Intermediate fen patches on a sloping rock outcrop in Koitelainen, Finnish Lapland

J. Laitinen[1], H. Kondelin[2] and R. Heikkilä[2]

[1]Department of Biology, University of Oulu, Finland
[2]Finnish Environment Institute, Joensuu, Finland

SUMMARY

Patches of intermediate fen, dominated by *Molinia caerulea, Trichophorum cespitosum* and *Loeskypnum badium* and resembling low aapa mire strings (lawn strings), were found on a sloping rock outcrop near the summit of Koitelainen Hill, central Finnish Lapland. Using eighteen 56-cm diameter plots and NMS-ordination we compared the vegetation of the patches to that of (A) corresponding larger fens belonging to a well-known north-Finnish mire site type *Loeskypnum badium* fen, (B) to that of narrow seepage soaks dominated by *Warnstorfia sarmentosa*, and (C) to that of a local heath patch. Ordination of the sample plots suggested a 'horizontal gradient' (general wetness) and three 'vertical gradients' (1: stability of the water regime; 2: poor-rich species; 3: frost action). Species richness increased along both the horizontal and the vertical gradient, from wet seepage areas to drier *Loeskypnum badium* fens, to intermediate fen patches and finally to the heterogeneous heath patch. We regard the fen patches of Koitelainen as belonging to an ecologically extreme group, the water-fluctuating lawn-fens. The water-fluctuating lawn-fens are characterised by a thin peat layer with high humification degree, caused by intermittent aeration during drought periods, as well as by the specific community composition, which is evidently partly structured by the seasonal drought tolerances of individual fen species.

KEY WORDS: boreal mire vegetation, indicator species groups, *Loeskypnum badium,* seasonal drought, vegetation gradient.

INTRODUCTION

Intermediate fens are transitional between poor fens and rich fens, and they are highly characteristic of boreal in contrast to nemoral areas (Sjörs 1952, Rydin *et al.* 1999, Sjörs & Gunnarsson 2002). *Loeskypnum badium* fen (Eurola *et al*. 1984, 1995), belonging to intermediate fens, is a Finnish mire site type originally described by Ruuhijärvi (1960) (*Drepanocladus badius Braunmoor-Weissmoor*) from northern Finland. Vegetation of this type usually occupies only small areas, being characteristic of gently sloping sites in fens in areas with relatively infertile (siliceous *etc.*) bedrock (Ruuhijärvi 1960). We noticed patches of vegetation resembling *Loeskypnum badium* fen, dominated by *Molinia caerulea, Trichophorum cespitosum* and *Loeskypnum badium* and resembling low aapa mire strings (lawn strings), in an unusual locality on a sloping rock outcrop near the southernmost summit of Koitelainen Hill. The term *patjasuo* (translation ´mattress mire´) was recently suggested for mire patches on sloping rock outcrops in Finland (Kaakinen *et al*. 2008), but published descriptions of the vegetation and its relationships to other vegetation seem to be lacking.

The first aim of this paper is to describe the plant community of the fen patches on the rock outcrop (hereafter 'rock') and to compare it to 1: local *Loeskypnum badium* fens (hereafter 'fen'); 2: small-sized *Warnstorfia sarmentosa* seepage areas (hereafter 'seep') occurring among *Loeskypnum badium* fens; and 3: to a local heath patch (hereafter 'heath'). We also compare the vegetation of these fen patches to that described elsewhere in north Fennoscandia. Secondly, we ask what vegetation gradients the ordination of sample plots suggests and how are the altitude, peat thickness and species richness reflected in the sample plot ordination.

METHODS

Study area

Koitelainen Nature Reserve (43,938 hectares), part of the Natura 2000 Ramsar area 'Koitelainen Mires', lies in the northern boreal forest zone (Hämet-Ahti 1981). Within the mire zone and section division of North Fennoscandia (Eurola & Vorren 1980), Koitelainen belongs to the NBs (Northern Boreal south) mire zone and to the relatively continental *Ledum* section, and specifically to its large eastern *Ledum palustre-Carex laxa* subsection (aapa mire subsection) east of the Fennoscandian mountain range (Figure 1). However, the abundance of *Calluna vulgaris* at higher altitudes on some parts of Koitelainen Hill indicates some local hygric oceanicity characteristic of higher altitudes (Eurola *et al*. 1982, Eurola & Kaakinen 1982, Eurola *et al*. 1991, Mikkonen-Keränen 1986, Paasovaara 1986) and/or it may be linked with the mafic bedrock type as shown by Laine & Nurmi (1971) in northern Lapland (West Inari). The bedrock of the Koitelainen area belongs to the Fennoscandian shield, and is composed of a mafic bedrock type (Mutanen 1997) which is suitable for rather demanding plant species. Mean annual temperature of the area (1931–1960) is -0.5 ºC, mean temperature in January is -13 ºC, mean temperature in July is +14 ºC and mean absolute minimum temperature (1931–1960) is -38 ºC (Alalammi 1987). Annual precipitation (1931–1960) is 550–600 mm, solid state precipitation as percentage of total precipitation is 45–50 %, duration of snow cover on open ground (1954/55–1972/73) is 210 days (seven months) in a year and the greatest winter snow depth in forests (1921–1960) is 80–85 cm (Alalammi 1987).

Koitelainen Hill (420 m a.s.l.) and the flat areas around it are situated in the municipality of Sodankylä in central Finnish Lapland, between the rivers Luiro and Kitinen. Aapa mires cover 60 % of the nature reserve, rich fens 3 % and boreal natural forests 24 %. The aapa mires around Koitelainen Hill are located at about 250 m a.s.l.

Koitelainen Hill itself is a hilly, stony and rocky area eight kilometres long and, at most, four kilometres wide (Figures 2, 3). The highest summits are half-vegetated and half-open, partly due to the abundant occurrence of rock outcrops and stones, although their positions in relation to altitudinal zones (belts) (Haapasaari 1988, Eeronheimo *et al*. 1992) have not been determined by specific vegetation studies. Various woodlands rich in mountain birch (*Betula pubescens* ssp. *czerepanovii*) occur in parts of the summit areas. The forest vegetation on the slopes of Koitelainen has not been studied either, but a variety of the boreal forest types

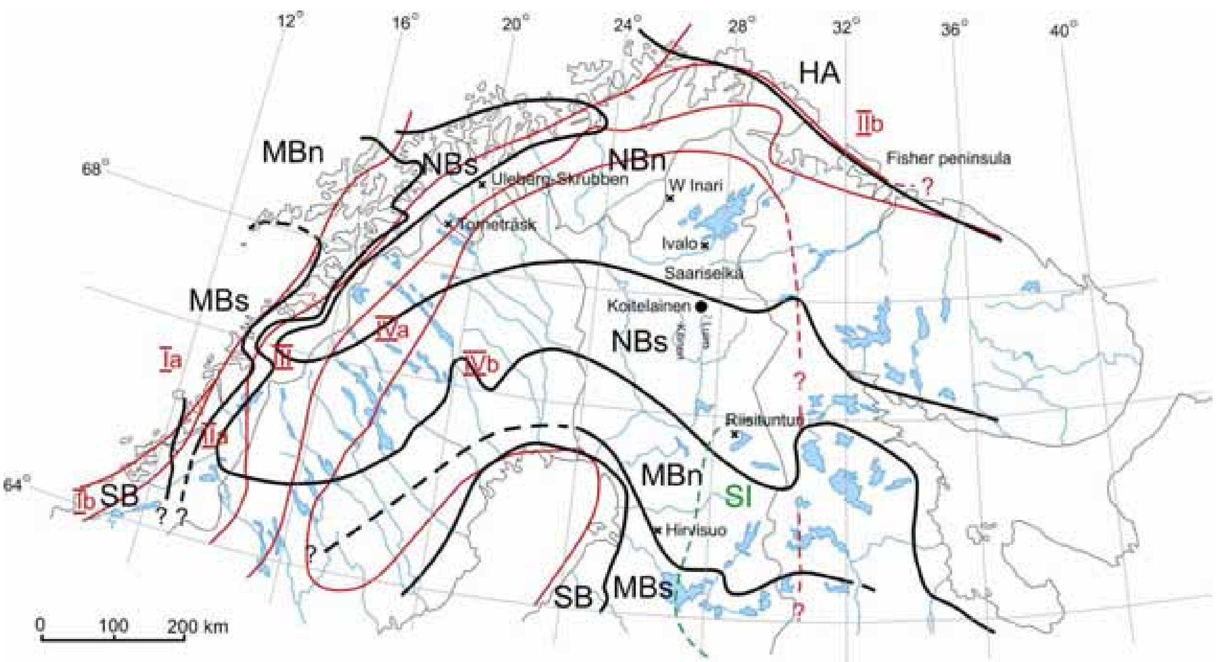

Figure 1. Location of Koitelainen Hill (●), other localities mentioned in the text (×), the mire zone and section division of Eurola & Vorren (1980) and the area with the sample plot material from sloping lawn fens (Sl) of eastern Finland (Havas 1961). Mire zones: SB = Southern Boreal, MBs = Middle Boreal south, MBn = Middle Boreal north, NBs = Northern Boreal south, NBn = Northern Boreal north, HA = HemiArctic. Mire sections: Ia = maritime *Dicranum groenlandicum-Sphagnum imbricatum* subsection, Ib = maritime *Sphagnum imbricatum* subsection, IIa = maritime *Racomitrium lanuginosum* section, IIb = northeastern subsection of section II without *R. lanuginosum*, III = transitional section, IVa = western subsection of the continental *Ledum palustre* section, IVb = eastern, continental *Ledum palustre-Carex laxa* subsection of the aapa mire subsection.

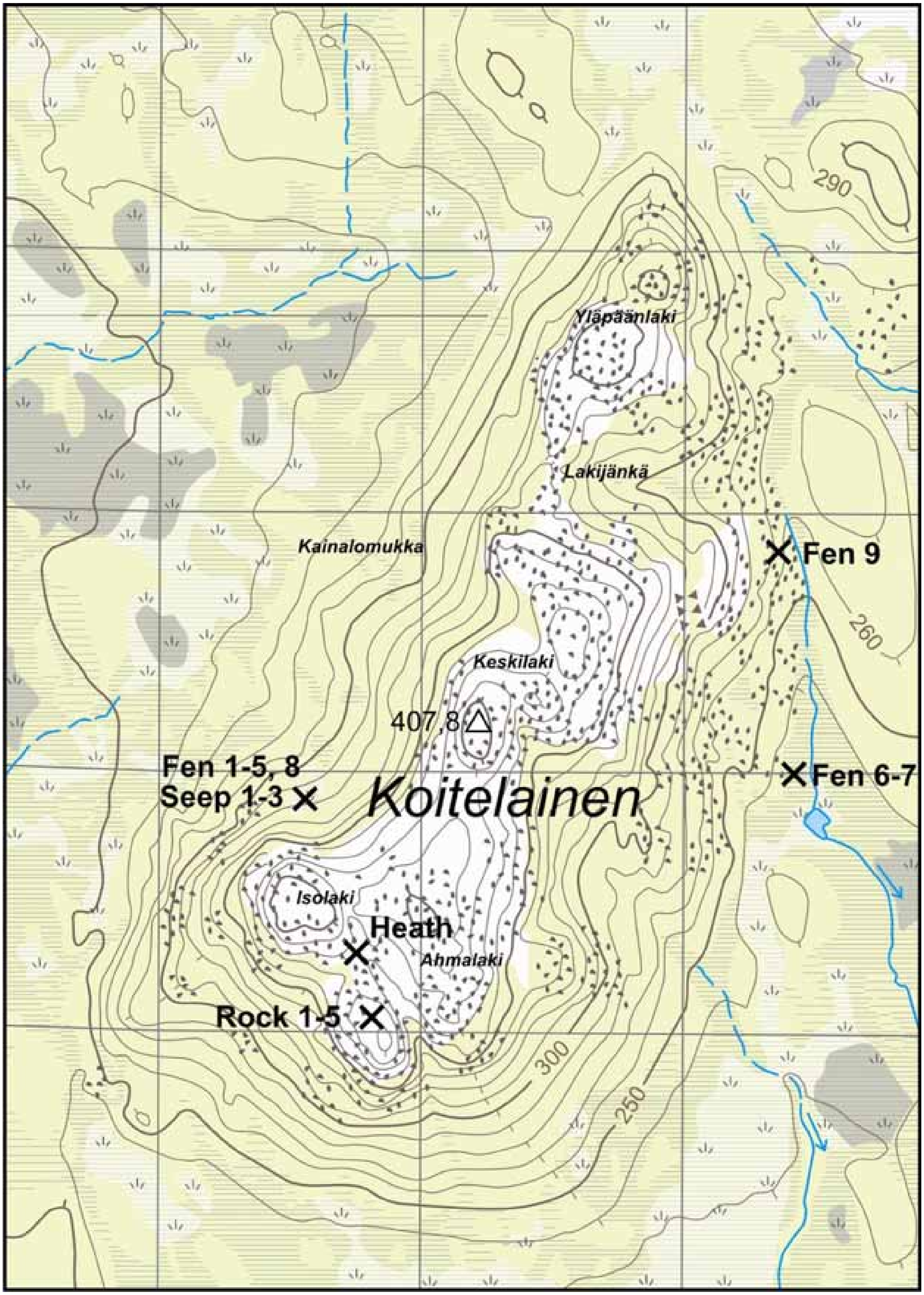

Figure 2. Koitelainen Hill, surrounding aapa mires and the locations of sample plots. The sides of the grid squares are 2 kilometres long, so that each square corresponds to 4 km².

Figure 3. General view of Koitelainen Hill, looking south-west from the Keskilaki summit towards the Isolaki summit. The trees behind the foreground boulders are mountain birch, and there is a sloping fen (the Isolaki Fen) on the opposite slope. August 1986. All photos by Jarmo Laitinen.

of northern Finland (Kalela 1961) are present. Locally, e.g. south of the top of Isolaki, there occur sparsely treed (pine) *Calluna vulgaris* heaths with *Tofieldia pusilla, Pinguicula vulgaris, Trichophorum cespitosum, Antennaria dioica, Festuca ovina, Diphasiastrum alpinum* and *Carex vaginata* (cf. Mikkonen-Keränen 1986). Small mires on the slopes and saddles of the summit areas of Koitelainen Hill are largely intermediate lawn fens (mostly *Loeskypnum badium* fen with small areas of *Paludella* spring fen). Poorer fens occur in small depressions (e.g. mud bottom flark fen with thin peat, dominated by *Trichophorum cespitosum*). The richest mire vegetation is represented by *Sphagnum warnstorfii* fens, *Campylium stellatum* fens and gently sloping rich pine fens. At lower altitudes (Kainalomukka area) there are herb-rich birch-spruce mires and some herb-rich forests with thin peat (according to the classifications of Eurola *et al.* 1984 and Eurola *et al.* 1995).

Fieldwork and nomenclature

Seventeen circular sample plots (56 cm diameter, 0.25 m²) were recorded during a trip to Koitelainen during 5–10 August 1986, and one sample plot was studied in September 1985 (Table 1, Figure 2). A small sample-plot size was used to compare the species composition and richness of vegetation patterns of very different sizes. Metallic circles were placed in homogeneous vegetation patches (fen patches on rock outcrops, *Warnstorfia sarmentosa* seepages) or in small-scale vegetation patterns (*Loeskypnum badium* fens, *Calluna*-*Trichophorum* heath). The percentage cover was estimated by eye. Some plant specimens were gathered for checking the identification of species, and they were determined later (2009) in the herbarium of Oulu University (OULU). Tauno Ulvinen determined the less-known moss *Oncophorus elongatus* (Hedenäs 2005, 2006, Ulvinen 2009) and some other moss and vascular plant specimens. Pekka Halonen determined lichen specimens. The *Oncophorus elongatus* specimen is deposited at OULU. The nomenclature of bryophytes follows Ulvinen *et al.* (2002), that of lichens Stenroos *et al.* (2011) and that of vascular plants Hämet-Ahti *et al*. (1998). Hepatics were not identifed but are recorded as a collective group.

Table 1. Localities, characteristics and species composition (% cover) of sample plots. Locality One (1) is the saddle between Isolaki and the southernmost summit; Locality Two (2) the northern head of the southernmost summit; Locality Three (3) the sloping fen north of Isolaki summit (the Isolaki Fen); Locality Four (4) the flat fen (aapa mire) at the eastern foot of Koitelainen Hill; and Locality Five (5) the eastern slope of the hill, near the foot.

Sample plot	**Heath**	**Rock 1**	**Rock 2**	**Rock 3**	**Rock 4**	**Rock 5**	**Fen 1**	**Fen 2**	**Fen 3**	**Fen 4**	**Fen 5**	**Fen 6**	**Fen 7**	**Fen 8**	**Fen 9**	**Seep 1**	**Seep 2**	**Seep 3**
Locality	1	2	2	2	2	2	3	3	3	3	3	4	4	3	5	3	3	3
Area of vegetation:																		
A: Homogenous veg. pattern	A						A	A	A	A	A	A	A	A	A			
P: Fen patches on rock outcrop		P	P	P	P	P												
S: Narrow soak in a fen																S	S	S
Sloping (S) or flat (F)	S	S	S	S	S	S	S	S	S	S	S	F	F	S	S	S	S	S
Location in mire basin:																		
M: Margin of mire basin							M	M				M	M					M
C: Centre of mire basin									C	C	C			C		C	C	
Altitude (m a.s.l.)	375	385	385	385	385	385	340	340	335	335	335	235	235	335	265	335	335	340
Organic layer (cm)	30	10	7	9	12	9	43	62	55	49	51	128	53	20	100	25	20	27
Species																		
TREES																		
Pinus sylvestris (sapling)	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
DWARF SHRUBS																		
Andromeda polifolia	1	0.5	0.5	0.5	+	0.5	1	0.5	0.5	0.5	+	0.5	0.5	+	0.5	+	0.5	0.5
Betula nana	-	-	-	-	-	2	-	-	-	-	-	-	+	-	+	-	-	1
Calluna vulgaris	10	+	-	1	2	+	-	-	-	-	-	-	-	-	-	-	-	-
Diphasiastrum alpinum	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Empetrum nigrum	-	+	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-
Huperzia selago	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vaccinium oxyc. + *microc*.	-	-	+	-	-	-	-	+	-	-	+	1	0.5	-	-	-	-	-
V. uliginosum	-	-	-	+	+	-	-	-	-	-	-	-	+	-	-	-	-	-
'SEDGES'																		
Carex dioica	-	-	-	-	-	-	-	0.5	-	-	-	-	-	+	-	-	+	1
C. lasiocarpa	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-
C. magellanica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-
C. pauciflora	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-
C. rostrata	-	-	-	-	-	-	-	-	5	0.5	5	3	15	0.5	-	20	25	-
Eriophorum angustifolium	-	-	-	-	-	-	0.5	0.5	+	0.5	+	0.5	0.5	+	30	0.5	1	5
E. vaginatum	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-
Trichophorum alpinum	-	-	-	-	-	-	-	-	-	-	-	-	0.5	-	-	-	-	-
T. cespitosum	25	30	15	7	10	20	40	50	40	30	50	20	2	40	0.5	-	-	-
GRASSES																		
Molinia caerulea	5	10	10	7	10	20	7	10	1	3	5	3	+	5	-	-	-	-
Nardus stricta	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Sample plot	**Heath**	**Rock 1**	**Rock 2**	**Rock 3**	**Rock 4**	**Rock 5**	**Fen 1**	**Fen 2**	**Fen 3**	**Fen 4**	**Fen 5**	**Fen 6**	**Fen 7**	**Fen 8**	**Fen 9**	**Seep 1**	**Seep 2**	**Seep 3**
FORBS																		
Antennaria dioica	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bartsia alpina	0.5	1	-	1	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-
Drosera longifolia	-	-	-	-	-	-	-	0.5	-	-	-	-	-	-	-	-	-	-
D. rotundifolia	-	-	-	-	-	-	-	-	0.5	1	-	-	-	-	-	-	-	-
Equisetum fluviatile	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
E. palustre	-	-	-	-	-	-	-	-	-	-	-	-	0.5	-	-	-	-	-
E. sylvaticum	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	0.5	0.5
Menyanthes trifoliata	-	-	-	-	-	-	-	-	1	5	0.5	+	-	-	-	-	-	-
Pinguicula vulgaris	-	-	0.5	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Potentilla palustris	-	-	-	-	-	-	-	-	0.5	-	+	+	+	+	-	+	-	-
Selaginella selaginoides	0.5	1	1	2	0.5	3	-	-	-	-	-	-	-	-	-	-	-	-
Solidago virgaurea	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tofieldia pusilla	0.5	0.5	1	10	1	5	-	-	-	-	-	-	-	-	-	-	-	-
MOSSES																		
Campylium stellatum	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dicranum drummondii	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Fissidens osmundoides	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hylocomium splendens	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Loeskypnum badium	0.5	20	30	80	80	80	100	70	100	90	40	100	50	0.5	1	-	-	-
Oncophorus elongatus	-	1	+	1	0.5	-	0.5	1	-	-	-	-	-	-	-	-	-	-
Paludella squarrosa	-	-	-	-	-	-	-	0.5	0.5	2	2	-	2	-	-	-	-	-
Pleurozium schreberi	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Racomitrium lanuginosum	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
R. microcarpon	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Scorpidium revolvens	-	10	-	-	-	-	-	-	0.5	-	-	-	-	10	-	-	-	-
S. scorpioides	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-
Straminergon stramineum	-	-	-	-	-	-	0.5	-	-	-	+	-	5	-	-	-	-	-
Warnstorfia sarmentosa	-	+	2	2	0.5	1	+	10	2	10	40	+	1	90	100	100	100	100
Sphagnum compactum	10	-	-	-	-	0.5	-	-	-	-	-	-	-	-	-	-	-	-
S. warnstorfii	+	-	-	-	-	-	-	-	-	-	3	-	40	-	-	-	-	-
LIVERWORTS																		
Hepaticae sp.	0.5	-	-	-	-	-	1	2	-	-	-	0.5	3	-	-	-	-	-
Ptilidium ciliare	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
LICHENS																		-
Cetraria islandica	0.5	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cladina stellaris	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C. stygia	0.5	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
Cladonia crispata	-	-	-	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C. ecmocyna	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C. phyllophora	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cladonia sp.	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Analysis methods

Vegetation data were estimated by eye as vertically projected independent cover. Percent cover was scored as classes, using 10 % intervals from 10 to 100. At the extremes, 1 % intervals were used. Summaries, outlier analysis and ordination were performed using the package PC-ORD 5 (McCune & Grace 2002). For numerical analyses, square root transformation was used to reduce the influence of high cover values. As a preliminary summary, mean, standard deviation, sum, minimum, maximum, skewness and kurtosis were calculated for both species and sample plots. From the average sum and standard deviation of species, the coefficient of variation (CV) was calculated. This CV of the totals of species after transformation was 241 %, which has a large effect on the analysis. However, as our hypothesis is that the cover of the vegetation on plots is influenced by hydrological conditions, no relativisation of species was made. Outlier analysis was done for the sample plots by calculating the distance of each plot from every other plot using the Sorensen distance measure. No pair exceeded a value of 2.0, so no plot was excluded.

Ecological gradients were revealed using non-metric multidimensional scaling (NMDS) using default settings (McCune & Grace 2002). The ordination diagrams were interpreted by fitting smooth thin-plate spline surfaces (iso-lines). The degree of smoothing was determined by cross-validation (Wood 2003). Altitude and thickness of the peat layer were used as ecological metrics; additionally the number of species in a plot (species density) was applied. Spline surfaces were determined in the R statistical environment (R Development Core Team, 2009) using package 'Vegan' (Oksanen *et al*. 2006).

Sample plot groups and localities

The localities of sample plots were selected in the field, mainly according to the physiognomy of the vegetation; i.e. according to the dominant species and location of the vegetation (the sample plot groups were 'heath', 'rock', 'fen' and 'seep'). At the same time, the placement of sample plots took into consideration species composition and mire type, according to the Finnish mire site typology which is itself based on species composition (Ruuhijärvi 1960, Eurola *et al*. 1984, 1995) (Table 1).

Heath

The only heath plot is from the saddle between Isolaki summit and the southernmost summit (Figure 2). The saddle slopes slightly towards the south-west, and small saplings of pine (*Pinus sylvestris*), small birches (*Betula pubescens*) and junipers (*Juniperus commumis*) occur there. In the middle of the *Calluna vulgaris* vegetation there was a small area with *Trichophorum cespitosum* and *Molinia caerulea* (Table 1). The sample plot is from this small area, where there were also water-filled pits in the rocks.

Rock 1–5

Sample plots from the intermediate fen patches on a rock outcrop are from the north head of the southernmost summit, towards the west on the upper part of the slope (Figure 2). The site is on a convex slope. Smooth, barren outcrops occur alternately with fen patches dominated by *Molinia caerulea* and *Trichophorum cespitosum* (Figure 4). The moss layer is sparse with *Loeskypnum badium* dominating. Sample plots are from the fen patches only (Table 1). Patches resemble aapa-mire strings (lawn strings) on a barren outcrop, being elongated along the contours. During the study, such a string had dammed up a water layer of three centimetres on the barren rock on the upslope side of the string.

Fen 1–9

Sample plots of *Loeskypnum badium* fen according to Ruuhijärvi (1960) and Eurola *et al*. (1984, 1995) are from three localities. Fen plots 1–5 and 8 are from the gently sloping lawn fen north of Isolaki summit (Figure 5). Plots Fen 6 and Fen 7 are from the flat fen (aapa mire) at the foot of the mountain, from its eastern side. Plot Fen 9 is from the eastern slope of the mountain, near the foot.

Seep 1–3

The seep plots are all from the same sloping fen as the bulk of fen plots, i.e. from the sloping fen north of Isolaki summit. Seepage areas, dominated by *Warnstorfia sarmentosa* and with a low cover of vascular plants (*Carex rostrata, Eriophorum angustifolium, Equisetum sylvaticum*), occurred as narrow soaks within the *Loeskypnum badium* fen that predominates in the Isolaki sloping fen. Plot Seep 3 is from near the upper margin of the fen, and plots Seep 1 and Seep 2 are from the central parts of the fen. Seepage areas generally occurred in Koitelainen as narrow seepage tracks on *Calluna* heaths with pine trees, or as soaks within fens (Figure 6).

RESULTS

Ordination of sample plots

The horizontal dimension in the ordination (Figure 7) reflected the decreasing cover of

Figure 4. String-like fen patches on the rock outcrop on the southernmost summit of Koitelainen Hill. Here, barren rock surfaces between the vegetation patches are covered with water after rain. August 1986.

Figure 5. The Isolaki sloping fen (*Loeskypnum badium* fen) to the north of the Isolaki summit of Koitelainen Hill. September 1985.

Figure 6. A *Warnstorfia sarmentosa* soak (about 0.5 m wide) with *Eriophorum angustifolium* and *Equisetum sylvaticum*, at the foot of the southern part of Koitelainen Hill. The seepage track begins from the heath and drains to a *Loeskypnum badium* fen. September 1985.

Warnstorfia sarmentosa from the left (seep plots) to the right (fen, rock and heath plots). The vertical dimension was reflected in that *Menyanthes trifoliata, Carex rostrata* and *Potentilla palustris* occurred only in the bottom part of the graph, while *Calluna vulgaris, Diphasiastrum alpinum Empetrum nigrum, Huperzia selago, Nardus stricta, Antennaria dioica, Bartsia alpina, Selaginella selaginoides, Tofieldia pusilla, Campylium stellatum, Sphagnum compactum* and lichens concentrated into the upper part of the graph.

The sample plots representing intermediate fen patches on the rock outcrop (Rock 1–5) and almost all the fen plots formed a relatively uniform-looking group in the ordination graph (Figure 7), but the areas covered by rock plots and fen plots did not overlap. The difference was that the fen patches have dwarf shrubs (*Calluna vulgaris, Empetrum nigrum (s.l.)*, *Vaccinium uliginosum*), certain herbs (*Tofieldia pusilla, Selaginella selaginoides, Bartsia alpina, Pinguicula vulgaris*), and mosses and lichens (*Sphagnum compactum, Ptilidium ciliare, Racomitrium microcarpon, Cetraria islandica, Cladina stygia, Cladonia* species) which are lacking in ‘normal’ *Loeskypnum badium* fens. Thus the rock plots have some floristic features in common with the heath plot (Table 1). *Oncophorus elongatus* occurs both in rock plots and in the fen plots.

Plots Fen 5 and Fen 8, situated in the middle of the graph, were transitional between fen plots and the seep plots situated on the left in the graph. Plots Heath and Fen 7 were at the top and bottom of the graph respectively, far from the other sample plots. This arose because Plot Fen 7 contained abundant *Sphagnum warnstorfii* together with species, such as *Carex lasiocarpa*, that were lacking or rare in other plots.

Environmental variables and species richness within the ordination

There was an altitude gradient from the flat fen sample plot Fen 7 to the other fen plots, and finally to the heath and rock plots (Figure 7, Table 1). The peat layer was generally thin and no uniform pattern for the whole ordination surface was found (Figure 7, Table 1). The abundance of species increased along the horizontal gradient from seep plots to all the other plots, and along the vertical gradient from the fen group to the group of rock plots and to the heath plot (Figure 7).

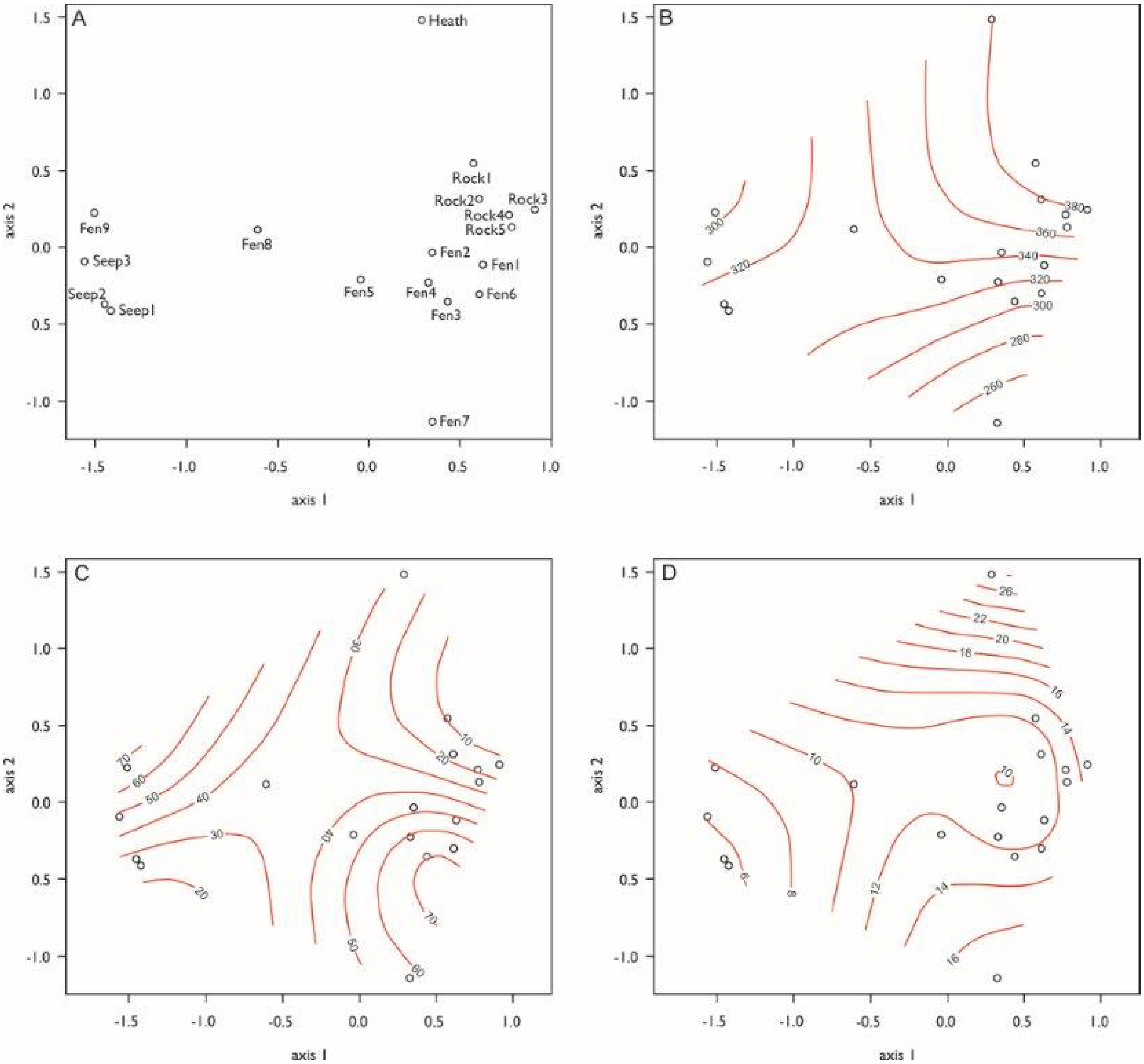

Figure 7. Ordination of the sample plots: (A) with sample plot labels; (B) with altitude (m a.s.l.) superimposed; (C) with peat thickness (cm) superimposed; and (D) with number of species superimposed.

DISCUSSION

Gradients, variables and species richness

The horizontal gradient from seep to fen and rock plots, reflecting the decreasing amount of *Warnstorfia sarmentosa,* can be interpreted to represent the general wetness of the ground surface, the seep plots occupying the wettest sites (flark level, carpet) and the rest of the plots the less wet sites (lawn and hummock levels) (Sjörs 1948, Eurola & Kaakinen 1978, Eurola *et al.* 1984, 1995) (Figure 7). The occurrence of *Warnstorfia sarmentosa* in a prominent position in relatively wet sites is shown in a comprehensive vegetation study of Persson (1961) in Swedish North Scandes.

The vertical dimension in the ordination graph (Figure 7) partly reflects the increasing general dryness of the ground surface (from bottom to top), but especially the variation from stable (bottom) to unstable (top) water regime; there is a larger number of species that are tolerant of seasonal drought according to Havas (1961) (*Molinia caerulea, Trichophorum cespitosum, Tofieldia pusilla, Selaginella selaginoides, Sphagnum compactum, Ptilidium ciliare, Campylium stellatum*) in the upper part of the graph (in rock plots and in the heath plot), while the indicators of stable water regime according to Laitinen (2008) (*Menyanthes trifoliata, Potentilla palustris, Carex rostrata*) occur only in the bottom part of the graph. The floristic indication of stable *versus* unstable water regime, including the effects on vegetation of fluctuation in water table level, seasonal drought of the surface peat and seasonal flooding (Auer 1922, Havas 1961, Heikkilä & Lindholm 1988, Laitinen 2008), is one of the least studied and little understood directions of variation in mire vegetation. Havas (1961) showed in his vegetation study, which included a temporal water-table measurement series, that the sloping fens of eastern Finland with stable and unstable water regimes have contrasting plant species groups and communities. Thirdly, the poor-to-rich direction of variation (Sjörs 1952, Sjörs & Gunnarsson 2002, Tahvanainen 2004)—i.e. the trophic gradient of Eurola & Kaakinen (1978), Eurola *et al*. (1984, 1995) and Heikkilä (1987)—is expressed in the vertical dimension in that the heath plot and the rock plots had more intermediate fen and rich fen indicators than the large fen group and the seep group. Finally, the indicators of frost action on mineral soil (in pine forest areas of the NBn Ivalo region north of Koitelainen) are more numerous in the upper part of the graph. These species include *Huperzia selago, Diphasiastrum alpinum, Selaginella selaginoides, Nardus stricta, Molinia caerulea, Trichophorum cespitosum, Tofieldia pusilla* and *Antennaria dioica* (Rintanen 1970). Thus, there may be some ecological link between the unstable water regime, frost action and the occurrence of intermediate to rich fen indicators. Plant species indicating unexpectedly high trophic status occur on sparsely vegetated frost ground sites in the NBn coniferous forest zone north of Koitelainen.

There was an altitude gradient (Figure 7) from the flat fen sample plot Fen 7 to the other fen plots and finally to the heath and the rock plots. Thus, the altitude gradient coincides closely with the stability of the water regime. Plots at higher altitudes have a more unstable water regime than the plot at the foot of the mountain. This simple pattern can be explained by a larger catchment area and, accordingly, a more continuous water supply at the foot of the mountain. A rather more complicated pattern might be revealed by sampling a larger number of plots, as the local conditions at each site exert great influence on the stability of the water regime.

The peat layer was generally thin (Figure 7) and no uniform pattern for the whole ordination surface was found. In the right half of the graph, peat thickness decreased as altitude increased; the rock plots at the highest altitude having the thinnest organic layer (10–20 cm), whereas the flat fen (Fen 7) at the foot of the mountain had the thickest (>60 cm) peat. In the left half of the graph, the exceptional plot Fen 9 had a thick peat layer (almost 70 cm), while the peat thickness at seep plots was only 20–30 cm (Table 1).

The abundance of species increased along the horizontal gradient from wetter to drier sites, which is a pattern generally seen in various boreal wetlands (Vitt *et al*. 2003, Whitehouse & Bayley 2005); and appearing clearly, for instance, within the alluvial-meadow vegetation series of large rivers (Kitinen, Luiro) around Koitelainen (Eurola 1967). Secondly, the species abundance increased from the fen group (the *Loeskypnum badium* fen of Ruuhijärvi 1960) to the group of rock plots (fen patches) and to the heath plot (Figure 7). The high species richness of the heath plot is best explained by the high environmental heterogeneity of the site. Environmental heterogeneity (occurrence of microhabitats) has been shown to correlate positively with the species richness in various habitats (Eriksson *et al*. 1995, Locky & Bayley 2006, Økland *et al*. 2008, Vitt *et al*. 1995, Whitehouse & Bayley 2005).

Intermediate *Molinia* fen patches at Koitelainen

The vegetation of the intermediate fen patches (rock plots) that we studied seemed to be close to that of the ‘normal’ *Loeskypnum badium* fens of Koitelainen, which fall into the corresponding mire site type of Ruuhijärvi (1960). However, the vegetation of the fen patches additionally resembles some of the *Molinia* meadow vegetation of Rintanen (1970: Table 8: plots 10, 15 and Fig. 16) by having *Loeskypnum badium.* The *Molinia* meadows were located in the southern part of the NBn mire zone of Eurola & Vorren (1980) (Raututunturit, Saariselkä and Luttojoki areas), and were thus more northerly than Koitelainen. The *Trichophorum cespitosum* peatland meadows of Laine & Nurmi (1971) in West Inari, occurring mainly in the same kind of (mafic) bedrock areas as Koitelainen, have many species in common with the fen patches of Koitelainen (*Trichophorum cespitosum, Tofieldia pusilla, Bartsia alpina*, *Pinguicula vulgaris*) although *Molinia* is lacking (it is rare in northern Lapland).

The fen patches of Koitelainen Hill, *Trichophorum cespitosum* - *Sphagnum compactum* - *Ptilidium ciliare* vegetation of Riisitunturi Hill (Havas 1961, Paasovaara 1986) and corresponding vegetation in the peripheral parts of the flat aapa mire complex Hirvisuo in the lowlands of the MBn zone of Finland (Laitinen *et al*. 2005, 2008a) represent one and the same ecological extreme end of mid- to north-boreal fen vegetation. The extremity appears in the pattern size (patches to small areas) and in the environment of the vegetation. The fen vegetation may be on a rock outcrop (Koitelainen Hill), on slopes (Riisitunturi Hill) or on flat, sandy substratum (Hirvisuo), but all the environments allow the loss of water from a thin peat layer, leading to repeated seasonal drought, evidently across the whole peat column (Laitinen *et al*. 2008b). The latter circumstance is not characteristic of mires proper as defined by Tahvanainen (2005), where the water table resides continuously within the peat layer. The latter seems to be in accordance with the conception of Rintanen (1970) and Laine & Nurmi (1971), who regard the NBn *Molinia* vegetation of Saariselkä and NBn *Trichophorum cespitosum* vegetation of West Inari as meadows. However, all of the extreme cases mentioned above may be viewed as belonging to a specific functional type of lawn mires with thin peat, namely the water-fluctuation lawn-fens (Laitinen 2008), whose best-known vegetation type *Trichophoro cespitosi-Sphagnetum compacti* occurs mainly in the subalpine belt of the boreal zone of northern Europe according to Dierssen (1995). A thin peat layer with high humification degree, caused by repeated aeration during drought periods, characterises the water-fluctuation lawn-fens; alongside the specific community composition, which appears to be partly structured by the seasonal drought tolerances of individual fen species (Havas 1961, Heikkilä & Lindholm 1988, Laitinen 2008, Laitinen *et al*. 2008b).

ACKNOWLEDGEMENTS

We thank Professor Karl-Dag Vorren, University of Tromsø, who provided us with information about north-Norwegian plant communities; Tauno Ulvinen and Pekka Halonen for determining some specimens; Pekka Kokko for company in the field; and Pirjo Appelgren for drawing the Figures. We also thank the editors of *Mires and Peat*, Professor R.S. Clymo and Dr Olivia Bragg, for improving the text quality and the structure of the article.

REFERENCES

Alalammi, P. (ed.) (1987) *Atlas of Finland, Folio 331, Climate.* National Board of Survey, Geographical Society of Finland, Helsinki.

Auer, V. (1922) Suotutkimuksia Kuusamon ja Kuolajärven vaara-alueilta. (Referat: Moorforschungen in den Vaaragebieten von Kuusamo und Kuolajärvi.) (Mire research in Kuusamo and the Kuolajärvi Danger Area). *Communicationes ex Instituti Forestalis Fenniae*, 6(1), 1–368 (in Finnish with German summary).

Dierssen, K. (1995) *Vegetation Nordeuropas (The Vegetation of Northern Europe)*. Verlag Eugen Ulmer, Stuttgart, Germany, 838 pp. (in German).

Eeronheimo, H., Virtanen, R., Sippola, A-L., Sepponen, P., Salmela, S. & Pikkupeura, R. (1992) Pallas-Ounastunturin kasvillisuus – Ounastunturin Pyhäkeron alue (Vegetation of Pallas-Ounastunturi fjell – Pyhäkero area of Ounastunturi). *Metsäntutkimuslaitoksen tiedonantoja*, 427, 1–119 (in Finnish).

Eriksson, Å., Eriksson, O. & Berglund, H. (1995) Species abundance patterns of plants in Swedish semi-natural pastures. *Ecography*, 18, 310–317.

Eurola, S. (1967) Über die Vegetation der Alluvialwiesen im Gebiet der geplanten Stauseen von Lokka und Porttipahta in Finnischen Lappland (On the vegetation of alluvial medows in the area of the planned reservoirs Lokka and Porttipahta in Finnish Lapland). *Aquilo Serie Botanica* 5, 1–119 (in German).

Eurola, S., Hicks, S. & Kaakinen, E. (1984) Key to Finnish mire types. In: Moore, P.D. (ed.) *European Mires*. Academic Press, London, 11–117.

Eurola, S., Huttunen, A., Huttunen, M. & Paasovaara, P. (1982) Kaksi rinnesuota Riisitunturin kansallispuistossa (The nature of two sloping mires in the Riisitunturi National Park, northern Finland (66º15´N, 28º35´E)). *Suo*, 33, 75–79 (in Finnish with English summary).

Eurola, S., Huttunen, A. & Kukko-oja, K. (1995) Suokasvillisuusopas (Mire vegetation guide) *Oulanka Reports*, 14, 1–85 (in Finnish).

Eurola, S. & Kaakinen, E. (1978) *Suotyyppiopas (Mire Site Type Guide).* WSOY, Porvoo-Helsinki-Juva, Finland, 87 pp. (in Finnish).

Eurola, S. & Kaakinen, E. (1982) The influence of an upland climate on the vegetation in the province of Kainuu, Eastern Finland. *Aquilo Serie Botanica*, 18, 10–15.

Eurola, S., Kaikkonen, K., Leinonen, S. & Sepponen, P. (1991) Forest vegetation of the upland areas of the province of Kainuu, eastern Finland. *Aquilo Serie Botanica*, 30, 1–23.

Eurola, S. & Vorren, K-D. (1980) Mire zones and sections in North Fennoscandia. *Aquilo Serie Botanica*, 17, 39–56.

Haapasaari, M. (1988) The oligotrophic heath vegetation of northern Fennoscandia. *Acta Botanica Fennica*, 135, 1–219.

Hämet-Ahti, L. (1981) The boreal zone and its biotic subdivision. *Fennia*, 159, 69–75.

Hämet-Ahti, L., Suominen, J., Ulvinen, T. & Uotila, P. (eds.) (1998) *Retkeilykasvio* (*Field Flora of Finland),* 4th edition. Finnish Museum of Natural

History, Botanical Museum, Helsinki, Finland, 656 pp. (in Finnish with English abstract).

Havas, P. (1961) Vegetation und ökologie der ostfinnischen Hangmoore (Vegetation and ecology of the east Finnish sloping mires). *Annales Botanici Societatis Zoologicæ Botanicæ Fennicae Vanamo*, 31(2), 1–188 (in German).

Hedenäs, L. (2005) *Oncophorus wahlenbergii* var. *elongatus* I. Hagen, an overlooked taxon in northern Europe. *Lindbergia*, 30, 32–38.

Hedenäs, L. (2006) *Oncophorus elongatus* gles knölmossa (*Oncophorus elongatus* sparse-tuber-moss). In: Hallingbäck, T., Hedenäs, S., Lönnell, N. & Weibull, H. Nationalnyckeln till Sveriges flora och fauna (*National Key to Sweden's Flora and Fauna*), Bladmossor: Sköldmossor–blämossor, Bryophyta: *Buxbaumia–Leucobryum*. ArtDatabanken, SLU, Uppsala, 302 pp. (in Swedish).

Heikkilä, H. (1987) The vegetation and ecology of mesotrophic and eutrophic fens in western Finland. *Annales Botanici Fennici*, 24, 155–175.

Heikkilä, R. & Lindholm, T. (1988) Distribution and ecology of *Sphagnum molle* in Finland. *Annales Botanici Fennici*, 25, 11–19.

Kaakinen, E., Kokko, A., Aapala, K., Kalpio, S., Eurola, S., Haapalehto, T., Heikkilä, R., Hotanen, J.P., Kondelin, H., Nousiainen, H., Ruuhijärvi, R., Salminen, P., Tuominen, S., Vasander, H. & Virtanen, K. (2008) Suot (Mires) In: Raunio, A., Schulman, A. & Kontula, T. (eds.) Suomen luontotyyppien uhanalaisuus - Osa 2: Luontotyyppien kuvaukset. (Threatened biotopes of Finland - Part 2: Descriptions of biotopes). *Suomen ympäristö*, 8/2008, 143–256 (in Finnish).

Kalela, A. (1961) Waldvegetationszonen Finnlands und ihre klimatischen Paralleltypen (Forest vegetation zones of Finland and their climatic parallel types). *Archivum Societatis Zoologicæ Botanicæ Fennicae "Vanamo"*, 16(suppl.), 65–83 (in German).

Laine, U. & Nurmi, J. (1971) Factors affecting vegetation and flora of anorthosite and granulite areas in western Inari, Finnish Lapland. *Reports from the Kevo Subarctic Research Station*, 8, 104–115.

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, 1–61.

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., Rehell, S. & Huttunen, A. (2005) Vegetation-related hydrotopographic and hydrologic classification for aapa mires (Hirvisuo, Finland). *Annales Botanici Fennici*, 42, 107–121.

Laitinen, J., Rehell, S. & Oksanen, J. (2008b) Community and species responses to water level fluctuations with reference to soil layers in different habitats of mid-boreal mire complexes. *Plant Ecology*, 194, 17–36.

Locky, D.A. & Bayley, S.E. (2006) Plant diversity, composition, and rarity in the southern boreal peatlands of Manitoba, Canada. *Canadian Journal of Botany*, 84, 940–955.

McCune, B. & Grace, J.B. (2002) *Analysis of Ecological Communities.* MjM Software Design, United States of America, 300 pp.

Mikkonen-Keränen, S. (1986) Riisitunturin ja Ison-Syötteen kivennäismaiden kasvillisuus (Vegetation of heathlands in Riisitunturi and Iso-Syöte Hills). *Oulun Yliopiston Oulangan Biologisen Aseman Monisteita*, 9, 39–50 (in Finnish).

Mutanen, T. (1997) Geology and ore petrology of the Akanvaara and Koitelainen mafic layered intrusions and the Keivitsa-Satovaara layered complex, northern Finland. *Geological Survey of Finland Bulletin*, 395, 1–233.

Økland, R.H., Rydgren, K. & Økland, T. (2008) Species richness in boreal swamp forests of SE Norway: The role of surface microtopography. *Journal of Vegetation Science,* 19, 67–74.

Oksanen, J., Kindt, R., Legendre, P. & O'Hara, R.G. (2006) *Vegan: Community Ecology Package.* R package version 1.8-2. http://cran.r-project.org/.

Paasovaara, P. (1986) Riisitunturin alueen suotyypeistä (On mire site types of Riisitunturi Hill). *Oulun Yliopiston Oulangan Biologisen Aseman Monisteita*, 9, 51–87 (in Finnish).

Persson, Å. (1961) Mire and spring vegetation in an area north of lake Torneträsk, Torne Lappmark, Sweden. *Opera Botanica*, 6(1), 1–187.

R Development Core Team (2009) *R: A Language and Environment for Statistical Computing.* R Foundation for Statistical Computing, Vienna, Austria.

Rintanen, T. (1970) On the vegetation and ecology of frost ground sites in eastern Finnish Lapland. *Annales Botanici Fennici*, 7, 353–374.

Ruuhijärvi, R. (1960) Über die Regionale Einteilung der Nordfinnischen Moore (On the regional zonation of north Finnish mires). *Annales Botanici Societatis Zoologicæ Botanicæ Fennicae Vanamo*, 31, 1–360 (in German).

Rydin, H., Sjörs, H. & Löfroth, M. (1999) Mires. *Acta Phytogeographica Suecica*, 84, 92–112.

Sjörs, H. (1948) Myrvegetation i Bergslagen (Mire vegetation in Bergslagen, Sweden). *Acta Phytogeographica Suecica*, 21, 1–299 (in Swedish with English summary).

Sjörs, H. (1952) On the relation between vegetation and electrolytes in North Swedish mire waters. *Oikos*, 2, 241–258.

Sjörs, H. & Gunnarsson, U. (2002) Calcium and pH in north and central Swedish mire waters. *Journal of Ecology*, 90, 650–657.

Stenroos, S., Ahti, T., Lohtander, K. & Myllys, L. (eds.) (2011) Suomen jäkäläopas (Lichen guide for Finland). *Norrlinia*, 21, 1–534 (in Finnish).

Tahvanainen, T. (2004) Water chemistry of mires in relation to the poor-rich vegetation gradient and contrasting geochemical zones of northeastern Fennoscandian Shield. *Folia Geobotanica*, 39, 353–369.

Tahvanainen, T. (2005) Diversity of water chemistry and vegetation of mires in the Kainuu region, middle boreal Finland. *University of Joensuu, PhD Dissertations in Biology*, 33, 30 pp.

Ulvinen, T. (2009) Isotihkusammal (*Oncophorus elongatus*) Suomessa (*Oncophorus elongatus* in Finland). *Bryobrotherella*, 12, 58–61 (in Finnish).

Ulvinen, T., Syrjänen, K. & Anttila, S. (eds.) (2002) Suomen sammalet – levinneisyys, ekologia, uhanalaisuus (Mosses of Finland – distribution, ecology and red list status). *Suomen ympäristö*, 560, 1–354 (in Finnish).

Vitt, D.H., Halsey, L.A., Bray, J. & Kinser, A. (2003) Patterns of bryophyte richness in a complex boreal landscape: Identifying key habitats of McCelland lake wetland. *The Bryologist,* 106(3), 372–382.

Vitt, D.H., Li, Y. & Belland, R. (1995) Patterns of bryophyte diversity in peatlands of continental western Canada. *The Bryologist*, 89, 218–227.

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.

Wood, S.N. (2003) Thin plate regression splines. *Journal of Royal Statistical Society B*, 65, 95–114.

Submitted 04 Jan 2011, final revision 13 Jly 2011
Editor: R.S. Clymo

Author for correspondence:
Dr. Jarmo Laitinen, Department of Biology, P.O. Box 3000, FI-90014 University of Oulu, Finland.
Tel:+358-40-5482 335; Fax: +358-8-553 1061; E-mail: jarmo.laitinen@oulu.fi