauno Ruuhijärvi dating from 1960. Sample plots formed a compositional gradient along NMDS 1 across three traditionally recognized peatland subzones of Finnish Lapland, and Cajanderian site types showed a poor–rich gradient along NMDS 2. Analysis-based major vegetation groups were related to the regional and the mire-expanse-to-margin gradient. Southerly-focused *Eriophorum gracile*–*Potentilla palustris*–*Stramineum stramineum* major group was interpreted as an indication of a more voluminous spring flood in a more oceanic climate, while northerly-focused *Carex rotundata*–*Trichophorum cespitosum* m. g. was interpreted as a reflection of a minor spring flood in a more continental climate. Regional communities were compatible with Cajanderian site types and showed new regional and vegetation-ecological features for site types. They were related to three European fen alliances, which represented boreal (*Stygio-Caricion limosae*), arcto-boreal-alpine (*Drepanocladion exanulati*) and widespread (*Scheuchzerion palustris*) vegetation.

## Introduction

Mires in treeless fjelds belong to the least studied peatland types in Finland. Such sites are scattered and very small in area; they are more numerous in Sweden and Norway, which host the mountain range of the Scandes (Moen 1999, Rydin *et al.* 1999). Finnish Lapland, here referred to as an

area roughly north of the Arctic Circle in Finland, is generally flatter and more low-lying with three different landscapes. The southernmost part (*Peräpohjola*) is characterized by *Picea abies* and *Pinus sylvestris* forests, the transitional zone north of it (Forest Lapland) is characterized by *P. sylvestris* forests and treeless fjelds, while the northernmost part (Fjeld Lapland) is char-

acterized by subalpine mountain birch (*Betula pubescens* ssp. *czerepanovii*) woodlands and treeless fjelds (Kalela 1958, 1961). Roughly the same three regions were applied for Cajanderian peatland complex types (*Moorkomplextypen*; Ruuhijärvi 1960). *Peräpohjola aapa*-mires (the main *aapa*-mire zone, Ruuhijärvi & Hosiaisuus 1987, see also Vitt *et al.* 1975) are characterized by a pattern of the wettest and largest flarks and narrow lawn strings. Forest Lapland *aapa*-mires are characterized by a pattern of broad and fragmented hummock-level strings, flarks, and small and partly frozen hummocks known as *pounu*. *Palsa*-mires in Fjeld Lapland are characterized by higher and frozen *palsa*-hummocks upwelling from and sinking back into the flarks. Eurola and Vorren (1980) assigned classic peatland regions of Finnish Lapland to boreal peatland subzones: the *Peräpohjola aapa*-mire zone (PeP) belongs to the northern boreal southern (NBs) peatland subzone, while hygrially more continental zones of Forest Lapland *aapa*-mires (ForL) and Fjeld Lapland *palsa* mires (FjeL) belong to the northern boreal northern (NBn) peatland subzone. Large areas with subalpine mountain birch woodlands in Finnish Fjeld Lapland, which actually include most of the *palsa* mire complexes studied by Ruuhijärvi (1960), were assigned to the northern oroboreal (NoB) zone *sensu* Haapasaari (1988). Oksanen and Virtanen (1995) and Virtanen *et al.* (1999) view the continental fjeld-dominated area east of the Scandes in northernmost Fennoscandia as an extension of the circumpolar hemiarctic zone (forest tundra), while Eurola and Vorren (1980) and Vorren *et al.* (1999) assigned it to the northern boreal zone and considered only a narrow strip in the northeastern coast of Fennoscandia to belong to the hemiarctic zone.

Flark fens are minerotrophic mires with the wettest surface level along the compositional gradient from the hummock level to lawn to the flark level (Sjörs 1948, Laitinen *et al.* 2008a). In Cajanderian mire classification (Cajander 1913, Ruuhijärvi 1960, Eurola 1962), mire site types (*Moortypen*) are rather narrowly-delimited (relatively homogenous) vegetation types, whereas mire site groups (*Moortypengruppen*; Eurola 1962) refer to high-level division of mire vegetation. ‘Cajanderian’ refers here to

the site types and groups tentatively described by Cajander (1913) and established later by Ruuhijärvi (1960) and Eurola (1962). Classification versions of Eurola and Kaakinen (1978) and Eurola *et al.* (1984, 1995, 2015) include six site-groups, whose original German reference names (Cajander 1913, Brandt 1948, Ruuhijärvi 1960, Eurola 1962) are *Bruchmoore* (*Picea abies* mires), *Reisermoore* (*Pinus sylvestris* mires), *Weissmoore* (poor fens), *Braunmoore* (rich fens), *Sumpfoore* (swamps i.e., treeless or treed mire vegetation dominated by littoral species) and *Quellmoore* (spring fens). Flark fens are included in poor fens (*Weissmoore*) and rich fens (*Braunmoore*).

In Cajanderian classification, vegetation units of whatever scale are thought to be fixed points in an ecological framework represented by three ‘mire gradients’: the trophic level or poor–rich gradient, the mire surface-level gradient, and the mire margin-expanse gradient (Ruuhijärvi 1960, Eurola *et al.* 1984, 1995, 2015, Ruuhijärvi & Lindholm 2006). This approach can be characterized as a three-gradient approach being used in the Nordic Countries (see Økland *et al.* 2001), which partly differs from British and central-European approaches (Wheeler & Proctor 2000, Hájek *et al.* 2006, Jiménez-Alfaro *et al.* 2014, Peterka *et al.* 2017). The primary division of six Finnish mire-site groups takes place along the mire margin-expanse gradient: poor fens, rich fens, and pine mires represent primarily mire expanse vegetation, while *Picea abies* mires, treeless and treed swamps and spring fens represent mire margin vegetation (cf. Økland *et al.* 2001).

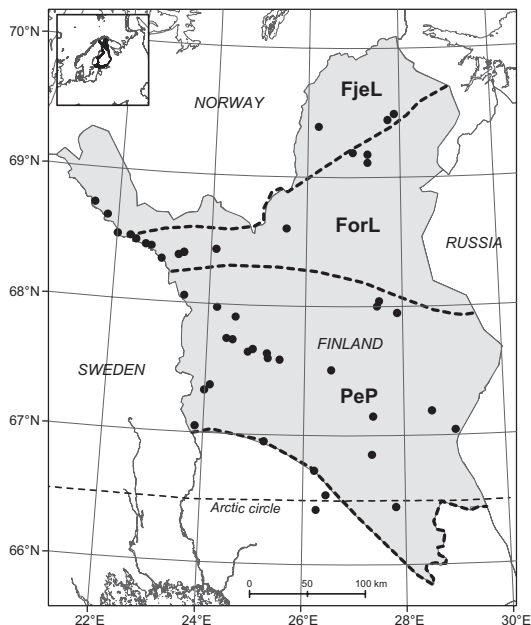
Seven Cajanderian mire site types (Ruuhijärvi 1960, 1983, Eurola 1962, Eurola *et al.* 1984, 1995, 2015) are included in the northern boreal flark-fen material of Ruuhijärvi (1960) (Table 1). He additionally described regional plant communities within site types, but their compositional relationships and regional patterns were not tested. Modern universal habitat-type conservation and ecological research call for a scrutiny of the regional plant communities in a larger, regional context (Peterka *et al.* 2017). Recently, phytosociological classification of fens from western Siberia to Europe and southeastern Greenland was harmonized by way of defining 13 alliances supported by the data, and creating

distribution maps for each alliance (Peterka *et al.* 2017). At present, that classification provides a coarse regional context for smaller-scale vegetation units from different parts of Europe and from different classification systems. Additionally, unsupervised vegetation classifications are used for smaller areas or as tests of the validity of supervised, formalized classifications (Vorren & Johansen 1990, Peterka *et al.* 2017). Pakarinen and Ruuhijärvi (1978) started the multivariate analysis of northern Finnish mire vegetation. We analysed a part of the sample plot material of Ruuhijärvi (1960) with the aim to find an unsupervised classification, which optimally considers the ecological variation shown by seven Cajanderian mire-site types and the regional variation within and among the three classic boreal peatland subzones (PeP, ForL, FjeL). We addressed three questions: (1) How does the vegetation hierarchy, shown by the cluster analysis, stress regional *vs.* ecological aspects within compositional gradients, and what species-richness patterns do flark fens have? (2) What new features do regional communities convey for Cajanderian mire site types and site groups? (3) How do regional communities of NB flark fens in Finnish Lapland relate to communities of treeless fjelds of Finnish Lapland, and to European fens, as shown by the recent phytosociological fen-classification?

## Material and methods

### Study area

Study area (*see* Fig. 1) included the northern



**Fig. 1.** Map of the study area. PeP = *Peräpohjola aapa-mire zone* (main *aapa-mire zone*), ForL = *Forest Lapland aapa-mire zone*, FjeL = *Fjeld Lapland aapa-mire zone*. The dots show site locations.

boreal (NB) peatland zone (Eurola & Vorren 1980) of Finland. Partly highly calcareous Kuusamo area in the southeastern corner of the NB peatland zone was excluded. The area belongs to the Fennosarmatian Precambrian bedrock block (Alalammi 1990) with glacial deposits. Annual mean temperatures just before the time of the field survey were from about  $-1$  to  $+0.5$  °C, and the effective temperature sum of the growing season from 800 to 600 °C (Kolkkki 1959 as cited in Ruuhijärvi 1960).

**Table 1.** Site types included in the analysis, their trophic level and original German site-type names and table numbers in Ruuhijärvi (1960).

Abbr.	Site types in English	Trophy	Original German site-type names [table number in Ruuhijärvi (1960)]
Sph	<i>Sphagnum</i> flark fens	Oligotrophic	<i>Sphagnum Rimpiveissmoore</i> [13]
Mud-Ol	Oligotrophic mud bottom flark fens	Oligotrophic	<i>Oligotrophe moosarme Rimpiveissmoore</i> [16]
Mud-Me	Mesotrophic mud bottom flark fens	Mesotrophic	<i>Mesotrophe moosarme Rimpiveissmoore</i> [17]
Fluit	<i>Warnstorfia fluitans</i> flark fens	Oligotrophic	<i>Drepanocladus fluitans Rimpiveissmoore</i> [14]
Ex	<i>Warnstorfia exannulata</i> flark fens	Mesotrophic	<i>Drepanocladus exannulatus Rimpiveissmoore</i> [14]
Sco	<i>Scorpidium scorpioides</i> flark fens	Eutrophic	<i>Scorpidium Rimpibraunmoore</i> [25]
Rev	<i>Scorpidium revolvens</i> flark fens	Eutrophic	<i>Drepanocladus revolvens Rimpibraunmoore</i> [26]

## Site types, sample plots and species nomenclature

We used only a part of the vegetation data [i.e., flark fens (*Rimpiweissmoore*, *Rimpibraunmoore*)] of the classic phytogeographic survey of Ruuhijärvi (1960: *see* tables 13, 14, 16, 17, 25 and 26) from northern Finland (*see* Fig. 1 for plot locations and Table 1 for site-type nomenclature). Sample-plot sizes of Ruuhijärvi (1960) varied and the plots were not placed in the field randomly but they were located in uniform-looking vegetation areas or patches. All the flark fen vegetation, except of *Calliergon richardsonii* flark fens with a restricted distribution, was analysed by us, including the flark fen sample plots from the Fjeld Lapland *palsa*-mire, the Forest Lapland *aapa*-mire and the *Peräpohjola aapa*-mire zones in Finnish Lapland and *Peräpohjola*. Nomenclature of vascular plants follows Hämet-Ahti *et al.* (1998), and that of mosses follows Ulvinen *et al.* (2002). Numbers of species (species richness) refer almost exclusively to vascular plants and mosses (Bryophyta), as only few hepatics were present in the original material.

## Nomenclature and description of analysis-based vegetation units

Analysis-based vegetation units of the highest level (major groups) were named according to characteristic species occurring in several of small-scale communities within that major group. Units of intermediate level (groups) were named according to dominant species in a large part of the group, and the lowest-level units (communities) were named according to species distribution patterns and the dominant or nearly-dominant species in the bulk of the community. Poor–rich status of the communities was assigned according to a Fennoscandian concept. Classic indicator species lists of Euroala and Kaakinen (1978), Euroala *et al.* (1984, 1995, 2015) and Euroala and Huttunen (2006) were used: oligotrophy in the lists corresponds to extreme-poor fen in our communities, mesotrophy to moderate-poor fen, meso-eutrophy to intermediate fen, and eutrophy to rich fen. Flark-level communities dominated by Hepaticae were

included in mud-bottom communities (Rydin & Jeglum 2013).

## Data analyses

The data were ordinated using non-metric multidimensional scaling, which is a robust ordination method for heterogeneous data (Minchin 1987). We used robust options of weak ties and classic stress (Kruskal 1964). We used Bray-Curtis' dissimilarity after Wisconsin double transformation of square-root-transformed data. The original data consisted of visually estimated cover percentage values, so we used square-root transformation to reduce the effect of highest cover values. In Wisconsin transformation, each species is first divided by its maximum abundances and then all sample plots are divided by their total abundances (Faith *et al.* 1987). This transformation gives the classical "strict" Bray-Curtis' measure (Yoshioka 2008) and also avoids the spurious dissimilarities in the data caused by different total abundances (Warton *et al.* 2012).

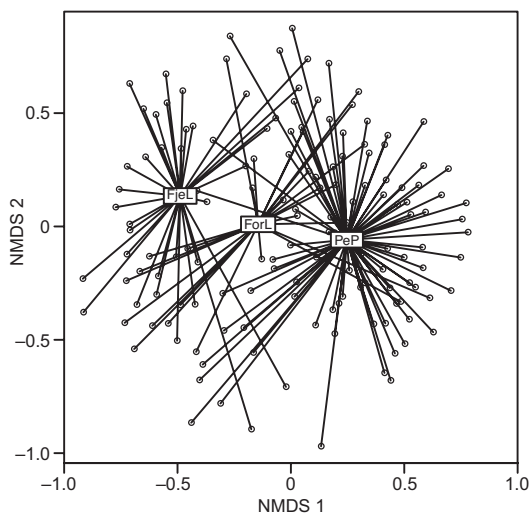
Cluster analysis was performed by hierarchic agglomeration of the original data so that at each step the increase in Shannon-Weaver's diversity index was minimized. Clustering does not use any explicit dissimilarity measure but gives homogeneous clusters in terms of their diversity. The idea is similar as in classic information clustering of Williams *et al.* (1966), but uses quantitative data.

All analyses were performed in the R statistical environment (R Core Team 2017) using add-on packages *vegan* (Oksanen *et al.* 2017; <https://cran.r-project.org/>) and *natto* (<https://github.com/jarioksa/natto/>).

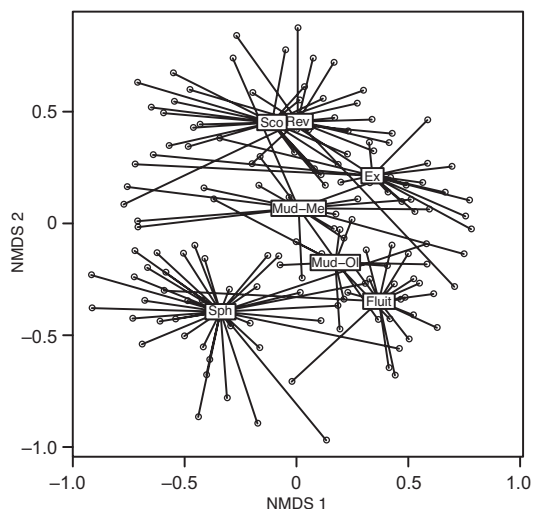
## Results

### Regional gradient in ordination

In the ordination (Fig. 2), there was a regional (climatic) gradient along the horizontal dimension (NMDS 1): peatland zones followed each other in the order in which they appear in the field from the north to the south (FjeL, ForL, PeP). The gradient was slightly oblique from the left top to the right bottom (Fig. 2).



**Fig. 2.** Ordination of sample plots for northern boreal regions. PeP = *Peräpohjola* (northern boreal southern), ForL = Forest Lapland, FjeL = Fjeld Lapland.



**Fig. 3.** Ordination of sample plots for site types. For site-type names, see Table 1.

### Site types in ordination

Plots of types defined by Ruuhijärvi (1960) largely overlapped in the ordination graph, but the centres of site types were situated highly relevantly in relation to each other (Fig. 3). Centres of the oligotrophic site types (Sph, Fluit, Mud-OI) were as a broad zone in the bottom part of the graph, those of the mesotrophic site types (Mud-Me, Ex) were as a narrow zone in the middle of the graph, while those of the rich-fen site types (Sco, Rev) were close to each other in the upper part of the graph. The vertical gradient (NMDS 2) corresponded to the poor–rich gradient. NMDS 1 varied towards *Warnstorffia exannulata* flark fens (Ex) and *W. fluitans* flark fens (Fluit). Direction of variation from bottom left (*Sphagnum* flark fen, Sph) to top right (all the other site types) in the ordination represented a minor moist–wet gradient.

### Cluster analysis: major groups, groups, communities

After several attempts, we found an analysis-based classification with 12 communities as an optimal solution to jointly consider the ecological variation in the classic site types (Sph,

Mud-OI, Mud-Me, Fluit, Ex, Sco, Rev) and the geographical variation in the classic peatland subzones (PeP, ForL, FjeL) (Fig. 4 and Table 2). In the first step, cluster analysis discriminated two, almost equally large, major groups. The *Carex rotundata*–*Trichophorum cespitosum* major group (communities 1–7) was on the left-hand side in the ordination (Fig. 5), and it was fairly evenly distributed in the three regions (FjeL, ForL, PeP). Characteristic species included *Betula nana* and *Vaccinium microcarpum*, less clearly *Carex pauciflora*, *Trichophorum alpinum*, *Carex livida*, *C. rariflora* and *Cetraria delisei*. The *Eriophorum gracile*–*Potentilla palustris*–*Straminergon stramineum* major group (communities 8–12) was in the ordination on the right-hand side (Fig. 5) with its centre in the southernmost region (PeP). That major group was additionally characterized by *Sphagnum obtusum*.

The second-level division differentiated four groups according to dominant moss species. The third-level division (not named) split the *Scorpidium scorpioides* group according to moss dominants (*S. scorpioides* vs. *S. revolvens*). The *Sphagnum lindbergii* group was divided into a *Hepaticae*-rich mud-bottom entity (community 5) and a *Sphagnum*-dominated entity (communities 6 and 7). *Warnstorffia exannulata*

group was split into an entity with rich-fen mosses and larger distribution (FjeL–ForL–PeP) (community 8), and an entity with no rich-fen mosses and a narrower (PeP) distribution (communities 9 and 10). *Warnstorfia fluitans* group was divided into a community dominated by *W. fluitans* (community 11) and a community dominated by *Sphagnum majus* (community 12).

### *Scorpidium scorpioides* group

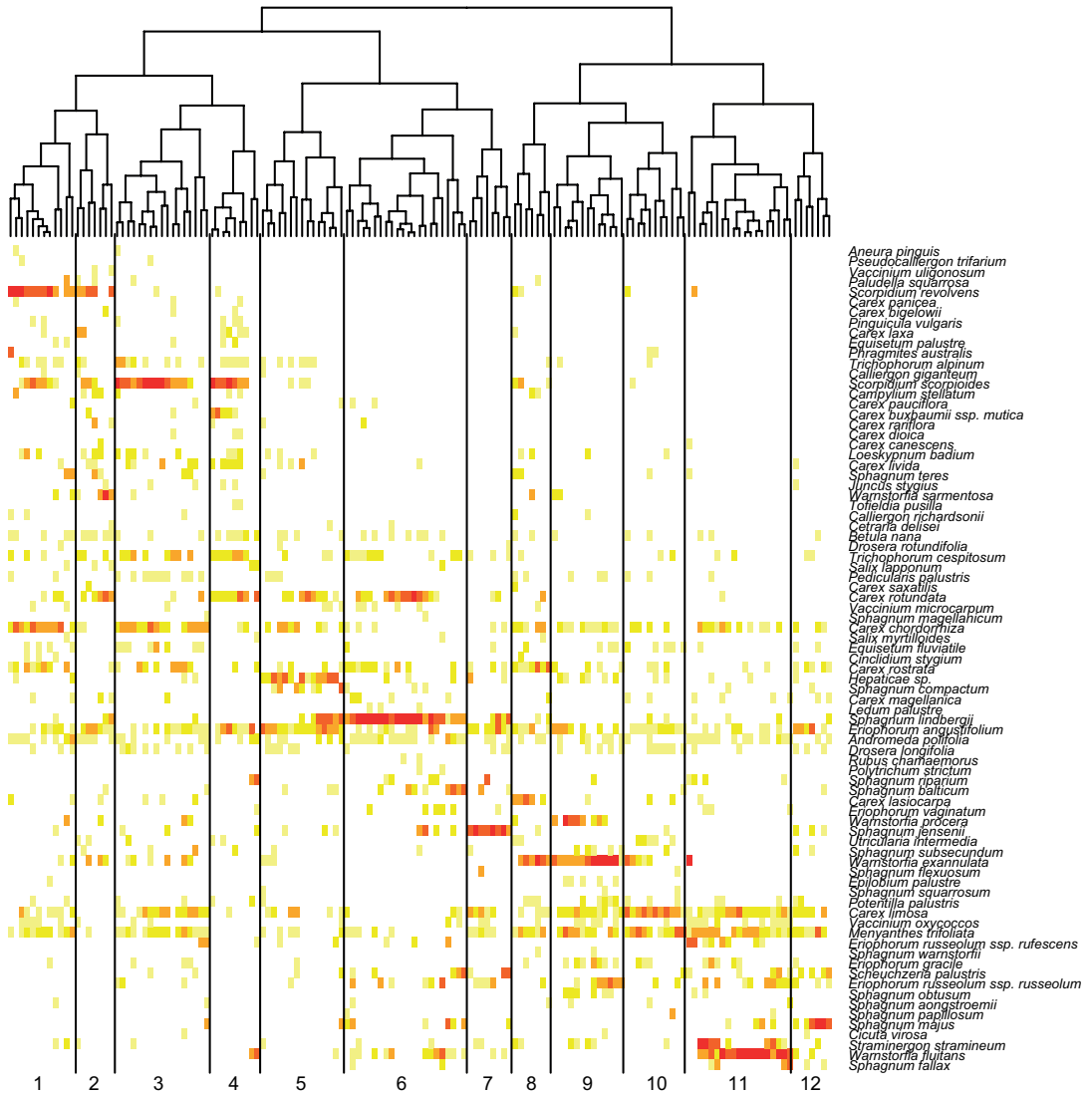
The *Scorpidium scorpioides* group (communities 1–4) was representative of moderately rich fens. The group was centred in the northernmost (FjeL) and southernmost (PeP) regions,

while in the transitional region (ForL) it was less common. *Scorpidium revolvens*, *Loesky-pnum badium*, *Equisetum palustre* and *Carex bigelowii* (infrequent) additionally characterized this group. Northern (FjeL) occurrences of *Menyanthes trifoliata* clearly outnumbered its occurrences in other groups, i.e., in poorer fens.

Community 1 [northern boreal (NB) *Carex chordorrhiza*–*Menyanthes trifoliata*–*Scorpidium revolvens* community]: Occupied the second highest number of plots belonging to the *Scorpidium scorpioides* group. The average number of species was 12 (range = 10–17). The signature species of the group, *Scorpidium scorpioides*, was scattered among the plots. *Cinclidium stygium* was almost exclusive to this commu-

**Table 2.** Sample plots distributed in regional plant communities of northern boreal flark fens of Finnish Lapland, related to the classic site types and peatland zones. “Major group” and “group” show the first- and second-level divisions from the cluster analysis. The community numbers (third-level division) refer to cluster numbers. A 12-cluster solution (12 plant communities) optimizes the classification in terms of the classic site types and classic peatland zones. Site types: Rev = *Scorpidium revolvens* flark fens, Sco = *Scorpidium scorpioides* flark fens, Sph = *Sphagnum* flark fens, Ex = *Warnstorfia exannulata* flark fens, Fluit = *Warnstorfia fluitans* flark fens, Mud-Me = Mesotrophic mud-bottom flark fens, Mud-Ol = Oligotrophic mud-bottom flark fens. Regions: FjeL = Fjeld Lapland, ForL = Forest Lapland, PeP = *Peräpohjola*. Zonal designations of regional plant communities: NB = northern boreal (*Peräpohjola*, Forest Lapland, mountain birch zone of Fjeld Lapland), NoB = northern oroboreal (mountain birch zone of Fjeld Lapland), NBs = northern boreal southern (*Peräpohjola*).

Major group/group/community	Site type							Region		
	Rev	Sco	SpH	Ex	Fluit	Mud-Me	Mud-Ol	FjeL	ForL	PeP
<i>Carex rotundata</i> – <i>Trichophorum cespitosum</i> major group										
<i>Scorpidium scorpioides</i> group										
1 NB <i>Car cho-Men tri-Sco rev</i> com.	10	1				1		3	2	7
2 NoB <i>Car rot-Eri ang-Sco rev</i> com.	4	1		2				6		1
3 NB <i>Car cho-Men tri-Sco sco</i> com.		14				2	1	1	5	11
4 NoB <i>Car rot-Eri ang-Sco sco</i> com.		7			2			9		
<i>Sphagnum lindbergii</i> group										
5 NB <i>Eri ang-Hepa</i> sp. com.			5			8	2	6	6	3
6 NB <i>Car rot-Sch pal-Sph lin</i> com.			21				1	7	8	7
7 NB <i>Eri ang-Sph jen</i> com.			8					1	1	6
<i>Eriophorum gracile</i> – <i>Potentilla palustris</i> – <i>Straminergon stramineum</i> major group										
<i>Warnstorfia exannulata</i> group										
8 NB <i>Car ros-Car las-War exa</i> com.		2		4		1		2	3	2
9 NBs <i>Car lim-Men tri-War exa</i> com.				11		2				13
10 NBs <i>Car lim-Men tri mud-bottom</i> com.				1		5	5			11
<i>Warnstorfia fluitans</i> group										
11 NBs <i>Car lim-Men tri-War flu</i> com.	1			1	17				2	17
12 NBs <i>Men tri-Sph maj</i> com.			4			1	2			7

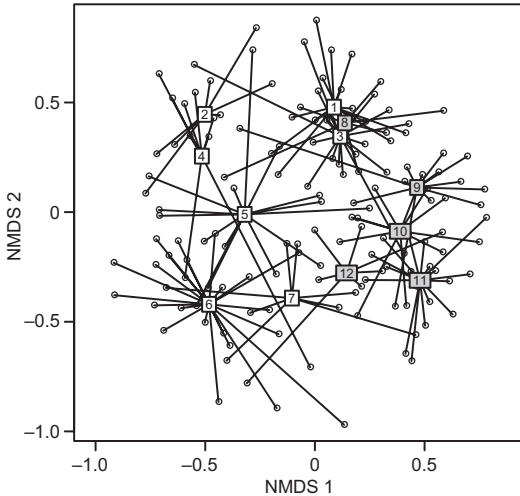


**Fig. 4.** Cluster analysis of the northern boreal flark fens in Finnish Lapland. For the names of communities 1–12, see Table 2. Sample plots (colour squares) are horizontally, species vertically. Dendrogram was created and species ordered by the first axes of correspondence analysis giving a diagonal structure of species occurrences. The colour scale is from pale yellow to dark red with cut points > 0%, 5%, 20%, 40% and 70% cover.

nity. *Menyanthes trifoliata*, *Carex rostrata*, *C. limosa* and partly *Trichophorum alpinum* were relatively evenly distributed among the plots, while *Equisetum fluviatile* and *Drosera longifolia* occurred less frequently.

Community 2 [northern oroboreal (NoB) *Carex rotundata*–*Eriophorum angustifolium*–*Scorpidium revolvens* community]: Typical of moderately rich to intermediate (to moderately poor) fens. The average numbers of species was

12 (range = 11–14). *Carex limosa*, *Equisetum fluviatile* and *Drosera longifolia* were absent, and *Menyanthes trifoliata* nearly absent. *Betula nana* was frequent, and *Warnstorfia exannulata* relatively frequent. Next division level showed a subdivision into a moderately rich sub-community dominated by *Eriophorum angustifolium*, *Scorpidium revolvens* and *S. scorpioides* and a spring-influenced sub-community dominated by *Carex rotundata* and *Warnstorfia sarmentosa*.



**Fig. 5.** Ordination of sample plots for 12 communities from the cluster analysis. For communities see Table 2. Centers of communities 1–7 belonging to major group 1 (*Carex rotundata*–*Trichophorum cespitosum* major group) are marked with white, while the centres of communities 8–12 belonging to major group 2 (*Eriophorum gracile*–*Potentilla palustris*–*Stramineogon stramineum* major groups) are marked with grey.

*Campylium stellatum* and *Carex rariflora* were most frequent in this community. *Carex saxatilis*, *C. bigelowii* and *C. laxa* were occasional.

Community 3 [northern boreal (NB) *Carex chordorrhiza*–*Menyanthes trifoliata*–*Scorpidium scorpioides* community]: Occupied the highest number of plots belonging to the *Scorpidium scorpioides* group. It was centred in the middle (ForL) and southern (PeP) parts of the study area. The average number of species was 11 (range = 4–18). *Carex limosa* was quite common and locally abundant. Among the communities of the *Scorpidium scorpioides* group, *Pedicularis palustris*, *Equisetum fluviatile* and *Drosera longifolia* were most frequent in this community, and *Scheuchzeria palustris* was found only in this community (in PeP).

Community 4 [northern oroboreal (NoB) *Carex rotundata*–*Eriophorum angustifolium*–*Scorpidium scorpioides* community]: The average numbers of species was 11, i.e. the same as in community 3 (range = 6–18), but there were more plots with a smaller number of species. *Menyanthes trifoliata*, *Equisetum fluviatile*, *Drosera longifolia* and *Carex lasiocarpa* were

absent, *Carex limosa* nearly so. *Trichophorum cespitosum*, *Carex buxbaumii* ssp. *mutica*, *C. livida* and *C. laxa* were more frequent than in any other community. *Betula nana* was frequent, *Trichophorum alpinum* relatively frequent. Occasional *Tofieldia pusilla* occurred only in this community. *Juncus stygius* and *Carex dioica* were most frequent in some plots. *Carex bigelowii* occurred occasionally. Unlike in all the other communities of this group, *Warnstorfia sarmentosa* and *W. exannulata* were absent.

### *Sphagnum lindbergii* group

*Sphagnum lindbergii* group (communities 5–7) was representative of extremely poor fens, and was distributed across all the three regions (PeP, ForL, FjeL). The group was further characterized by *Sphagnum balticum*.

Community 5 [northern boreal (NB) *Eriophorum angustifolium*–Hepaticae spp. community]: Representative of moderately poor and partly extremely poor fens. The average numbers of species was 9 (range = 5–15). *Eriophorum angustifolium* dominated in the field layer of most of plots, and only rarely *Carex rotundata* was dominant (in Forest Lapland). *Trichophorum alpinum* was fairly frequent. *Carex limosa* and especially *Menyanthes trifoliata* were sparse. Dominants in the bottom layer were either Hepaticae spp. (mud-bottom, in most plots) or *Sphagnum lindbergii*. *Sphagnum compactum* was relatively frequent and partly abundant.

Community 6 [northern boreal (NB) *Carex rotundata*–*Scheuchzeria palustris*–*Sphagnum lindbergii* community]: Representative of extremely poor fens with a low average number of species (8; range = 4–13). This was a community with a pronounced within-community compositional variation related to NBn (FjeL, ForL) and NBs (PeP) subzones as the next division level showed a regional subdivision into NBn and NBs sub-communities. In the NBn sub-community, *Carex rotundata* and *Sphagnum lindbergii* were dominant (majority of plots), and *Scheuchzeria palustris* was lacking. In the NBs sub-community, *Scheuchzeria palustris*, *Sphagnum balticum* and partly *S. majus* were



dominant, and *Carex rotundata* was lacking. *Warnstorfia fluitans* was relatively frequent, and *Eriophorum vaginatum* and *Vaccinium microcarpum* were most frequent.

Community 7 [northern boreal (NB) *Eriophorum angustifolium*–*Sphagnum jensenii* community]: The average number of species was very low (7; range = 5–10). It was common in plots of the southern part of the northern boreal zone (PeP). *Sphagnum lindbergii* was abundant in about half of the plots, and *Eriophorum russeolum* ssp. *russeolum* occurred in half of the plots. *Carex limosa* and *Menyanthes trifoliata* were fairly frequent. *Scheuchzeria palustris* was dominant in two southern (PeP) plots, while *Carex rotundata* was present in two northern (ForL, FjeL) plots.

#### *Warnstorfia exannulata* group

*Warnstorfia exannulata* group (communities 8–10) was principally representative of moderately poor (mesotrophic) fens. *Carex lasiocarpa* weakly characterized the group, and the group was centred in the south (PeP).

Community 8 [northern boreal (NB) *Carex rostrata*–*Carex lasiocarpa*–*Warnstorfia exannulata* community]: Representative of moderately poor to moderately rich fens. The average number of species was 10 species (range = 9–18). In the ordination (Fig. 5), the community was close to moderately rich-fen communities 1 and 3 because of the presence of *Scorpidium scorpioides* and *Sphagnum teres*. *Scorpidium revolvens*, *Campylium stellatum* and *Loeskyppnum badium* occurred in two plots of the seven. *Menyanthes trifoliata* was common and partly abundant. *Carex chordorrhiza* was frequent, *C. limosa* relatively frequent, and *Potentilla palustris* was present in almost half of plots. *Carex laxa* was occasional.

Community 9 [northern boreal southern (NBs) *Carex limosa*–*Menyanthes trifoliata*–*Warnstorfia exannulata* community]: Occupied the highest number of plots belonging to the *Warnstorfia exannulata* group. The average number of species was 11 (range = 6–14). *Carex chordorrhiza* was quite common. *Eriophorum angustifolium*, *Carex limosa* and *Menyanthes*

*trifoliata* were the field-layer dominants in one sub-community, and *Eriophorum russeolum* ssp. *russeolum* was the dominant in another sub-community. The main species in two plots of the former sub-community were *Eriophorum angustifolium*, *Warnstorfia exannulata* and *W. sarmen-tosa*. *Epilobium palustre* and *Sphagnum obtusum* were almost exclusive to this community. *Eriophorum gracile* was most frequent. *Warnstorfia procera* and *Sphagnum subsecundum* were most typical of this community.

Community 10 [northern boreal southern (NBs) *Carex limosa*–*Menyanthes trifoliata* mud-bottom community]: Representative of moderately poor and extremely poor fens. The average number of species was 7 (range = 5–21). *Eriophorum angustifolium* was most common, while *Carex chordorrhiza* was less frequent. *Equisetum fluviatile* was more frequent than in other communities of the *Warnstorfia exannulata* group. *Utricularia intermedia* was typical of this community. *Drosera longifolia* was relatively frequent. *Warnstorfia exannulata* occurred only in some plots. *Trichophorum alpinum*, *Scorpidium scorpioides*, *Sphagnum subsecundum*, *S. teres* and *Loeskyppnum badium* were occasional.

#### *Warnstorfia fluitans* group

*Warnstorfia fluitans* group (communities 11–12) was principally representative of extremely poor fens. *Sphagnum fallax* characterized the group. The group was centred in the southern region (PeP).

Community 11 [northern boreal southern (NBs) *Carex limosa*–*Menyanthes trifoliata*–*Warnstorfia fluitans* community]: Occupied the highest number of plots belonging to the *Warnstorfia fluitans* group. The average number of species was 9 (range = 5–14). *Vaccinium oxycoccos* was frequent, and *Carex chordorrhiza* and *Andromeda polifolia* were relatively frequent. In a larger sub-community, *Eriophorum russeolum* ssp. *rufescens* was quite dominant along with *Carex limosa* and *Menyanthes trifoliata*. In a smaller sub-community, *Eriophorum russeolum* ssp. *russeolum* dominated along with *Carex limosa* and *Menyanthes trifoliata*. *Straminergon stramineum* was typical to this community.

*Sphagnum majus* occurred with moderate frequency. *Sphagnum riparium* rare, and *S. fallax* was quite typical of this and the next community.

Community 12 [northern boreal southern (NBs) *Menyanthes trifoliata*–*Sphagnum majus* community]: The average number of species was 9 (range = 5–17). *Scheuchzeria palustris* was clearly typical of this community. *Eriophorum angustifolium* and *Carex limosa* were equally frequent. *Sphagnum jensenii* was more frequent than *S. lindbergii* and *S. balticum*.

### Number of species in relation to compositional gradients

Number of species increased along the trophic or poor–rich gradient, while no relation was found either between the species number and the geographic gradient, or the species number and the mire-expanse-to-margin gradient (Fig. 7).

## Discussion

### Compositional gradients and species richness in NB flark fens

Hierarchical levels in the cluster analysis show the vegetation structure and hence may also refer to scales at which the compositional gradients operate. Compositional gradient associated with the largest scale division in the cluster analysis for northern boreal flark fens refers to mire-expanse-to-margin gradient (Sjörs 1948), because the name-giving species (*Carex rotundata*, *Trichophorum cespitosum*) and characteristic species (*Betula nana*, *Vaccinium microcarpum*, *Trichophorum alpinum*, *Carex pauciflora*, *C. livida*, *C. rariflora*, *Cetraria delisei*) of the first major group are clear-cut mire expanse species, while the name-giving species (*Eriophorum gracile*, *Potentilla palustris*, *Straminergon stramineum*) and characteristic species (*Sphagnum obtusum*) of the latter major group are mire margin species (Eurola & Huttunen 2006). This is an important result as mire-expanse-to-margin is a prominent gradient across treeless vegetation in flark fens; mire margin vegetation according to Økland et al. (2001) refers to treed vegetation,

contrary to the concept of Ruuhijärvi (1960), Eurola et al. 1984, 1995, 2015 and Ruuhijärvi and Lindholm (2006). The main gradient, however, is additionally context-dependent: Sjörs (1946), Malmer (1986), Sjörs & Gunnarsson (2002), Tahvanainen (2004) and Hájek et al. (2006) found the poor–rich gradient to be the principal gradient within mires. Specifically, the mire margin vegetation in northern boreal flark fens of Finnish Lapland refers to *Sumpfigkeit* (Ruuhijärvi 1960), or swamp influence, which is ecohydrologically interpreted as a surface water influence (Eurola et al. 1984, 1995, 2015) referring to supply of additional nutrients via moving mire water or flood water (cf. the fertility gradient of Hájek et al. 2006). As in our NMDS ordination, the reciprocal averaging from all kinds of mires in northern Finland by Pakarinen and Ruuhijärvi (1978) showed the mire margin to expanse as the gradient related to the first axis. It is significant that the largest-scale ecological gradient in our material in flark fens is highly parallel with the regional (geographic) gradient (FjeL to ForL to PeP). Classic studies report that the volume of the *aapa*-mire spring flood from snow meltwater is most intense in hygrially more oceanic main *aapa*-mire zone (Ruuhijärvi & Hosiaislouma 1987), i.e. in the southernmost part of Finnish Lapland (PeP). Our analysis produced a result similar to the classic opinion and supports the interpretation that the volume of the spring flood from snow meltwater is the primary regional variable structuring the vegetation within northern boreal flark fens.

Poor–rich gradient (Sjörs 1948, Sjörs & Gunnarsson 2002, Tahvanainen 2004) shows another essential variation across northern boreal flark fens of the Finnish Lapland. In the ordination of flark fens the gradient is related to NMDS 2 dimension and appears in the vegetation units of the cluster analysis at the second division level, i.e. at and below the level of groups. Trophic sequence of classic site types was also well reflected in the reciprocal averaging analysis of Pakarinen and Ruuhijärvi (1978) for all the northern Finnish peatland material. Our *Scorpidium scorpioides* group with moderate-rich flark fens has a bimodal distribution in NB zone of Finland with the focus in the northernmost (Fjeld Lapland) and in the southernmost (*Peräpoh-*

*jola*) subzones, on both sides of the transitional subzone (Forest Lapland). It may be due to sampling, but the result agrees with a pattern reported formerly: Forest Lapland of Finland is regarded as an area with less eutrophic vegetation (rich fens, e.g.) than areas south and north of it (Ruuhijärvi 1960, Eurola & Vorren 1980).

Carpets–mud-bottom variation of flark fens (Sjörs 1948, Laitinen *et al.* 2008a) appears in the vegetation units of the cluster analysis only at the third and fourth division levels. Mire surface level is generally regarded as a small-scale gradient (Økland *et al.* 2001) as compared with poor–rich and margin–expanse gradients. Mud-bottom plots of flark fens in our material represent a narrow transitional zone between the plots of poor-fen carpets and those of rich-fen carpets, and the mud-bottom in *aapa*-mire flarks seems to reflect the physiognomy (and physical processes) of the site rather than a specific species composition. *Utricularia intermedia*, however, clearly favours mud-bottom, as it focuses on northern boreal southern (NBs) *Carex limosa*–*Menyanthes trifoliata* mud-bottom community (10). It is noteworthy that the areas occupied by the NB *Eriophorum angustifolium*–Hepaticae spp. community have a drier mire surface level than the areas occupied by the NBs *Carex limosa*–*Menyanthes trifoliata* mud-bottom community. The former community is characterized by a dense Hepaticae-cover and several plots are dominated by a flark-level *Sphagnum lindbergii*, while in the latter community Hepaticae are less common within the mud bottom and *Warnstorfia exannulata* is present in some plots. The result agrees with the original result of Ruuhijärvi (1960: 293) and the climatic characterization of Eurola and Vorren (1980), who stress that the northern boreal northern (NBn) subzone (ForL, FjeL) with a more continental climate favours the formation of flarks slightly drier (*Sphagnum* flarks) than those in the main *aapa*-mire zone (NBs) with a hygrially more oceanic climate and a more voluminous spring flood. According to Ruuhijärvi (1960), Eurola and Vorren (1980) and Eurola *et al.* (2015), the voluminous spring flood of the NBs subzone especially favours the abundance of *Warnstorfia* species in flark fens.

NB *Eriophorum angustifolium*–Hepaticae spp. community (5) shows compositional and

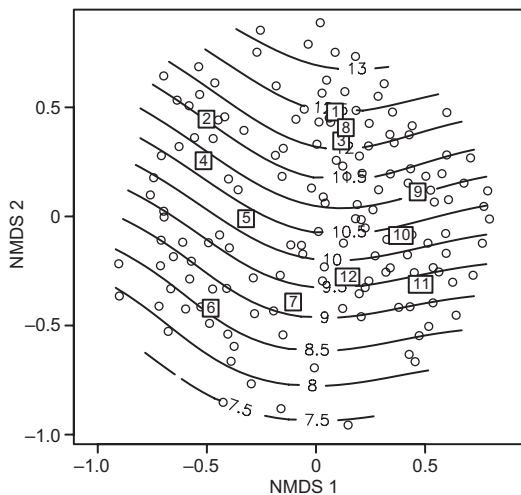


Fig. 7. Average species numbers in the ordination of flark-fen sample plots. Central points of communities are shown with squares and the community numbers are in squares. For community names, see Table 2.

species-richness features associated with seasonal drought of the peat surface layer: they are dominance of *Eriophorum angustifolium*, presence of *Sphagnum compactum*, scarcity of *Menyanthes trifoliata* and a relatively low number of species (Laitinen 2008). According to Ruuhijärvi (1960), species-poor *Eriophorum angustifolium* mud-bottom flarks at the margins of *Peräpohjola aapa*-mires represent seasonally dry (while spring-flooded) flark fens (for seasonally dry sloping lawn fens, see Havas 1961). Compositional gradient from continuous moisture to seasonal drought, however, seems of less importance in a regional flark-fen data, and the seasonally dry end of the gradient appears in special cases to be associated with a water-permeable mineral soil and an extremely thin peat layer (5–30 cm; Laitinen 2008 and the literature cited therein).

Average species richness of flark fens was extremely low (7.5–13) (Fig. 7). This was expected, as flark fens represent the wettest habitats of boreal mires (Ruuhijärvi 1960, Eurola *et al.* 1984, 1995, 2015), and a decreasing species richness from drier to wetter sites is a pattern generally seen in various boreal wetlands (Eurola 1967, Vitt *et al.* 2003, Whitehouse & Bayley 2005). Also the taxonomic diversity of diatoms decreased from hummocks to hollows in hemiboreal Estonian bogs (Küttim *et*

al. 2017). Within studied flark fens, the species richness was positively related to the poor–rich gradient but not to the geographic gradient or the mire–expanse-to-margin gradient. At a larger geographic scale, the species richness is generally expected to decrease along increasing latitude (Willing *et al.* 2003): south-to-north environmental variation within the northern boreal zone (up to its northern oroboreal part) seems so slight that it does not affect the species richness of flark fens.

### Cajanderian classification of flark fens

Apart from community 8, our ordination of flark fens (Fig. 5) clearly differentiated the communities belonging to two mire-site groups (*Moortypengruppen*): poor fens, i.e. *Weissmoore*, and rich fens, i.e. *Braunmoore*. Instead, the first division level in the cluster analysis did not divide flark fens according those mire-site groups (Fig. 4 and Table 2). Similarly, the analysis by Pakarinen and Ruuhijärvi (1978) showed that in a six-factor solution, a *Rimpi* (flark) factor could be interpreted along with five factors referring to the current mire site groups (*Reisermoor* (pine bog) factor, *Weissmoor* (poor fen) factor, *Braunmoor* (rich fen) factor, *Bruchmoor* (*Picea abies*–*Betula pubescens* mire) factor, and *Sumpf*–*Carex* (swamp) factor). Pakarinen and Ruuhijärvi (1978) postulated that those factors refer to six major directions of variation (*Variationsrichtungen*; Tuomikoski 1942) and that the factors additionally can be thought to refer to corresponding vegetation units. Accordingly, a placement of flark fens as a new boreal mire-site group (*Rimpimoore*) in the Cajanderian classification cannot be totally factored out.

Because seven classic site types (*Moortypen*) of flark fens (Table 1) and the twelve regional communities from the cluster analysis are fairly compatible, communities highlight the regional variation of site types. Mainly *Sphagnum*-dominated communities 6, 7 and 12 (Fig. 5), which in the ordination are situated along the horizontal (regional, mire expanse-margin) gradient, show that *Sphagnum* flark fens (*Sphagnum Rimpiveissmoore sensu* Ruuhijärvi 1960) are clearly differentiated into regional communities, and

the southernmost of them (community 12, NBs *Menyanthes trifoliata*–*Sphagnum majus* community) reaches the end of the vegetation gradient with diminutive mire margin features (*Sphagnum fallax*, abundance of *Menyanthes trifoliata*). Mainly mud-bottom-dominated communities 5 and 10 indicate that the distinction between oligotrophic and mesotrophic mud-bottom flark fens (*oligotrophe moosarme Rimpiveissmoore*, *mesotrophe moosarme Rimpiveissmoore*) is not self-evident. Instead, they indicate that mud bottom flark fens have an ecological–regional pattern resembling that of *Sphagnum* flark fens of Ruuhijärvi (1960) with a widespread (NB) mire expanse community (5) belonging to *Sphagnum lindbergii* group, and a NBs community (10) belonging to *Warnstorfia fluitans* group with some features of mire margin vegetation (*Eriophorum gracile*, *Potentilla palustris*, *Equisetum fluviatile*). Ordination of communities 1 to 4 (moderate-rich flark fens) shows that the regional variation in *Rimpibraunmoore*, mainly characterized by dominant vascular plants, is more evident than the variation of Cajanderian site types reflecting dominant moss species (*Scorpidium Rimpibraunmoore*, *Drepanocladus revolvens Rimpibraunmoore*). A close position of classic *Scorpidium Rimpibraunmoore* to mud-bottom flark fens, especially to mesotrophic mud-bottom flark fens (*mesotrophe Moosarme Rimpiveissmoore*), was suggested by the site-type combination of sample plots within the NB *Carex chordorrhiza*–*Menyanthes trifoliata*–*Scorpidium scorpioides* community (3) (Table 2).

### Flark fens of treeless fjelds and a European context of NB flark fens

Vegetation surveys of mires in treeless fjelds of Finnish Lapland stem from low fjelds and a low-oroarctic zone (Haapasaari 1988). Outermost northwest Finnish Lapland (*Käsivarsi*) and the middle oroarctic zone close to the Scandes (Virtanen & Eurola 1997) is outside that area. The classic survey by Kalliola (1939) shows four small-scale vegetation units, which correspond to the regional communities resulting from our cluster analysis. *Eriophorum polys-*

*tachyum–Calliargon sarmentosum–Drepanocladus exannulatus* Soziation (Kalliola 1939) has a lot in common with two plots with the same three dominants in community 9. Highly species-poor patches with *Eriophorum angustifolium* and *Warnstorfia sarmentosa* as dominants are encountered further south (up to mid-boreal zone) at peatland margins with little evidence of groundwater influence (Laitinen *et al.* 2011, 2016). The oroarctic *Carex rotundata–Calliargon sarmentosum–Drepanocladus exannulatus* Soziation corresponds to those plots of community 2 which are dominated by *Carex rotundata*, *Warnstorfia sarmentosa* and partly *Sphagnum lindbergii*. Further, the oroarctic *Carex rotundata–Sphagnum lindbergii* Soziation corresponds to our community 6. Finally, the relatively species-rich (8–14 species) oroarctic *Carex rostrata–Drepanocladus exannulatus* Soziation corresponds to community 8. *Menyanthes trifoliata*, however, is quite common in the NB community and is totally missing from the oroarctic community, as is boreal *Carex lasiocarpa* (Väre & Partanen 2009).

Regional flark-fen communities of northern boreal Finnish Lapland probably fall into three European fen alliances recognized by Peterka *et al.* (2017) (see Appendix), i.e. *Stygio-Caricion limosae* (boreal topogenic brown-moss fens), *Drepanocladion exannulati* (arcto-boreal-alpine non-calcareous fens), and *Scheuchzerion palustris* (*Caricion rotundatae* according to Kalliola 1939). It is noteworthy that the flark-fen communities of Finnish Lapland considered here seem to correspond to boreal (*Stygio-Caricion limosae*), to arcto-boreal-alpine (*Drepanocladion exannulati*), and to widespread (*Scheuchzerion palustris*) European alliances, not to the arcto-alpine alliance (*Caricion atrofusco-saxatilis*) of Peterka *et al.* (2017) present in the Scandes and the Alps. The southern to mid-boreal *Rhynchospora alba* flark fens (Ruuhijärvi 1960, Heikkilä 1987) do not reach the NB peatland zone of the Finnish Lapland either.

## Acknowledgements

The article is dedicated to the memory of docent Pekka Pakarinen, who began the analyses of classic peatland sample

plot materials across Finland. Miia Parviainen was funded by the EU Life + LIFEPEATLANDUSE-project (LIFE 12 ENV/FI/000150).

## References

- Alalammi P. 1990: Geologia [Geology]. — In: *Atlas of Finland*: 123–126. National Board of Survey Geographical Society of Finland, Helsinki. [In Finnish with English summary].
- Brandt A. 1948: Über die Entwicklung der Moore im Küstengebiet von Süd-Pohjanmaa am Bottnischen Meerbusen. — *Annales Botanicæ Societatis Zoologicae Botanicæ Fennicae Vanamo* 23(4): 1–134.
- Cajander A.K. 1913: Studien über die Moore Finnlands. — *Acta Forestalia Fennica* 2(3): 1–208.
- Eurola S. 1962: Über die regionale Einteilung der Südfinnischen Moore. — *Annales Botanicæ Societatis Zoologicae Botanicæ Fennicae Vanamo* 33(2): 1–243.
- Eurola S. 1967: Über die Vegetation der Alluvialviesen in Gebit der geplanten Stauseen von Lokka and Porttipahta in Finnischen Lapland. — *Aquilo Serie Botanica* 5: 1–119.
- Eurola S. & Kaakinen E. 1978: *Suotyyppiopas*. — WSOY, Porvoo.
- Eurola S., Hicks S. & Kaakinen E. 1984: Key to Finnish mire types. — In: Moore P.D. (eds.), *European mires*: 11–117. Academic press, London.
- Eurola S. & Huttunen A. 2006: Mire plant species and their ecology in Finland. Finland — land of mires. — *The Finnish Environment* 23: 127–144.
- Eurola S. & Vorren K.-D. 1980: Mire zones and sections in North Fennoscandia. — *Aquilo Serie Botanica* 17: 39–56.
- Eurola S., Huttunen A. & Kukko-oja K. 1995: Suokasvillisuusopas. — *Oulanka Reports* 14: 1–85.
- Eurola S., Kaakinen E., Saari V., Huttunen A., Kukko-oja K. & Salonen V. 2015: *Sata suotyyppiä. Opas Suomen suokasvillisuuden tuntemiseen*. — Thule Institut, Oulanka Research Station, University of Oulu.
- Faith D.P., Minchin P.R. & Belbin L. 1987: Compositional dissimilarity as a robust measure of ecological distance. — *Vegetatio* 69: 57–68.
- Haapasaari M. 1988: The oligotrophic heath vegetation of northern Fennoscandia and its zonation. — *Acta Botanica Fennica* 135: 1–219.
- Hájek M., Horsák M., Hájková P. & Ditě D. 2006: Habitat diversity of central European fens in relation to environmental gradients and an effort to standardize fen terminology in ecological studies. — *Perspectives in Plant Ecology, Evolution and Systematics* 8(2): 9–114.
- Hämet-Ahti L., Suominen J., Ulvinen T. & Uotila P. (eds.) 1998: *Retkeilykasvio [Fjeld flora of Finland]*, 4th ed. — Finnish Museum of Natural History, Botanical Museum, Helsinki. [In Finnish with English summary]
- Havas P. 1961: Vegetation und Ökologie der ostfinnischen Hangmoore. — *Annales Botanicæ Societatis Zoologicae Botanicæ Fennicae 'Vanamo'* 31: 1–188.

- Heikkilä H. 1987: The vegetation and ecology of mesotrophic and eutrophic fens in western Finland. — *Annales Botanici Fennici* 24: 155–175.
- Jiménez-Alfaro B., Hájek M., Ejrnaes R., Rodwell J., Pawlikowski P., Weeda E.J., Laitinen J., Moen A., Bergamini A., Aunina L., Sekulová L., Tahvanainen T., Gillet F., Díte D., Hájková P., Corriol G., Kondelin H. & Díaz T.E. 2014: Biogeographic patterns of base-rich fen vegetation across Europe. — *Applied Vegetation Science* 2013: 367–380.
- Kalela A. 1958: Über die Waldvegetationszonen Finnlands. — *Botaniska Notiser* 111(1): 353–368.
- Kalela A. 1961: Waldvegetationszonen Finnlands und ihre klimatischen Paralleltypen. — *Archivum Societatis Zoologicae Botanicae Fennicae 'Vanamo'* 16: 65–83.
- Kalliola R. 1939: Pflanzensoziologische Untersuchungen in der alpinen Stufe Finnisch-Lappland. — *Annales Botanicae Societatis Zoologicae Botanicae Fennicae 'Vanamo'* 13(2): 1–321.
- Kruskal J.B. 1964: Nonmetric multidimensional scaling: a numerical method. — *Psychometrika* 29: 1–28.
- Küttim L., Küttim M., Puusepp L. & Sugita S. 2017: The effects of ecotope, microtopography and environmental variables on diatom assemblages in hemiboreal bogs in Northern Europe. — *Hydrobiologia* 792: 137–149.
- Laitinen J. 2008: Vegetational and landscape level responses to water level fluctuations in Finnish, mid-boreal aapa mire-aro wetland environments. — *Acta Universitatis Ouluensis A* 513: 1–69.
- Laitinen J., Kukko-oja K. & Huttunen A. 2008a: Stability of the water regime forms a vegetation gradient in minerotrophic mire expanse vegetation of a boreal aapa mire. — *Annales Botanici Fennici* 45: 342–358.
- Laitinen J., Heikkilä R. & Kondelin H. 2011: Intermediate fen patches on a sloping rock outcrop in Koitelainen, Finnish Lapland. — *Mires and Peat* 8: Art. 6, available at [http://pixelrauschen.de/wbmp/media/map08/map\\_08\\_06.pdf](http://pixelrauschen.de/wbmp/media/map08/map_08_06.pdf).
- Laitinen J., Oksanen J., Maliniemi T., Kaakinen E., Aapala K. & Rehell S. 2016: Ecological, topographic and successional patterns across wetlands in a rugged land uplift coast in Nyby, northern Finland. — *Fennia* 194: 89–116.
- Malmer N. 1986: Vegetational gradients in relation to environmental conditions in northwestern European mires. — *Canadian Journal of Botany* 64: 375–383.
- Minchin P.R. 1987: An evaluation of relative robustness of techniques for ecological ordinations. — *Vegetatio* 69: 89–107.
- Moen A. 1999: Vegetation. — In: *National Atlas of Norway*. Norwegian Mapping Authority, Hønefoss.
- Økland R.H., Økland T. & Rydgren K. 2001: A Scandinavian perspective on ecological gradients in north-west European mires: reply to Wheeler & Proctor. — *Journal of Ecology* 89: 481–486.
- Oksanen L. & Virtanen R. 1995: Topographic, altitudinal and regional patterns in continental and suboceanic heath vegetation of northern Fennoscandia. — *Acta Botanica Fennica* 153: 1–80.
- Pakarinen P. & Ruuhijärvi R. 1978: Ordination of northern Finnish peatland vegetation with factor analysis and reciprocal averaging. — *Annales Botanici Fennici* 15: 147–157.
- Peterka T., Hájek M., Jiroušek M., Jiménez-Alfaro B., Aunina L., Bergamini A., Dítě D., Felbaba-Klushyna L., Graf U., Hájková P., Hettenbergerová E., Ivchenko T.G., Jansen F., Koroleva N.E., Lapshina E.D., Lazarević P.M., Moen A., Napreenko M.G., Pawlikowski P., Plesková S., Sekulová L., Smagin V.A., Tahvanainen T., Thiele A., Bitá-Nicolae C., Biurrun I., Brisse H., Čušterevska R., De Bie E., Ewald J., FitzPatrick Ú., Front X., Jandt U., Kacki Z., Kuzemko A., Landucci F., Moeslund J.E., Pérez-Haase A., Rašomavičius V., Rodwell J.S., Schaminée J.H.J., Šilc U., Stančić Z. & Chytrý M. 2017: Formalized classification of European fen vegetation at the alliance level. — *Applied Vegetation Science* 20: 124–142.
- R Core Team 2016: R: A language and environment for statistical computing. — *R Foundation for Statistical Computing*, Vienna, Austria.
- Ruuhijärvi R. 1960: Über die Regionale Einteilung der Nordfinnischen Moore. — *Annales Botanici Societatis Zoologicae Botanicae Fennicae 'Vanamo'* 31(1): 1–360.
- Ruuhijärvi R. 1983: The Finnish mire types and their regional distribution. — In: Gore A.J.P. (ed.), *Mires: swamp, bog, fen and moor*: 47–67. *Ecosystems of the world* vol. 4B, Elsevier, Amsterdam.
- Ruuhijärvi R. & Hosiaislouma V. 1987: Mires 1: 1000000. — In: *Atlas of Finland*: 141–143, Map Appendix 2. Natural Board of Survey & Geographical Society of Finland, Helsinki.
- Ruuhijärvi R. & Lindholm T. 2006: Ecological gradients as the basis of Finnish mire site type system. — *The Finnish Environment* 23: 119–125.
- Rydin H., Sjörs H. & Löfroth M. 1999: Mires. — *Acta Phytogeographica Suecica* 84: 91–112.
- Rydin H. & Jeglum J.K. 2013: *The biology of peatlands*, 2nd ed. — Oxford University Press, Oxford.
- Sjörs H. 1946: Myrvegetation I övre Långanområdet I Jämtland. — *Arkiv för Botanik* 22 A (6): 1–96.
- Sjörs H. 1948: Myrvegetation i Bergslagen. — *Acta Phytogeographica Suecica* 21: 1–299.
- Sjörs H. & Gunnarsson U. 2002: Calcium and pH in north and central Swedish mire waters. — *Journal of Ecology* 90: 650–657.
- Tahvanainen T. 2004: Water chemistry of mires in relation to the poor-rich vegetation gradient and contrasting geochemical zones of the north-eastern Fennoscandian Shield. — *Folia Geobotanica* 39: 353–369.
- Tuomikoski R. 1942: Untersuchungen über die Vegetation der Bruchmoore in Ostfinnland. I. Zur Methodik der pflanzensoziologischen Systematik. — *Annales Botanici Societatis Zoologicae Botanicae Fennicae 'Vanamo'* 17(1): 1–203.
- Ulvinen T., Syrjänen K. & Anttila S. (ed.) 2002: Suomen sammalet — levinneisyys, ekologia, uhanalaisuus. — *Suomen Ympäristö* 560: 1–354.
- Väre H. & Partanen R. 2009: *Suomen tunturikasvio*. — Metsäkustannus, Hämeenlinna.
- Virtanen R. & Eurola S. 1997: Middle oroarctic vegetation in Finland and middle-northern arctic vegetation on Svalbard. — *Acta Phytogeographica Suecica* 82: 1–64.

- Virtanen R., Oksanen L., & Razzhivin V. 1999: Topographic and regional patterns of tundra heath vegetation from northern Fennoscandia to the Taimyr Peninsula. — *Acta Botanica Fennica* 167: 29–83.
- Vitt D.H., Achuff P. & Andrus R.E. 1975: The vegetation and chemical properties of patterned fens in the Swan Hills, north-central Alberta. — *Canadian Journal of Botany* 53: 2776–2795.
- Vitt D.H., Li Y. & Belland R. 2003: Patterns of bryophyte richness in a complex boreal landscape: identifying key habitats of McClelland lake wetland. — *Bryologist* 106: 372–382.
- Vorren K.-D. & Johansen B. 1990: Synopsis and numerical analysis of the pre-, sub-, and low-alpine mire vegetation of the Uleberg-Skrubben area, North Norway. — *Aquilo Serie Botanica* 28: 79–92.
- Vorren K.-D., Euroala S. & Tveraabak U. 1999: The lowland terrestrial mire vegetation about 69°N lat. in northern Norway. — *Tromsø* 84: 1–90.
- Warton D.I., Wright S.T. & Wang Y. 2012: Distance-based multivariate analyses confound location and dispersion effects. — *Methods in Ecology & Evolution* 3: 89–101.
- Wheeler B.D. & Proctor M.C.F. 2000: Ecological gradients, subdivisions and terminology of north-west European mires. — *Journal of Ecology* 88: 187–203.
- Whitehouse H.E. & Bayley S. 2005: Vegetation patterns and biodiversity of peatland plant communities surrounding mid-boreal wetland ponds in Alberta, Canada. — *Canadian Journal of Botany* 83: 621–637.
- Williams W.T., Lambert J.M. & Lance G.N. 1966: Multivariate methods in plant ecology. V. Similarity analyses and information-analysis. — *Journal of Ecology* 54: 427–445.
- Willing M.R., Kaufman D.M. & Stevens R.D. 2003: Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. — *Ecology, Evolution and Systematics* 34: 273–309.
- Yoshioka P.M. 2008: Misidentification of the Bray-Curtis similarity index. — *Marine Ecology Progress Series* 368: 309–310.

**Appendix.** European fen alliances, some diagnostic species, distribution characters for alliances and regional flark-fen communities of Finnish Lapland roughly related to alliances. Northern boreal (NB) peatland regions are shown for communities: FjEL = Fjeld Lapland, ForL = Forest Lapland, NBs = northern boreal southern i.e. *Peräpohjola* (PeP). Alliances are assigned to central-European poor-rich categories of fens, while regional flark-fen communities of Finnish Lapland are assigned to corresponding Scandinavian and Finnish categories. Classic Finnish trophic levels are in brackets.

Alliances	Some diagnostic species	Distr. character	NB flark-fen communities	NB regions
<b>CALCAREOUS &amp; EXTREMELY RICH FENS</b>				
<i>Caricion viridulo-trinervis</i>	<i>Salix reprens</i> , <i>Carex trinervis</i> , <i>Juncus anceps</i>	Atlantic dune-slack fens		
<i>Caricion davallianae</i>	<i>Carex davalliana</i> ; Island and N Scandinavia: stands dominated by <i>Eleocharis quinqueflora</i>	Temperate calcareous fens		
<i>Caricion atrofusco-saxatilis</i>	<i>Carex capillaris</i> , <i>Juncus triglumis</i> , <i>Salix reticulata</i>	Arcto-alpine calcareous fens		
<b>RICH FENS</b>				
<i>Stygio-Caricion limosae</i>	<i>Scorpidium scorpioides</i>	Boreal topogenic brown-moss fens	MAINLY MODERATELY-RICH FENS NoB <i>Car rot-Eri ang-Sco sco com.</i> NoB <i>Car rot-Eri ang-Sco rev com.</i> NB <i>Car cho-Men tri-Sco rev com.</i> NB <i>Car cho-Men tri-Sco sco com.</i>	FjEL FjEL (NBs) FjEL (ForL) NBs (FjEL) ForL NBs
<i>Sphagno warnstorffii-Tomentypnion nitentis</i>	<i>Sphagnum warnstorffii</i> , <i>Tomentypnum nitens</i> , <i>Aulacomnium palustre</i>	Sphagnum-brown-moss rich fens		
<i>Saxifrago-Tomentypnion</i>	<i>Hamatocaulis vernicosus</i> , <i>Brachythecium mildeanum</i> , <i>Stellaria crassifolia</i>	Continental to boreo-continental brown-moss-rich fens		
<b>RICH-MODERATELY-RICH FENS</b>				
<i>Narthecio scardici</i>	<i>Pinguicula balcanica</i> , <i>Plantago gentianoides</i>	Alpine fens with Balkan endemics		
<i>Caricion stantisi</i>	<i>DuPontia fisheri</i> , <i>Calliergon turgescens</i> , <i>Ranunculus hyperboreus</i> , <i>Calliergon richardsoni</i>	Arctic brown-moss rich fens		
<b>MODERATELY-RICH FENS</b>				
<i>Anagallido tenellae-Juncion bulbosi</i>	<i>Anagallis tenella</i> , <i>Juncus bulbosus</i> , <i>Hypericum elodes</i>	Ibero-Atlantic moderately-rich fens	MAINLY MODERATELY POOR (mesotrophic) FENS	

continued



## Appendix. Continued.

Alliances	Some diagnostic species	Distr. character	NB flark-fen communities	NB regions
<i>Drepanocladiion exannulati</i>	<i>Drepanocladus exannulatus</i> , <i>Calliergon sarmentosum</i>	Arcto-boreal-alpine non-calcareous fens	NB <i>Eri ang-Hepa</i> sp. com. NB <i>Car ros-Car las-War exa</i> com. NBs <i>Car lim-Men tri-War exa</i> com. NBs <i>Car lim-Men tri mud-bot</i> com.	Fjøl ForL (NBs) Fjøl ForL NBs NBs NBs
<i>Caricion fuscae</i>	<i>Viola palustris</i> , <i>Agrostis canina</i>	Mainly temperate moderately-rich fens		
POOR FENS <i>Sphagno-Caricion canescentis</i>	<i>Sphagnum recurvum</i> agg., <i>Vaccinium oxycoccos</i> agg., <i>Polytrichum commune</i>	Mainly temperate-boreal poor fens		
DYSTROPHIC HOLLOWES <i>Scheuchzerion palustris</i>	<i>Sphagnum cuspidatum</i> , <i>Scheuchzeria palustris</i> , <i>Sphagnum majus</i> , <i>Drepanocladus fluitans</i> , <i>Rhynchospora alba</i>	Dystrophic hollows; in boreal region larger areas	EXTREMELY POOR (oligotrophic) FENS NB <i>Car rot-Sch pal-Sph lin</i> com. NBs <i>Eri ang-Sph jen</i> com. NBs <i>Car lim-Men tri-War flu</i> com. NBs <i>Men tri-Sph maj</i> com.	Fjøl ForL NBs (Fjøl) (ForL) NBs (ForL) NBs NBs