Mire margin to expanse gradient in part relates to nutrients gradient: evidence from successional mire basins, north Finland

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SUMMARY

To study the relationship between mire vegetation and ecological variables we tested the Finnish hypothesis that the mire margin to expanse gradient in vegetation composition relates to a gradient of solutes (main plant nutrients) in the soil that is separate from the mainly pH related poor–rich gradient. Successional mire basins where mire margin to expanse is the prominent gradient were surveyed. An indirect method (Ellenberg indicator values) and direct measurements (phosphorous concentrations, pH) were used to assess the relationship between the mire margin to expanse and nutrients gradients. Vegetation with indicators of Subtype A mire margin vegetation (assumed to reflect surface water flow) correlated best with Ellenberg nitrogen values, whereas Subtype B (assumed to reflect groundwater influence) correlated best with Ellenberg reaction values. Subtype C (supposed to reflect mineral soil influence) did not correlate with these Ellenberg values. The study provides information about the complexity of the vegetational gradients. In general, water flow seems to be related to the poor–rich gradient, but surface water flow is also related to the nutrients gradient. Subtype C (influence of mineral soil) seems to differ from the other two subtypes of the mire margin to expanse gradient and also from the poor–rich gradient. It is prominent on forested sites, where the water table is comparatively deep.

KEY WORDS: Ellenberg indicator values, mire gradients, poor–rich gradient

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INTRODUCTION

Compositional gradients in mire vegetation are a central research topic in boreal and temperate mire ecology (Malmer 1986, Wheeler & Proctor 2000, Økland _et al_. 2001a, Jassey _et al_. 2014). There are differences of opinion about even major gradients in various geographical areas, about their relationships with measurable environmental factors, about their interrelationships, and about terminology. The relationship between the poor to rich gradient (denoting pH) and the gradient of solute concentrations or fertility (denoting availability of the main plant nutrients) was a major issue in the debate on mire gradients and subdivisions between British (Wheeler & Proctor 2000) and Scandinavian researchers (Økland _et al_. 2001a). The British proposed that fertility as a mire gradient was separate from the poor to rich gradient, whereas Scandinavian authors considered that environmental variables associated with either of these gradients formed a single complex gradient that correlated with the poor to rich gradient in vegetation. In Scandinavia it has more recently been proposed that the term 'mire margin' should be reserved solely for treed vegetation (swamp forest) (Økland _et al_. 2001a). In continental Central Europe a new proposal presented by Hájek _et al_. (2006) related the major fen types to both the poor to rich gradient and the fertility gradient, where fertility refers to the proportion of nutrient-demanding forbs and grasses. North American researchers (Bridgham _et al._ 1996) have recommended the separation of gradients denoting pH and nutrients. In boreal Alberta, Vitt & Chee (1990) distinguished between a nutrients gradient that was especially associated with variations in vascular plant occurrence and a poor to rich gradient associated with variations in bryophyte occurrence. A recent Canadian study of ombrotrophic mires (bogs) and minerotrophioc laggs found that the differences in main plant nutrients were more prominent than differences in pH or base cations (Paradis _et al_. 2015).

In Scandinavia, the concept of three major mire gradients (poor to rich, hummock to mud bottom, mire margin to mire expanse) (Sjörs 1948, Fransson 1972, Malmer 1986, Moen _et al_. 2012) has almost attained the status of a paradigm in mire ecology. The

margin to expanse gradient (Sjörs 1948) was introduced to describe the vegetation patterns of raised bogs with diverse marginal parts (laggs) and more monotonous central parts. This gradient has also been considered fitting for aapa mires (Ruuhijärvi 1960), where the variation arises mainly in minerotrophic vegetation. The same three major gradients have been considered in Finland (Ruuhijärvi 1960, Eurola *et al.* 1984, 1995, 2015; Ruuhijärvi & Lindholm 2006), where the importance of a fertility gradient for forestry (Reinikainen 1988) has increased the interest. Here, the development towards peatland forests has been shown to correlate with nutrients and peat thickness (Eurola & Holappa 1985) and the occurrence of mire margin vegetation (Hotanen & Vasander 1992). The Scandinavian mire margin to expanse gradient of Sjörs (1948) was divided into subgroups with a specific ecohydrological interpretation for each subgroup. The subgroups of mire margin vegetation (Eurola *et al.* 1984, 1995, 2015), the corresponding gradients (Tuomikoski 1942, 1955; Ruuhijärvi 1960) and their ecohydrological interpretations (Eurola *et al.* 1984, 1995, 2015) are not well known outside Finland. In general, it is hypothesised that mire margin influence appearing in the vegetation is a supplementary nutrient effect (Eurola *et al.* 1984, 1995, 2015). The gradient in vegetation composition from mire expanse to mire margin appears as three subtypes:

A: gradient towards vegetation of littoral areas ("*Sumpfigkeit*"; Brandt 1948, Ruuhijärvi 1960, Eurola 1962) (typical indicators *Potentilla palustris, Lysimachia thyrsiflora, Calliergon cordifolium*; additional nutrients thought to come from limnogenous water or from water moving through a loose peat layer);

B: gradient towards vegetation of springs ("*Quelligkeit*"; Ruuhijärvi 1960, Eurola 1962) (typical indicators *Warnstorfia sarmentosa, Warnstorfia exannulata, Sphagnum teres, Helodium blandowii, Philonotis* sp.; additional nutrients thought to be introduced by groundwater emerging from mineral soil); and

C: gradient towards the vegetation of boreal mesic heath forests ("*Bruchmoorigkeit*"; Ruuhijärvi 1960, Eurola 1962) (typical indicators *Picea abies, Carex globularis, Equisetum sylvaticum, Sphagnum girgensohnii*; additional nutrients thought to come from the mineral soil beneath the thin peat layer).

Mire expanse influence appearing in the vegetation as the lack of mire margin species belonging to Subtypes A–C above is interpreted as an inherent plant nutrient influence (self-sufficiency)

(Eurola 1969; Eurola *et al.* 1984, 1995, 2015). This implies the occurrence and dominance of true mire species (Eurola & Huttunen 2006), e.g. most of the *Sphagnum* mosses. However, the Finnish hypothesis that the mire margin direction of compositional variation relates to the soil nutrient (nitrogen etc.) gradient is poorly tested, and the relationships between the poor to rich and margin to expanse gradients have not been thoroughly studied. Additionally, the relationship between the boreal margin to expanse gradient and the Central European fertility gradient has not been considered.

Research methods for the relationships between compositional gradients and environmental factors include preliminary evaluations based on the vegetation (indirect surveys) and direct measurements for environmental factors assumed to be associated with the compositional gradients. Ellenberg indicator values for nitrogen and soil reaction are allocated to different plant species (Ellenberg *et al.* 1991). This provides an indirect method for assessing the relationships between species composition and the environment when only vegetation data are available. The nitrogen value can be taken to reflect the overall production of vegetation (Hill & Carey 1997, Schaffers & Sykora 2000) and hence the concentrations of all the main plant nutrients (N, P, K). The reaction value can be considered to reflect soil pH.

In the research reported here, we first tested the validity of the Ellenberg indicator values against environmental variables for our study area, then asked how self-sufficiency (mire expanse vegetation) and the three Finnish subtypes of the mire margin direction of compositional variation relate to main nutrient concentrations and the acidity (reaction/pH) of the soil. We used Ellenberg indicator values (for nitrogen and reaction) as an indirect method, and measurements of the phosphorous content of the soil and the soil-water pH as a direct method. The result of applying the indirect method with a fairly large dataset was checked using the direct method with a small dataset.

METHODS

Study area

The Finnish land uplift coast of the Bothnian Bay (Kakkuri 1985) was chosen as the study area for interpretation of the mire margin to expanse gradient because all subtypes of the mire margin to expanse gradient and all grades of the poor to rich gradient (Rehell & Heikkilä 2009, Rehell & Laitinen 2014, Laitinen *et al.* 2016) are well represented there, enabling comparisons. Most of the sites are classified

as minerotrophic; true ombrotrophy can be found on small areas in the peripheral parts of the oldest mire systems (Rehell & Laitinen 2014). Sequences of virgin mire basins in both morainic (Ryöskäri–Kairavaara) and sandy (Hailuoto–Rokua) terrain (Figure 1) were included (Rehell & Heikkilä 2009). The underlying bedrock is composed mainly of siliceous granitoid gneiss and of migmatite with diabase joints and other more basic veins (in Ryöskäri–Kairavaara) and mainly of a sedimentary siltstone (in Hailuoto–Rokua) (Geological Survey of Finland 1997). The area lies within the mid-boreal forest (Kalela 1958, 1961) and peatland (Ruuhijärvi 1960) zones.

Vegetation sampling
Habitats for vegetation studies included seashore meadows and thickets in the littoral belt, together with mires and paludified heath forests inland. The species composition of 158 sample plots (normally single 10 m × 10 m (100 m^2) squares but in some special cases several squares joined together) was studied (Rehell & Laitinen 2014). The plots were located along local transects that were placed across successional mire basins so that both the areas near watersheds and the parts with voluminous water flow (Laitinen *et al.* 2007a) were represented. In some localities two transects (perpendicular to one another) were needed to obtain information about hydrologically different situations. Sample plots were placed at intervals of 100 metres along the local transects. Where a plot would have fallen partly on a mineral soil island or small water body, one plot was recorded on each side of the island or pond. Principal topographical patterns (hummocks, lawns, flarks, etc.) were mapped in these (large) sample plots. Within each of the large sample plots, smaller plots (1 m²) (Laitinen *et al.* 2008) were studied on each mire surface level to get a valid view of the whole large sample plot. A total of 468 plots of area 1 m² were investigated. Cover percentages of species were evaluated by eye in the 1 m² plots, and cover values for each large sample plot were calculated as averages of the values for 1 m² plots, weighted according to the proportions of different mire surface levels mapped for the large plot. A total list of species was made for each 100 m² plot, and species occurring in the large plots but not in any of the 1 m² plots were added to the results for 1 m² plots representing the mire surface levels in which the additional species were found. A 0.1 percentage cover value was recorded for such species. For 17 sample plots, two or even more 100 m^2 squares were combined to get a broader view of some particular sites. This was done because the data were also used for a study of the initiation and development of microtopographical
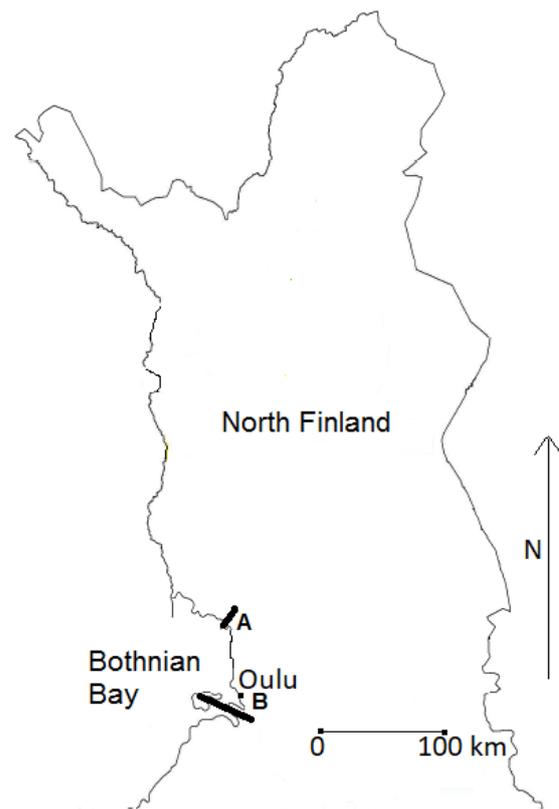

Figure 1. Outline map of northern Finland showing the location of the study area. A: sites in moraine topography; B: sites in sandy topography.

levels during the aapa mire succession (Rehell *et al.* 2012). When calculating the mean cover values of species for whole mire basins, all deviations from the normal sample plot size and density were taken into account (Rehell & Laitinen 2014). The studied transects are presented in Rehell *et al.* (2012).

Fieldwork was carried out for the moraine terrain in July–September 2001 and 2002, and for the sandy topography in July–September 2003. Nomenclature follows Hämet-Ahti *et al.* (1998) for vascular plants and Ulvinen *et al.* (2002) for mosses. Hepatics and lichens were mostly determined at genus level.

Vegetation analysis
Ellenberg indicator values (Ellenberg *et al.* 1991) were used to evaluate indirectly the relationships of cover values for different plant species (weighted means for large sample plots) to environmental factors. For Ellenberg reaction the cover values for both vascular plants and mosses were used. For nitrogen, the percentage cover values for only vascular plants were used, because values for moss species are not provided in the literature. In calculating the Ellenberg values for reaction, the percentages of plant species were modified to

highlight the importance of even small percentages of indicator species by using the square roots of the values so that the 1–100 scale reduced to 1–10. Although the Ellenberg indicator values and their usage stem from the temperate zone, only a few species were lacking in this boreal zone location.

The species indications for the subtypes (A–C) of mire-margin gradient were derived from Eurola *et al.* (1984, 1995, 2015) (indicator species of *Sumpfigkeit, Quelligkeit, Bruchmoorigkeit*). The poor to rich classes suggested by Rehell & Heikkilä (2009) were used, but the indications of single species were derived from the trophic-level indications suggested by Eurola *et al.* (1984, 1995, 2015) and Eurola & Huttunen (2006).

Geochemical sampling and analysis
The material for the nutrients analyses was collected for a study of the geochemistry of young lake basins and their catchment areas (Siira 2013, 2017), so all sites were situated fairly near the coast. Four of the sites included in that study were situated in the sample plots of the present mire vegetation study. Concentrations of PO_4 (phosphate) were used because phosphorus is thought to be a critical nutrient for plant growth in both boreal forested peatlands (Päivänen 1989) and pristine bogs and fens (Richardson & Marshall 1986, Koerselman & Verhoeven 1995), sometimes together with nitrogen (Bridgham *et al.* 1996, Pérez-Corona & Verhoeven 1996). The results of the analysis method we selected were the amounts of phosphorus that are directly available to plants or can become available through biological processes, but this method was found to be unsuitable for analysing nitrogen availability.

The sites of the geochemical studies differed principally in relation to the mire margin to expanse gradient. Two of the sites were rich *Scorpidium*-flark-level fens with large catchment areas on moraine terrain. At the first of these the vegetation showed a strong mire margin effect (surface and groundwater influence as well as mineral soil influence, the peat layer being 25 cm thick with a thin layer of gyttja at its base). At the other studied *Scorpidium*-flark fen the vegetation showed a clear mire-expanse character (no clear mire-margin indicators, peat layer 135 cm thick). The other two sites were moderately poor fens located between sandy beach ridges. The first of these had a clear mire-margin character (lush swamp dominated by *Equisetum fluviatile*, 40 cm peat layer with a thin layer of gyttja above the sand); whereas the second had a clear mire-expanse character (sedge fen with relatively uniform *Sphagnum* carpet and 40 cm of *Carex* peat directly above the sandy substratum).

The samples for nutrients analyses were taken from the top 40 cm of the peat layer or, on sites with thin peat layers, from the whole of the peat layer plus the underlying gyttja layer. This was thought to represent the main rooting layer for vascular plants. Profiles were taken from this layer with a metal cylinder 11 cm in diameter. Different peat horizons were analysed separately. The samples were dried for 24 hours at 60 °C. The extraction was carried out by adding 0.5 g of pulverised sample to 50 ml of 0.1 M HCl. The time for extraction was 12 hours. After that the samples were shaken mechanically and filtered (through filter paper). The amount of phosphorus was determined spectrometrically, using the ascorbic acid method modified for soil samples (Matt 1970). The results were calculated as phosphorus (P) concentration in a soil sample (mg kg^{-1} or ppm) for the whole surface layer.

pH was measured only in young mires near the coast, where intensive mapping of vegetation (Rehell & Heikkilä 2009) and geochemical studies (Siira 2013) were also performed. These sites can be classified as minerotrophic fens with all types of mire margin and mire expanse vegetation. Overall, 16 of the pH measurements from these studies could be correlated with vegetation data; samples were taken from large patterns with uniform vegetation. The water samples were collected in bottles from small holes dug in the moss layer and measured in the laboratory a few hours later.

Water table depth
The hydrotopographical levels of the studied sites (hummock, lawn, carpet, mud-bottom) were mapped during the fieldwork (Rehell *et al.* 2012). The mean water table level for each sample plot was calculated from the percentages of its hydrotopographical levels together with their mean water table depths and ranges of fluctuation, based on the measurements of Laitinen *et al.* (2008).

Validity and correspondence of the methods and regression analyses
The validity of the Ellenberg indicator values for a boreal study area was assessed by comparing the Ellenberg values with measured pH values and PO_4 concentrations. The cover values for species considered in Finnish literature to indicate different subtypes of mire-margin influence were compared with the Ellenberg indicator values for reaction and nitrogen, as well as with the measured pH and phosphorous concentrations.

Because the correspondence between variables was often curvilinear, we used regression analysis with polynomial curves and goodness-of-fit tests

under Gaussian error (Venables & Ripley 2002). We applied second-order polynomial regression, and only when the goodness-of-fit tests indicated that the second-degree term was insignificant, we used linear regression. When the linear regression was also insignificant according to the goodness-of-fit test, no regression line was shown. This is the standard procedure in analysing nested response models (Venables & Ripley 2002). We also considered using generalised additive models (Venables & Ripley 2002), but these were never significantly better than simpler polynomial regression. The goodness of fit of the selected model was expressed as the coefficient of determination (R^2). We used orthonormal polynomials in regression models. This is a standard procedure in modern statistical software for numerical precision, but the regression coefficients have no real relation to the original scale of variables. The polynomial regression coefficients are hardly ever interesting; the main result is the graphical response curve (Venables & Ripley 2002).

RESULTS

Validity and correspondence of the methods
Ellenberg reaction value showed a linear relationship with locally measured pH values, whereas there was no relationship between nitrogen and pH values (Figure 2). The relationship of Ellenberg values to PO_4 concentrations (Figure 3) was based on such limited data that only tentative conclusions could be drawn. The measured phosphorous concentrations seemed to have an unclear linear positive relationship with Ellenberg nitrogen values but not with Ellenberg reaction values.

Surveying the ecological variables indirectly by vegetation analysis
The indicator species of mire-margin subtype A (*Sumpfigkeit*) had some positive correlation with both Ellenberg values, but the correlation with nitrogen values was significant. The indicator species of mire-margin subtype B (*Quelligkeit*) had clear correlation with Ellenberg reaction values but not with Ellenberg nitrogen values (Figures 4 and 5). Subtype C (*Bruchmoorigkeit*) showed practically no correlation with Ellenberg values of either type; the sites with the largest percentages of indicators had relatively low Ellenberg nitrogen and reaction values. Mire expanse influence is manifest as a lack of mire margin indicators and mall values for both Ellenberg reaction and nitrogen. Indicators of Subtype B (*Quelligkeit*) are practically non-existent in the sites with small values for Ellenberg reaction or nitrogen.
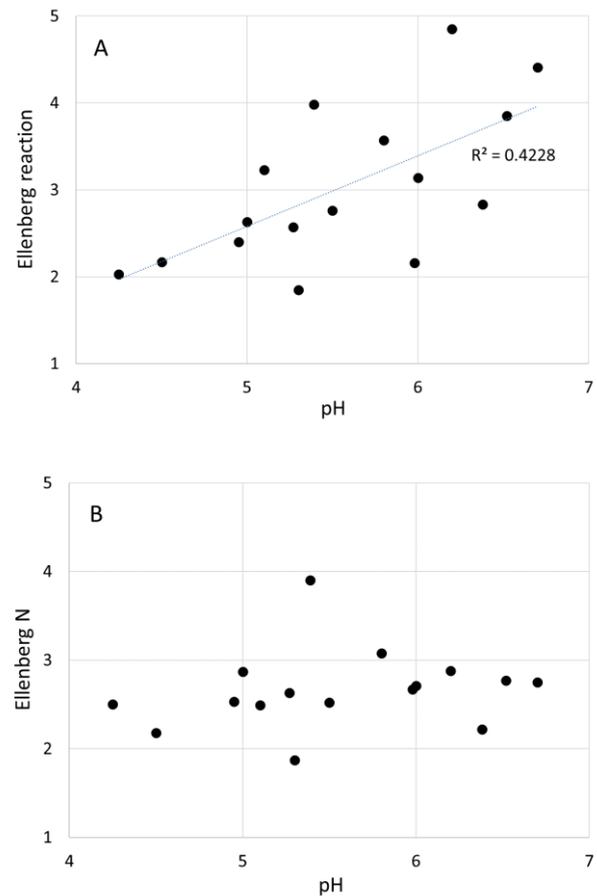

Figure 2. The relationships of the Ellenberg indicator values for (A) reaction and (B) nitrogen with measured pH values.
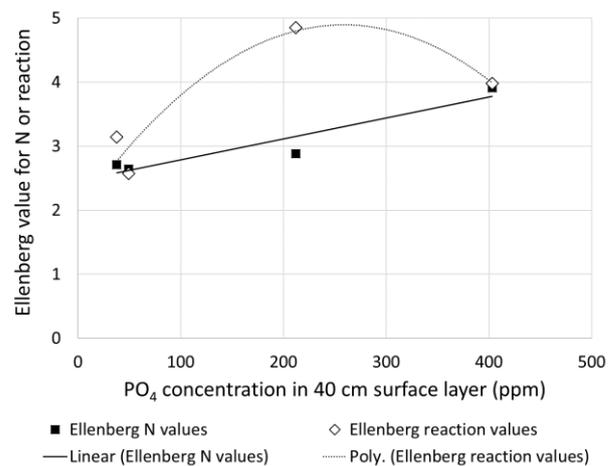

Figure 3. Ellenberg indicator values for N and reaction (y-axis) in relation to measured PO_4 concentrations (x-axis) in a 40 cm layer of surface peat and sediment. Trend lines are shown but the correlations are not statistically significant due to the small number of occurrences.
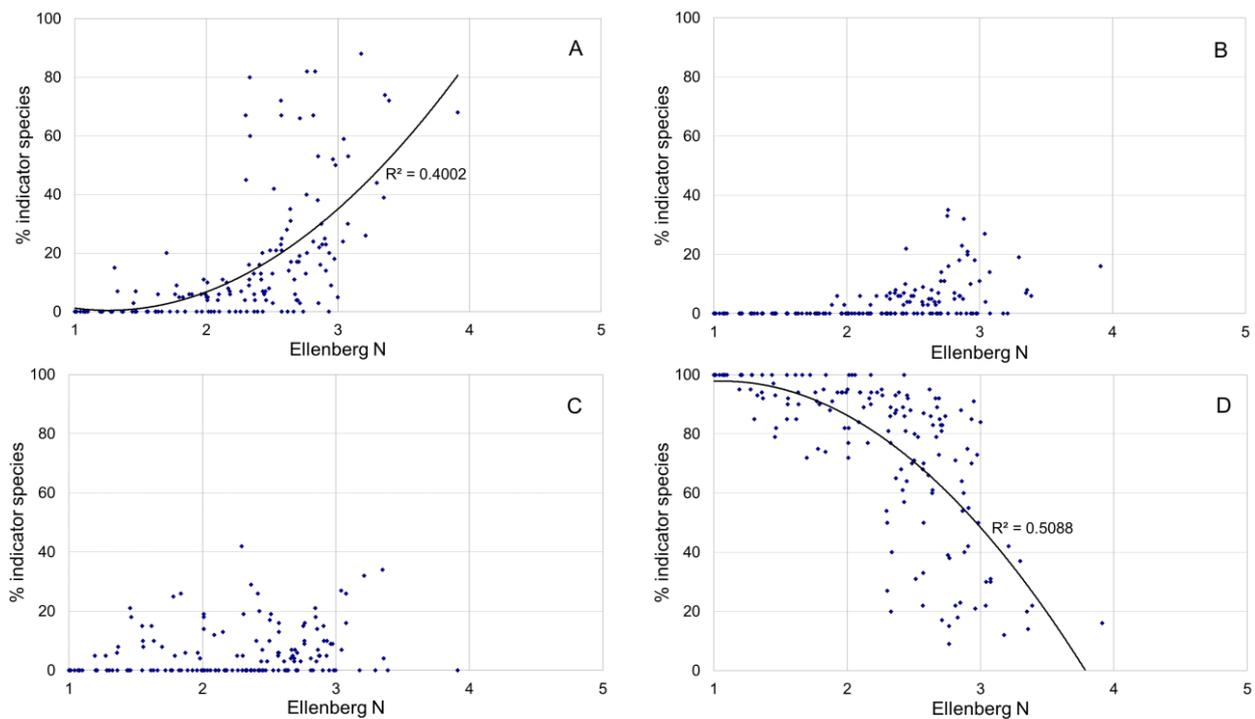
Figure 4. Percentages of plant species indicating mire margin to expanse gradient (y-axis) in relation to Ellenberg nitrogen value (x-axis). Subtypes of mire margin influence are (A) *Sumpfigkeit*, (B) *Quelligkeit* and (C) *Bruchmoorigkeit*. (D) refers to mire expanse vegetation including indifferent species. Percentages of plant species indicators for mire margin–expanse gradient are derived from the presence-absence data for vascular plants and mosses. Ellenberg nitrogen values are derived from cover values for vascular plants. Regression lines are shown only for correlations with statistical significance ($R^2 > 0.4$).
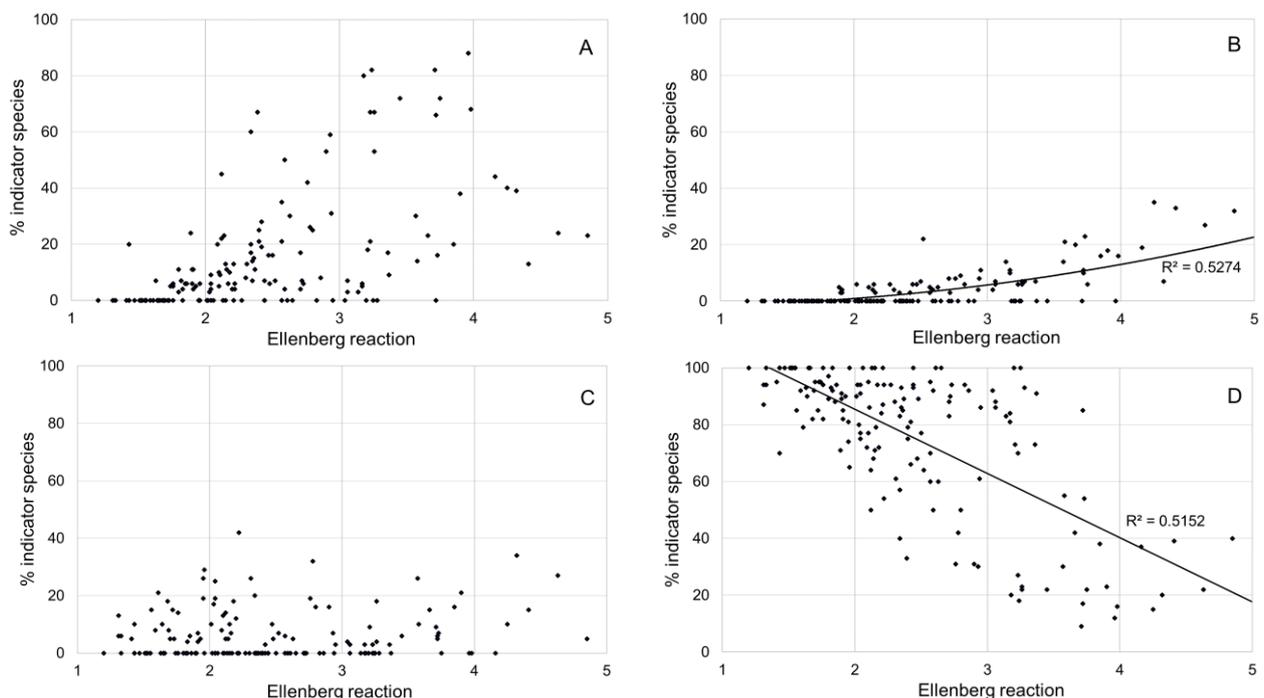

Figure 5. Percentages of plant species indicating mire margin to expanse gradient (y-axis) in relation to Ellenberg reaction value (x-axis). Subtypes of mire margin influence are (A) *Sumpfigkeit*, (B) *Quelligkeit* and (C) *Bruchmoorigkeit*. (D) refers to mire expanse vegetation including indifferent species. Percentages of plant species indicators for mire margin–expanse gradient are derived from the presence-absence data for vascular plants and mosses. Ellenberg nitrogen values are derived from cover values for vascular plants. Regression lines are shown only for correlations with statistical significance ($R^2 > 0.4$).

Direct measurements of pH and P

Cover values for species indicating Subtype A (*Sumpfigkeit*) seemed to have positive, linear relationships with measured PO_4 concentrations in the soil (Figure 6). However, they had only limited explanation power as the number of samples was small. The cover values for species indicating Subtype B (*Quelligkeit*) had no or slightly unimodal relationships with PO_4 concentrations. Species indicating Subtype C (*Bruchmoorigkeit*) were extremely scanty (0–5 % of species in the plots) and there was no evident correlation (not shown). Cover values of mire expanse species (self-sufficiency) and indifferent species showed only a weak negative correlation with PO_4 concentrations (not shown, as they can be regarded as the residual shared between all mire margin indicators).

There was a positive linear relationship between measured pH and mire margin indicators of Subtype B (*Quelligkeit*) (Figure 7B), whereas indicators of Subtype A (*Sumpfigkeit*) showed an
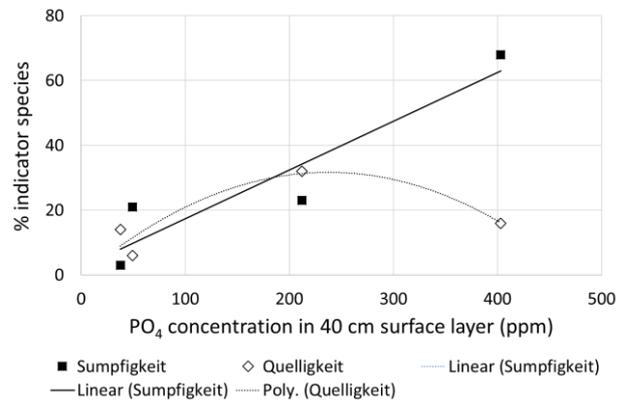

Figure 6. Indicators of mire margin influence (*Sumpfigkeit* meaning surface water influence and *Quelligkeit* groundwater influence) (y-axis) in relation to measured PO_4 concentrations (x-axis) in a 40 cm layer of surface peat and sediment. Trend lines are shown but the correlations are not statistically significant due to the small number of occurrences.
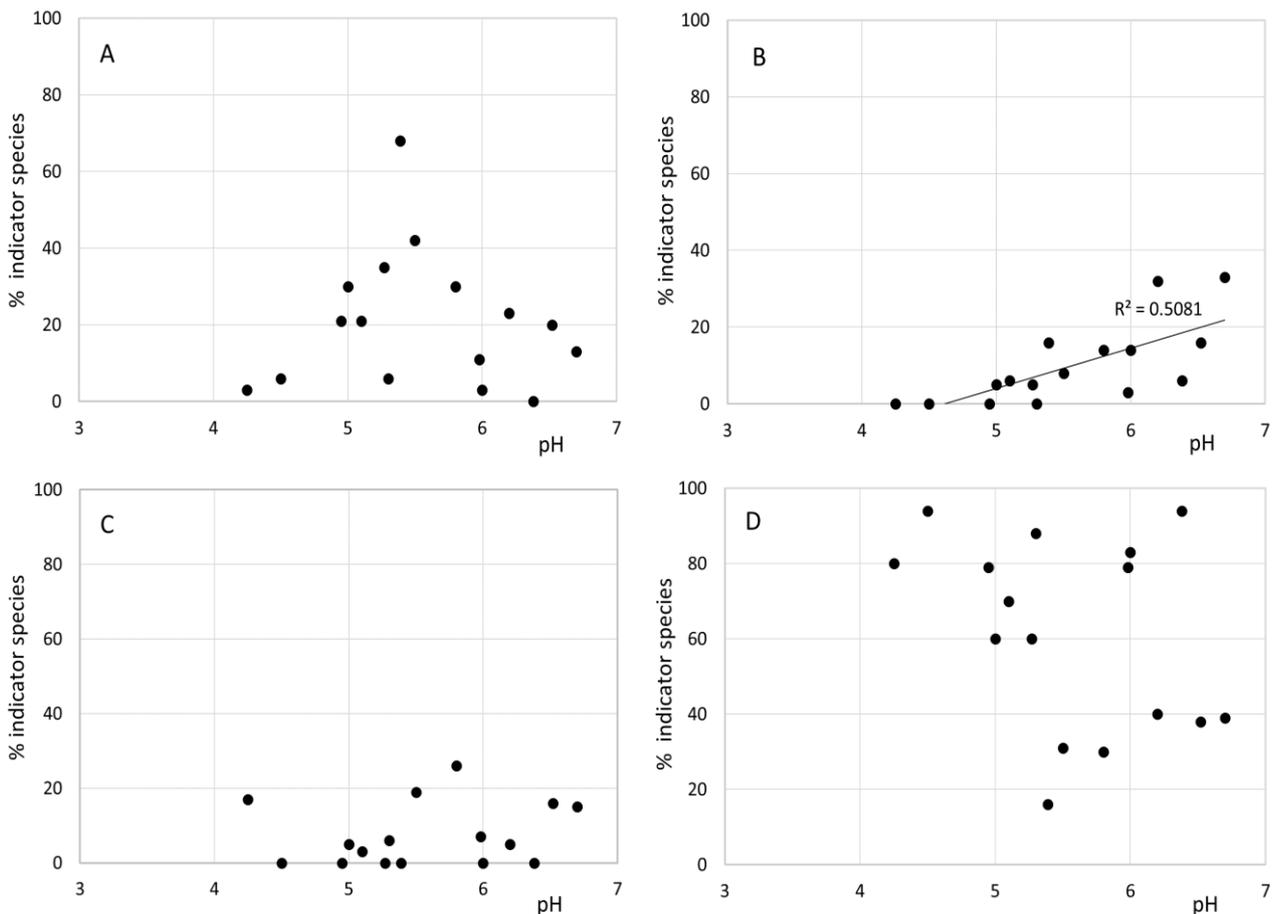

Figure 7. The relationship between the percentage of indicators of mineral soil influence (A) *Sumpfigkeit*, (B) *Quelligkeit*, (C) *Bruchmoorigkeit*, (D) mire expanse and indifferent (y-axis) and pH (x-axis). The regression line in (B) shows a statistically significant correlation.

unclear unimodal (hump-shaped) relationship (Figure 7A). There was no relationship between the percentage of indicators for Subtype C (*Bruchmoorigkeit*) and measured pH values (Figure 7C). Mire expanse and indifferent vegetation showed no evident relationship with measured pH values (Figure 7D).

Water table depth in relation to mire margin to expanse indicators
The indicators of Subtype C (*Bruchmoorigkeit*) became more abundant as the mean water table fell deeper beneath the ground surface. These indicators had a very prominent role (at least 10 % of all species) on about 80 % of sample plots with water table deeper that 25 cm and were absent from sample plots with mean water table depth less than 5 cm. In contrast, indicators of Subtypes A and B (*Sumpfigkeit* and *Quelligkeit*) were concentrated in wetter sample plots (Figure 8).
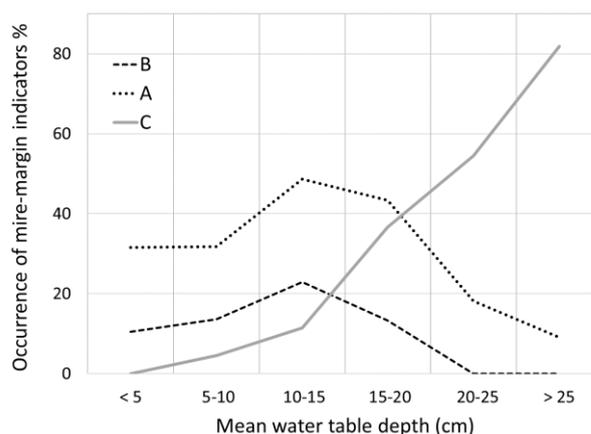

Figure 8. The relationship between mean water table depth in the large sample plots and the occurrence of mire margin indicators (probability that at least 10 % of species are indicators of the particular subtype of mire margin influence) for the three categories A (*Sumpfigkeit*), B (*Quelligkeit*) and C (*Bruchmoorigkeit*).

DISCUSSION

Ellenberg indicator values
Ellenberg indicator values (Ellenberg *et al*. 1991), which were developed for temperate central Europe, seem to be valid for our boreal study area, as the expected results were obtained when Ellenberg reaction and nitrogen values were tested against locally measured pH values (Figure 2). Both the indirect method (using Ellenberg nitrogen values) and the direct method (using measured soil phosphorous concentrations) turned out to similarly explain the relationship between the compositional mire margin to expanse gradient and solute (plant nutrient) levels in the soil, which was the central topic of our survey (Figure 3). Ellenberg indicator values were used recently for other investigations in boreal areas by Laitinen *et al*. (2007b), who compared the depth and duration patterns of water table fluctuations with Ellenberg indicator values for moisture, and evaluated the pH and fertility characteristics of mire complexes against Ellenberg values for reaction and nitrogen. Our small test and the results of Laitinen *et al*. (2007b) establish some validity of the Ellenberg indicator values for the boreal area and the possibility that vegetation data may be used with caution for preliminary evaluations of moisture and geochemical characteristics of boreal peatlands. Therefore, the use of Ellenberg values together with other information about indicator species seems to provide an opportunity to assess nutrient status and pH without direct measurements in the boreal zone as well as in temperate locations.

Ecohydrological interpretation for boreal mire margin vegetation indicating surface water flow
Our results provide a basis for a partly new understanding of Finnish mire margin vegetation and its classical ecohydrological interpretation as a supplementary nutrient effect (Eurola *et al*. 1984, 1995, 2015). According to these results, Subtype A (*Sumpfigkeit*) (Tuomikoski 1942, 1955; Brandt 1948, Ruuhijärvi 1960), which is traditionally correlated with surface water flow, corresponds best to the Central European Ellenberg nitrogen values. Additionally, the correspondence of indirect and direct methods supports the idea that the indicators of this subtype associate most readily with the moderately poor to intermediate status of the poor–rich gradient (Eurola *et.al* 1984, 1995). Surface water flow is known to be essential for the transition from ombrotrohic to minerotrophic conditions (e.g., Kulczynski 1948). It also seems to associate clearly with increased amounts of supplementary solutes which may be regarded as chiefly main plant nutrients (at least P and N), although the determination method used does not allow detailed conclusions at the level of elements. In this research, scrutiny of the Ellenberg N value was based on cover values for vascular plants. This is in accordance with the fact that, in boreal Finland, the most intensive surface water influence can be found in swamps (*Sumpfmoore*) (Brandt 1948, Eurola *et al*. 1984, 1995), which are characterised by scanty moss cover and a well-developed vascular plant layer with

abundant biomass (Eurola 1969, Eurola *et al.* 1984, 1995). As stated in the introduction, Vitt & Chee (1995) suggest that the variation in vascular plant occurrence on the mires of boreal Alberta relates best to nutrient levels, while that of mosses is more closely associated with the poor to rich gradient. A clear increase in the coverage of vascular plants indicating *Sumpfigkeit* and a decrease in the moss cover were the main trends in vegetation observed by Huttunen *et al.* (1996) on mires used for absorbing main nutrients from the flowing surface water of overland flow treatment systems. As a conclusion from our study we suggest that the influence of the main nutrients (nitrogen, phosphorus, etc.) on mire vegetation, and especially on the field layer of vascular plants, should also be taken into consideration in boreal Fennoscandia. This highlights the importance of main nutrients in the ecology and dynamics of boreal mires.

Groundwater influence and rich fens

Mire margin gradient subtype B (*Quelligkeit*) (Ruuhijärvi 1960), which is traditionally associated with groundwater influence (Ruuhijärvi 1960, Eurola 1962), proved to have an evident relationship with the poor–rich gradient (pH and Ellenberg reaction values) but only weak relationships with Ellenberg nitrogen values and phosphorous concentrations. This outcome can be interpreted as a weak relationship with nutrient gradient and, furthermore, with the overall productivity and vascular plant biomass of the site (Vitt & Chee 1990, Hill & Carey 1997, Schaffers & Sykora 2000). The result and its interpretation match well with the physiognomic pattern generally recognised in springs with a dominance of mosses and a diminutive cover of vascular plants (Persson 1961). In our study area, additionally, indicators of groundwater influence (*Quelligkeit*) were positively related to Ellenberg soil reaction values and to pH. This accords with the interpretation of Vitt & Chee (1990), that mosses relate to the poor–rich gradient more clearly than to the vascular plants. Our result for the relationship between groundwater influence and the poor–rich gradient (indicators of groundwater influence are abundant in intermediate and rich fens but nonexistent in poor fens) additionally shows a hydrogeological pattern, in that intermediate and rich fens in the study area seem to be dependent on groundwater discharge areas. The pattern is displayed primarily by fens with mire margin vegetation near the Bothnian Bay coast, but also more generally by such fens located inland but outwith specific calcareous areas (Ruuhijärvi 1960, Persson 1961; Laitinen *et al.* 2011, 2016).

Picea abies mires and mineral soil influence

Mire margin vegetation subtype C (*Bruchmoorigkeit*) (Tuomikoski 1942, Ruuhijärvi 1960, Eurola 1962), with no evident correlation to either of the Ellenberg values, seems to be more or less separate from both the poor–rich and the nutrient gradient. This kind of vegetation (*Picea abies* mire) is traditionally correlated with thin peat and clear influence of the underlying mineral soil. The result suggests that *Picea abies* mire occupies a different position among other types of mire margin vegetation than among boreal mire vegetation in general.

Ecohydrologically, one may assume that the mineral soil influence relating to *Picea abies* mires is at least partly independent of the water-flow rate in peat, unlike surface water influence (*Sumpfigkeit*) and groundwater influence (*Quelligkeit*). Wheeler & Proctor (2000), for example, suggest that the ecological basis of the mire margin to expanse direction of variation may lie in rates of water flow affecting the rates of uptake and turnover of limiting nutrients. Independence of the mineral-soil influence from the water-flow rate is illustrated by the fact that this subtype of mire margin vegetation (*Bruchmoorigkeit*) actually represents hummock-level vegetation with relatively deep water table, whereas surface-water influence (*Sumpfigkeit*) and groundwater influence (*Quelligkeit*) are associated with mire margin vegetation and water-table levels near the ground surface (Ruuhijärvi 1960; Eurola *et al.* 1984, 1995). The strong interdependence between vegetation indicating *Picea abies* mires and water table depth (Figure 8) is partly due to the dataset, since most of the sites are clearly minerotrophic and hummock-level vegetation typical of ombrotrophic bogs is rare. The *Picea abies* mires also typically have thin peat layers and in this way resemble wide forested laggs with thin peat (Paradis *et al.* 2015) and large water table fluctuations.

According to an ecological definition of mire (Tahvanainen 2005), waterlogging in mires occurs in an organic soil layer within which the water table can be located. According to this definition, all of the *Picea abies* mires are not 'proper' mires in an ecological sense, and perhaps the ecology of *Picea abies* mires should rather be viewed from the point of view of the ecology of boreal (mesic heath or herb-rich) forests (Tonteri *et al.* 1990), although a shallow peat layer and often a relatively uniform cover of *Sphagnum* do characterise spruce mire vegetation (Ruuhijärvi 1960, Eurola 1962, Korpela & Reinikainen 1996). This does not imply that *Picea abies* mire vegetation (Ruuhijärvi 1960, Eurola 1962) should be classified as boreal forest in the sense of, for example, Finnish forest site types on mineral soil

(Kalela 1961), but only that (especially) the nutrient ecology of Fennoscandian *Picea abies* mires (boreal *Picea abies* swamp forests) largely remains to be studied (cf. the studies of water table levels and species richness of Økland *et al*. 2001b, 2003; and of Halvorsen *et al*. 2008). According to our results, the mineral-soil influence (*Bruchmoorigkeit*) not only clearly differs from other subgroups of mire margin influence (*Sumpfigkeit, Quelligkeit*), but also seems to be clearly separate from the poor–rich gradient, which is largely regarded as being central to characterising mire vegetation or, specifically, mire expanse vegetation (Tahvanainen 2004). Also, in this respect, mineral-soil influence (*Bruchmoorigkeit*), which is typical for forested peatlands, represents features that are most clearly foreign to mire expanse vegetation. Thus, the gradient from forested to open mires can be taken to form an independent direction of variation in minerotrophic vegetation. Partly contrary to expectations, our ecological analysis in a way supports the physiognomic mire margin concept of Økland *et al*. (2001), according to which mire margin vegetation refers, essentially, to treed vegetation.

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