

Thirty years of vegetation dynamics in the Rospuda fen (NE Poland)

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SUMMARY

Little is known about the vegetation dynamics of fens, and especially of hydrologically undisturbed examples. We described the vegetation of an undisturbed mesotrophic rich fen (percolation mire) in 2006–2008 and 2016 and compared our results with vegetation records from the 1980s to identify any longer-term changes. Eight vegetation types were distinguished. On the whole, the vegetation of the mire has remained very stable throughout the last 30 years. However, detailed comparisons of permanent plots recorded twice in the last ten years indicated an expansion of shrubs in patches of *Sphagnum* - small sedge vegetation. There were also several less prominent changes in the abundance of particular species in other mire vegetation types: (1) an increase of sedges, reeds and *Calliergonella cuspidata* at the expense of rich-fen moss species in communities of brown moss - small sedge; (2) a change in composition of the moss layer in pine - birch fen woodland; (3) an increase of reedbed species and reduced *Alnus glutinosa* abundance in flooded riparian alder woodland; and (4) a decline of wetland herbs and mosses in alder spring fen woodland at the edges of the valley.

KEY WORDS: biodiversity, ecosystem stability, long-term vegetation studies, percolation mire, rich fen

INTRODUCTION

Percolation rich fens are mires with a stable supply of base-rich groundwater percolating through the peat body (Joosten *et al.* 2017). Examples in the temperate zone which have been severely damaged by agricultural drainage are now a focus for restoration and conservation efforts (e.g. Wheeler & Shaw 1995, Kotowski *et al.* 2016). However, nature conservation practitioners often face a dilemma in choosing the most appropriate target status for such systems. The question is, which changes in vegetation represent the natural dynamics of the undisturbed ecosystem, as opposed to the progress of its anthropogenic degradation? The dilemma arises because undisturbed reference ecosystems are scarce and documented time series of vegetation dynamics in such systems are lacking. Palaeoecological records (e.g. Michaelis 2002) show that these fens have remained stable for hundreds of years in the past; but nowadays most are unstable and dependent on active conservation management to prevent succession towards scrub and forest (Middleton *et al.* 2006). Responsible choices of conservation strategies for these ecosystems (e.g. the introduction of mowing versus passive conservation) require an ability to distinguish between changes caused by human activities, such as alteration of the hydrological regime (van Diggelen *et al.* 2006) or eutrophication

(Verhoeven *et al.* 1996), and changes expressing natural fluctuations.

One of the last large, well-preserved percolation rich fen systems remaining in Central Europe can be found in the valley of the Rospuda River in north-east (NE) Poland. There have been proposals to create a nature reserve in the lower Rospuda valley since the early 1980s (Sokołowski 1988, 1989, 1996) and, although this goal has not been realised, a detailed description of the area's vegetation was prepared in the 1980s as partial documentation for the proposed nature reserve (Sokołowski 1996). The existence of this study provides an opportunity to track vegetation dynamics in the lower Rospuda valley over the last 30 years.

Open rich fen vegetation can thrive as both natural and semi-natural (mown) plant communities, which makes it difficult to choose adequate conservation strategies on the basis of single vegetation surveys. Several authors have observed that major vegetation changes in fens have followed a cessation of mowing, which was once a common practice in these ecosystems all over Europe (e.g. Pałczyński 1985, Moen 1990, Peintinger & Bergamini 2006) but largely ceased in the second half of the 20th century. Mowing was usually accompanied by some level of drainage, which could be the reason for expansion of woody species after abandonment. On the other hand, Schipper *et al.* (2007) argued that the removal of mown litter may alone cause enhanced

decomposition and compaction of the uppermost soil layers, leading to increased insulation and warming of the peat, and thus predispose a mown site to scrubbing-over after abandonment even if it has not been drained.

A study of recent vegetation dynamics in the Rospuda mire could substantially contribute to this debate. Mowing was certainly practised here, ceasing in the early 1980s as on most European fens (see the comparison of aerial photographs from 1970, 1997 and 2016 in Figure 1). However, the mire has never been drained. Moreover, the palaeoecological study of Jabłońska *et al.* (2014) shows that open fen vegetation has been present on the Rospuda mire for hundreds of years and remains largely unchanged today, despite the documented period of mowing. On this basis we hypothesise that the open character of the Rospuda fen is maintained, and the growth of trees, shrubs and hummock mosses suppressed, by the combination of stable water table with unaltered, little-decomposed and nutrient-poor peat.

The objectives of this article are: a) to present the full results of vegetation studies carried out at Rospuda in 2006–2008 and previously summarised (only) by Jabłońska *et al.* (2011); b) to verify whether any directional changes in the cover of vegetation layers (trees, shrubs, herbs, mosses), as well as in species composition, have occurred in different zones of the mire during the last ~10 years (from 2006–2008 to 2016); and c) to compare our 2006–2008 vegetation data with vegetation records from the 1980s reported by Sokołowski (1996) and, thus, identify any signs of vegetation changes in the mire

over the 20 years from the early 1980s to 2006–2008. Thus, overall, the variability of vegetation over the last 30 years should be accessible from the data at our disposal. In addition to providing a reference point for rich fen conservation and restoration, we aim to document the vegetation of the mire in the Rospuda valley as a justification for its protection, which was recently the focus of a ‘hot’ conservation campaign against an infrastructural development project (Niedziałkowski *et al.* 2013; see also the *post-scriptum* part of Discussion for more details).

METHODS

Study site

The Rospuda valley (from 53° 56' 40" N, 22° 52' 40" E to 53° 53' 00" N, 22° 58' 8" E) is located in NE Poland at the junction of three European mire regions, namely: the nemoral-submeridional fen region, where percolation fens are typical and abundant; the continental fen and bog region; and the typical raised bog region (Moen *et al.* 2017). During the last glaciation (which ended ca. 11,700 years ago) the valley was a sub-glacial channel that drained glacial meltwater. After the glacier had retreated, a lake formed in the present lower reaches of the river, then shallowed as a result of gyttja deposition until it was overgrown by fen vegetation to form the Rospuda mire (Jabłońska *et al.* 2014).

The catchment area of the mire (excluding the catchments of tributaries and upper reaches of the Rospuda river) is estimated to be approximately five

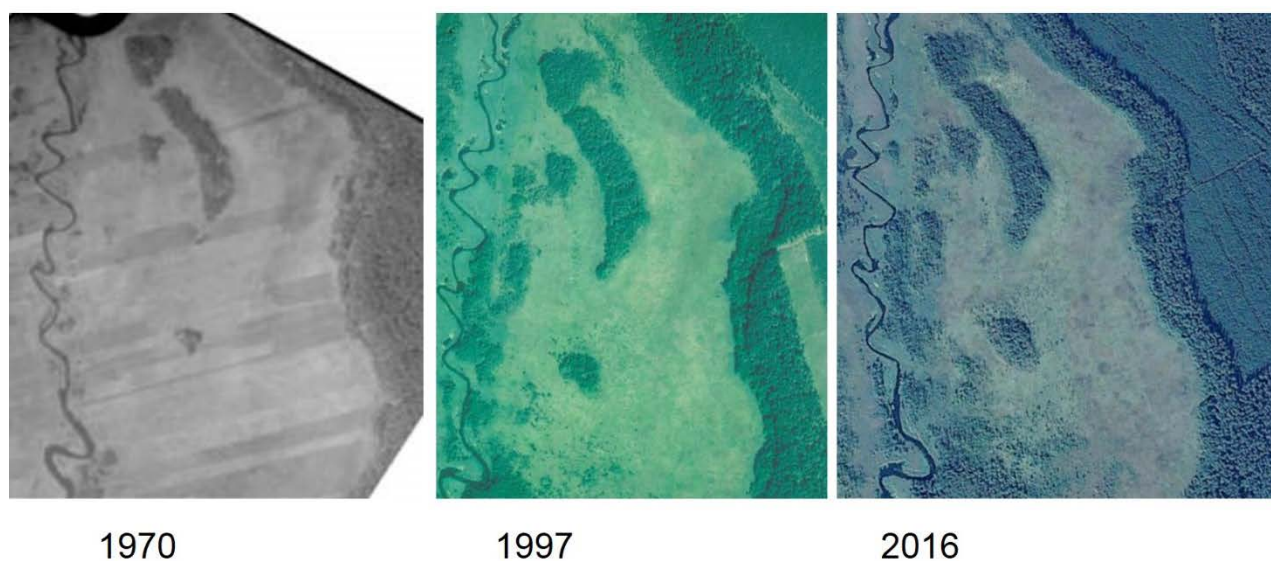


Figure 1. Aerial photographs of the southern basin of the Rospuda mire in 1970, 1997 (images obtained from Geodesic and Cartographic Documentation Center, PL) and 2016 (image source: Google Earth, CNS/Airbus).

times the area of the mire itself, which covers about 600 hectares and reaches 1400 metres across at its widest point. Most of the catchment is a sandy outwash plain covered by managed pine forests; but there are villages, arable fields and meadows at its outer edges.

The Rospuda mire can be described as a percolation mesotrophic rich fen on the basis of the following characteristics: (1) as is typical for percolation fens (Joosten *et al.* 2017), the mire has a stable supply of groundwater that maintains the water table level almost constantly at the mire surface, elastic and porous weakly decomposed peat, and a diffuse flow of groundwater through a porous peat body over a substantial depth; (2) as is typical for rich fens (Joosten *et al.* 2017), the mire is supplied with groundwater enriched with base ions; and (3) as is typical for mesotrophic fens (Joosten *et al.* 2017), the mire is characterised by peat water with moderate solute concentrations and hosts nutrient-limited vegetation dominated by short sedges and mosses. This is one of the very few fens in Europe that have never been drained, and the only management in its non-forested parts has been extensive mowing which ceased in the early 1980s. The vegetation exhibits a natural zonation from the valley margin to the river, with open brown moss - sedge vegetation occupying the largest area in the southern part of the valley (lower basin) where peat development started by terrestrialisation of the glacial lake and has remained stable for hundreds of years (Jabłońska *et al.* 2014). ¹⁴C dating has confirmed that the two-metre-thick layer of uniform brown moss - small sedge peat in the lower Rospuda basin was initiated about 1200 years BP (authors' unpublished data). The mire is now a unique location for biodiversity protection, with abundant rare and endangered plant species (e.g. *Carex chordorrhiza*, *C. dioica*, *Betula humilis*, *Eriophorum gracile*, *Hamatocaulis vernicosus*, *Liparis loeselii*, *Meesia triquetra*, *Paludella squarrosa*, *Saxifraga hirculus*, *Scirpus hudsonianus*; for the full list of rare species see Pawlikowski *et al.* (2010)).

Data collection

In the period 2006–2008 we made 308 phytosociological relevés at 10-metre intervals along five transects crossing the mire (Figure 2). The dimensions of relevés were 5 m × 5 m in herbaceous vegetation, 10 m × 5 m in shrub vegetation and 10 m × 10 m in forest. In the latter two vegetation types, relevés were directly adjacent to each other along the transect, whereas in herbaceous communities they were separated by 5 m gaps. The relevé data were compiled into a phytosociological table for each

transect. One relevé within each vegetation type per transect was selected as a 'permanent' sampling plot, giving 2–6 sampling plots for each vegetation type and 27 in total. These were marked with dipwells (0.5 m long, 0.2 m at base perforated) in which the level of the water table was measured every 15 days for two years (2007–2008). In 2009 we photographed the sampling plots to record vegetation physiognomy.

At the end of June 2016 we repeated the phytosociological relevés, measured the water table level once and took repeat photographs of the 27 sampling plots. That year we also re-assessed the cover of each vegetation layer in 225 relevés along the transects (excluding forest relevés on Transects I and IV as well as the whole of Transect V, which is almost completely forested, because our focus was on open mire communities).

From the 1980s survey data of Sokołowski (1996) we digitised 138 phytosociological relevés excluding those in aquatic plant communities (*Hydrocharitetum morsus-ranae*), vegetation on mineral soils (i.e. *Glycerietum nemoralis-plicatae*, *Phalaridetum arundinaceae*, *Caricetum gracilis*), and mesic forests and grasslands located outwith the peatland.

Nomenclature follows Rutkowski (1998) for vascular plants, Ochyra *et al.* (2003) for mosses and Hodgetts (2015) for liverworts.

Data analysis

To verify whether any changes occurred in the vegetation of the mire during the last ~10 years (between the 2006–2008 and 2016 field surveys), we compared: (1) cover of individual vegetation layers in 225 pairs of relevés recorded at the same locations on the transects; (2) species composition in 27 pairs of relevés located in the permanent sampling plots; (3) water level measurements in the sampling plots; and (4) photographs of the sampling plots. Results of the analysis of vegetation layer cover were presented graphically for each transect. We also calculated mean values (and 95 % confidence intervals) for changes of cover in all open fen vegetation types. Species composition for relevés located in the permanent sampling plots was compared between the two survey dates using detrended correspondence analysis (DCA), in order to reveal potential changes between samples in the context of variability of the mire vegetation as a whole. We estimated changes as relative change per plot (RCPP) by dividing the vegetation shift for each plot along the first and second DCA axes by the whole span of relevés along both DCA axes, as follows:

$$RCPP = \frac{|(AI_{xt2} - AI_{xt1}) \times (AII_{xt2} - AII_{xt1})|}{(AI_{max} - AI_{min}) \times (AII_{max} - AII_{min})} \quad [1]$$

where: AI_{xt2} and AI_{xt1} are the first-axis scores for Plot x in 2016 and 2006–2008, respectively; AII_{xt2} and AII_{xt1} are the second-axis scores for the same plot and dates; AI_{max} and AI_{min} are the maximum and minimum scores along the first axis; and AII_{max} and AII_{min} are the maximum and minimum scores along the second axis. We then calculated a mean value (and 95 % confidence intervals) for the 27 permanent sampling plots. We also compiled a table showing changes in cover of particular species found in the sampling plots. This simple comparison technique was chosen because some of the vegetation types were represented by an insufficient number of sampling plots (minimum 2) for meaningful statistical analysis.

In search of evidence for vegetation changes in the mire over the previous 20 years, we compared 138 phytosociological relevés from the 1980s (Sokołowski 1996) with our 308 relevés from 2006–2008 plus 32 additional relevés recorded in 2010–2013 at random locations within vegetation types that were poorly represented along the transects, namely:

alder woodland, low-productivity rich fen and some semi-aquatic (including tall sedge) communities. This analysis was done using DCA, and was complemented with boxplots summarising the variation within the 1980s and recent datasets. For the DCA analysis, species were aggregated following Peterka *et al.* (2017); except for *Carex flava* agg., *Plagiomnium affine* agg. and *Sphagnum recurvum* agg., which were considered separately.

RESULTS

Description of vegetation in 2006–2008

Phytosociological relevés from 2006–2008 (Supplement 1) were classified into eight vegetation types and summarised in a synoptic table (Table A1 in Appendix). The vegetation types were: (1) brown moss - small (and slender) sedge fen, (2) *Sphagnum* - small sedge fen, (3) brown moss - tall sedge fen, (4) tall sedge - reed fen, (5) pine - birch fen woodland

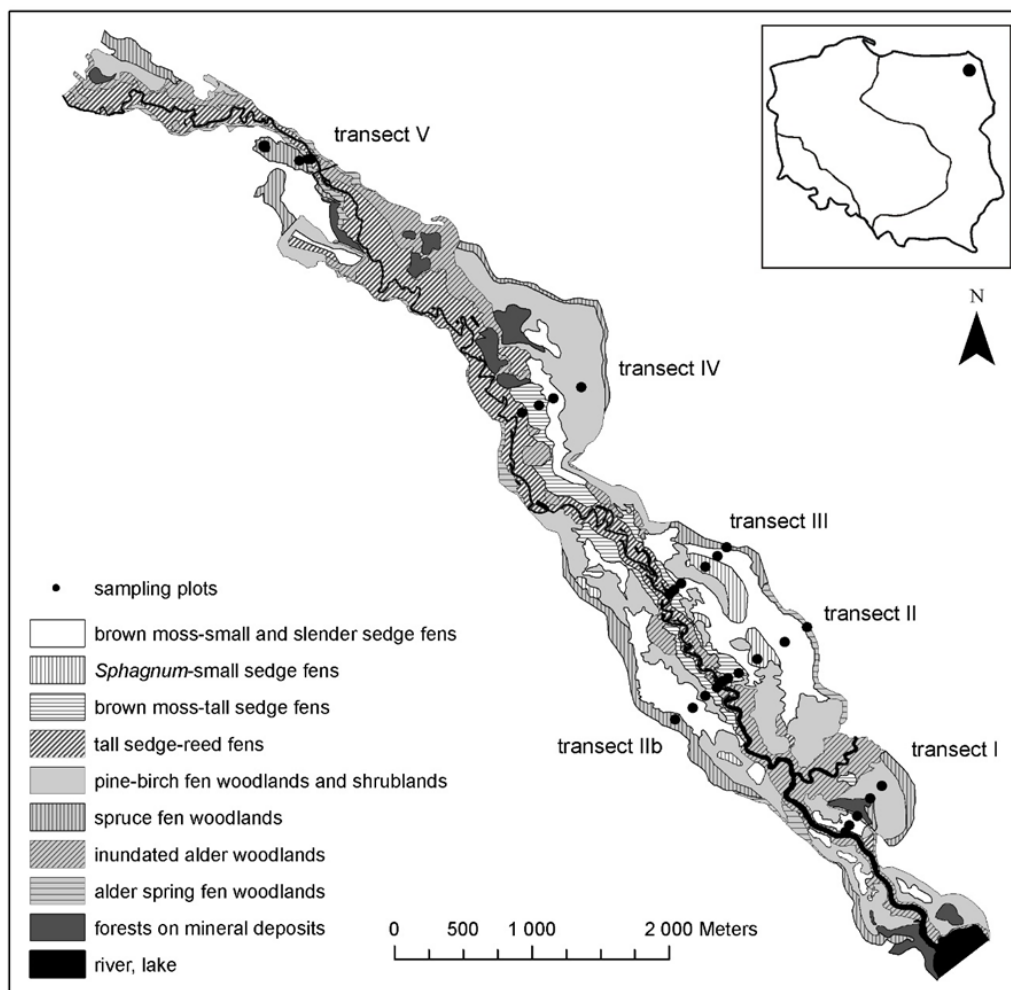


Figure 2. Location of the Rospuda valley and schematic vegetation map with sampling transects (after Jabłońska *et al.* 2011).

and shrubland, (6) spruce fen woodland, (7) inundated alder woodland, and (8) alder spring fen woodland (see Jabłońska *et al.* (2011) for detailed descriptions).

Each of the five transects started in fen woodland vegetation (Type 5, 6 or 8) at the mire margin and ended in inundated alder woodland (Type 7) or tall sedge - reed fen (Type 4) at the bank of the Rospuda river. Brown moss - small sedge fen (Type 1) communities occurred on Transects I, II, Iib, III and IV, and *Sphagnum* - small sedge fen (Type 2) on Transects II and III. Transect I crossed about 100 m of brown moss - small sedge fen (Type 1) vegetation (Table S1.1 in Supplement 1) and Transect II passed through the largest area of Type 1 (extending for over 300 m along the transect) as well as approximately 180 m of Type 2 (Table S1.2). On Transect Iib there was a zone of Type 1 about 180 m wide (Table S1.3). Transect III had a Type 1 zone ~ 100 m wide then a patch of Type 2, also ~ 100 m wide, followed by a

mineral 'wooded island' with shallow peat and Type 5 vegetation, behind which there was another 100 m wide zone of Type 1 (Table S1.4). Transect IV passed through a Type 1 zone about 80 m wide (Table S1.5).

Comparison of the cover of vegetation layers in open fen communities over the 10-year period 2006–2008 to 2016

In Type 1 communities we noted the following tendencies: (1) in Transect I, the tree cover increased from 0 to 5 %, the shrub cover and the cover of herbs decreased (from ~ 20 % to 5 % in several places), whereas the cover of mosses did not change (Figure 3); (2) the cover of all layers remained unchanged along Transect Iib (Figure 3); (3) in Transect II, the cover of the tree layer was unchanged, small changes in the shrub layer were noticed, and cover of the herb and moss layers increased slightly in the majority of relevés (Figure 4); (4) in Transect III, the tree layer

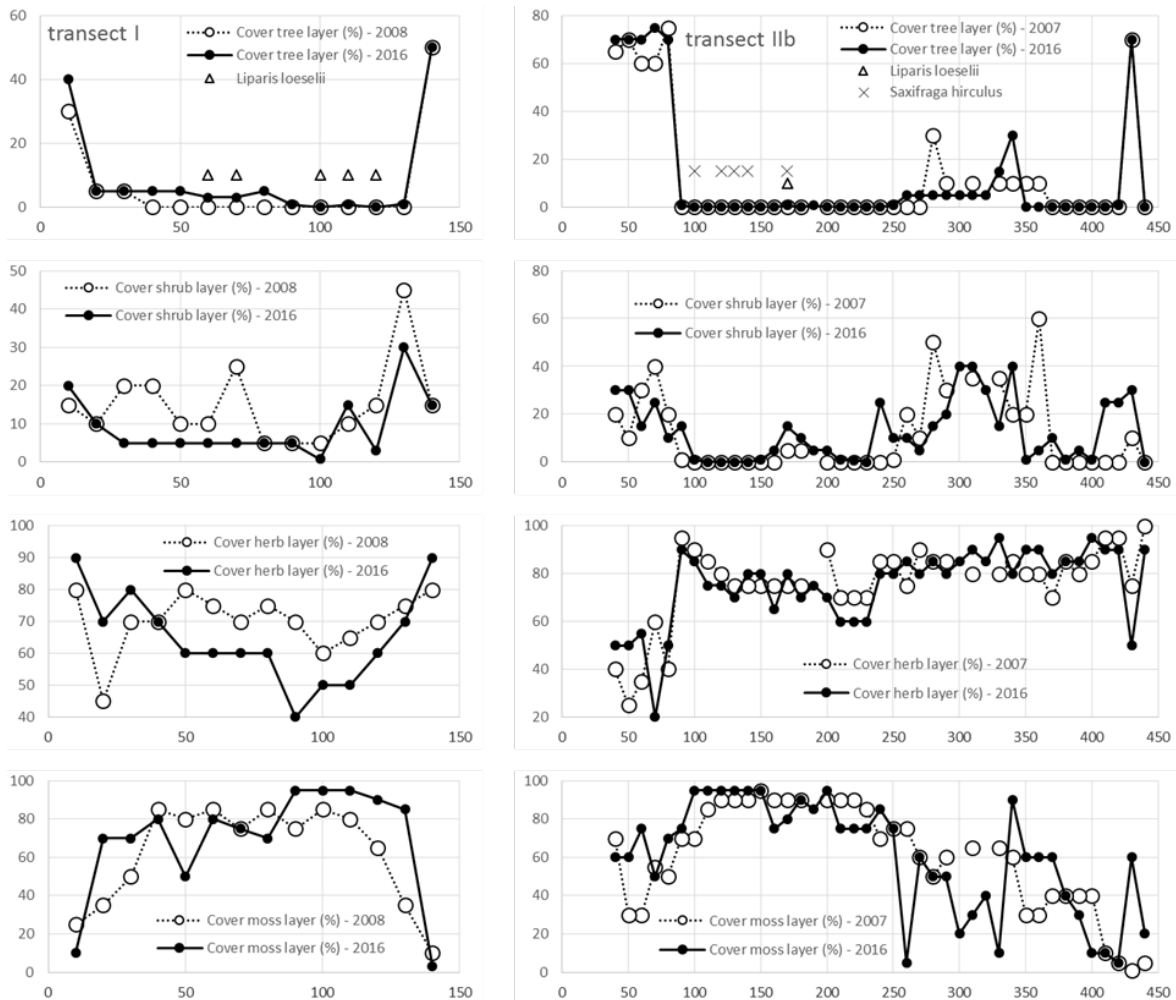


Figure 3. Cover of tree, shrub, herb and moss layers along the non-forested part of Transect I (on the western side of the mineral island within the Rospuda mire) and along Transect Iib, in 2007/2008 and 2016. Relevés with *Liparis loeselii* and *Saxifraga hirculus* in 2007/2008 are marked. In Figures 3–6, all panels show variation in cover along the transect, from mire margin (left side of graph) to the Rospuda river (right side of graph).

stayed relatively unchanged but we observed an increase in shrub layer cover (to >20 %) and a decrease in herb layer cover in the Type 1 zone at the edge of the valley, whereas in the Type 1 zone behind the ‘wooded island’ there was no evidence of change in the shrub and herb layers but the cover of mosses slightly decreased (Figure 5); (5) in Transect IV, we did not record any expansion of trees, but we observed a decline of the shrub layer, an increase of the herb layer and a slight decrease in cover of the moss layer (Figure 6).

In Type 2 communities we noticed the following changes: a decrease of herb layer cover in Transect II (Figure 4) and, in Transect III, an increase of shrub layer cover (to >70 % in one plot) and a decrease of herb layer cover from 80 % to ~40 % (Figure 5).

Comparisons of the cover of tree, shrub, herb and moss layers in open fen vegetation (Types 1–4) between 2006–2008 and 2016, analysed jointly for Transects I, II, IIb, III and IV (Figure 7), revealed that: (1) the mean difference in tree layer cover was close to zero in all of these vegetation types (the 95 % confidence interval (CI) includes zero for Types 3 and 4 and is small (zero to ~0.5 %) for Types 1 and 2); (2) an increase in shrub layer cover occurred in

Type 2 (95 % CI for the change in mean is 7–20 %) whereas no change in this layer was evident for the other three types (95 % CI for the change in mean was relatively narrow and included zero); (3) cover of the herb layer decreased in Type 2 (95 % CI for the change in mean is ~7 % to >25 %), remained stable in Type 1, and increased slightly in the other two vegetation types; (4) no change in moss layer cover was evident.

Comparison of species composition in fen communities over the 10-year period 2006–2008 to 2016)

Generally, no changes were evident within representative patches of any of the vegetation types during the 10-year period, as indicated by both the relevés (Figure 8) and the photographs (Supplement 2). The DCA-based analysis of changes in vegetation composition on the permanent sampling plots revealed that the mean relative change per plot (*RCPP*) was 0.15 % (95 % CI = 0.07–0.25 %). The maximum *RCPP* observed was 1 % for the sampling plot located in Type 4 vegetation on Transect V.

A more detailed analysis of the abundance of particular species in the relevés revealed the

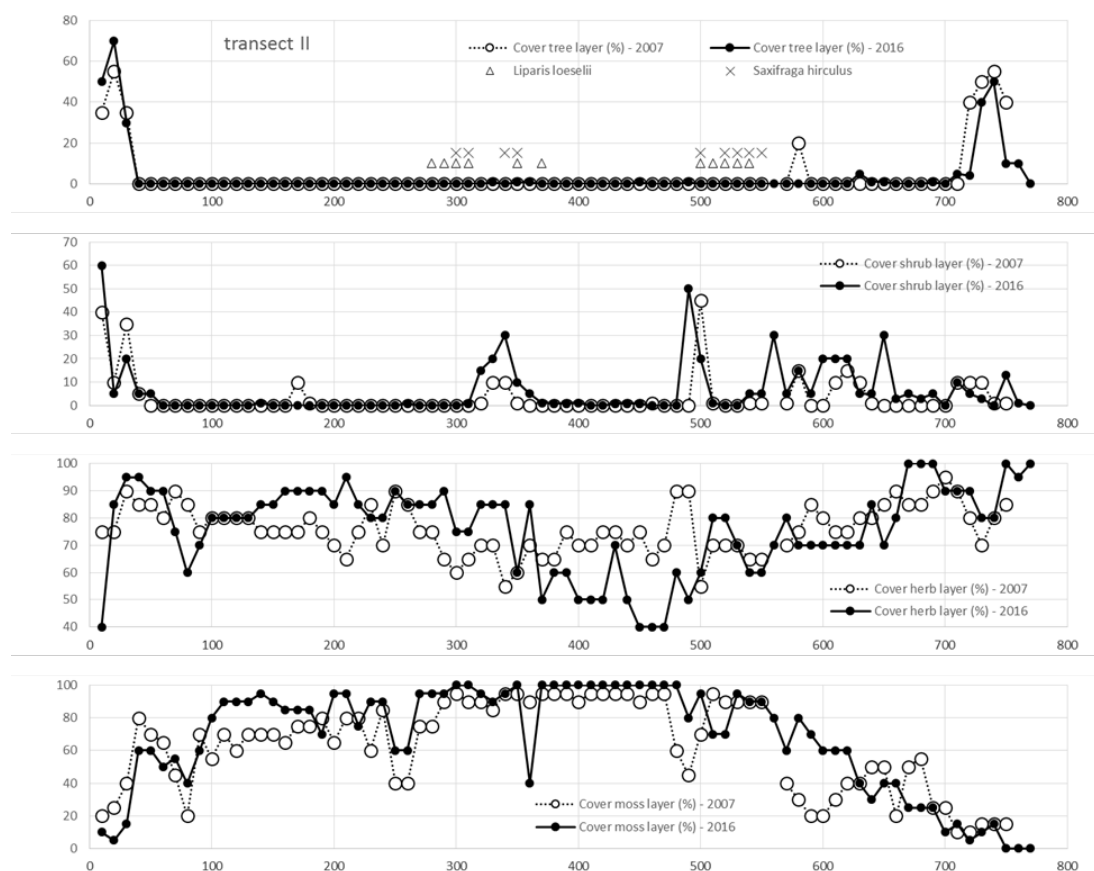


Figure 4. Cover of tree, shrub, herb and moss layers along Transect II, in 2007 and 2016. Relevés with *Liparis loeselii* and *Saxifraga hirculus* in 2007 are marked.

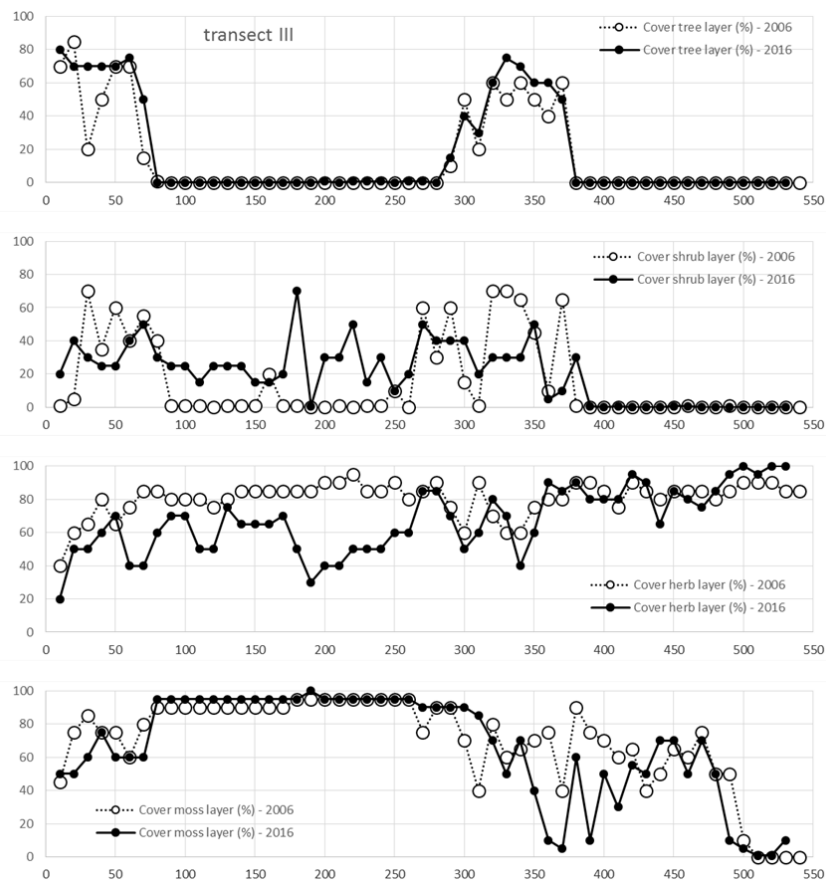


Figure 5. Cover of tree, shrub, herb and moss layers along Transect III, in 2006 and 2016.

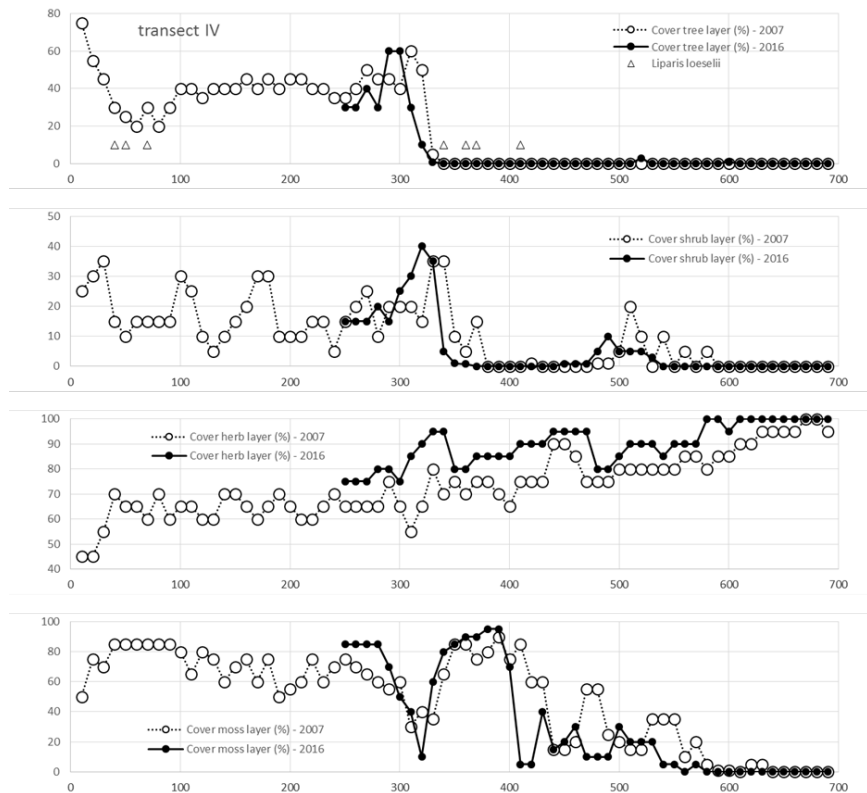


Figure 6. Cover of tree, shrub, herb and moss layers along Transect IV, in 2007 and 2016. Relevés with *Liparis loeselii* in 2007 are marked. The forested part of the transect was not sampled in 2016.

following changes: (1) in Type 1 (brown moss - small sedge fen), a change in composition of the moss layer, i.e. an increase in representation of *Calliergonella cuspidata* at the expense of the rich fen species *Calliergon giganteum* and *Campylium stellatum* and an increase of sedges and reeds; (2) in Type 2 (*Sphagnum* - small sedge fen), an expansion of trees and shrubs and a decline of *Vaccinium oxycoccos*; (3) in Type 5 (pine - birch fen woodland), a change in composition of the moss layer, i.e. a decline in *Sphagnum* and an increase in species characteristic of drier environments (*Brachythecium rutabulum*, *Dicranum scoparium*, *Hylocomium splendens*, *Plagiomnium cuspidatum*); (4) in Type 7 (riparian inundated alder woodland), an increase of reedbed species (*Phragmites australis*, *Thelypteris palustris*) and a decline of *Alnus*, and (5) in Type 8 (alder spring fen woodlands), a decline in herb species characteristic of wet environments (*Caltha*

palustris, *Cirsium oleraceum*, *Equisetum fluviatile*, *Menyanthes trifoliata*, *Thelypteris palustris*) and in moss species (Table A2 in Appendix).

Comparison of relevés over the 20-year period from the early 1980s to 2006–2008

Overall, no changes in the vegetation of the Rospuda mire were detected between the 1980s (Sokołowski 1996) and 2006–2008; the clusters of black and grey points in the DCA, as well as respective ranges in the boxplots, practically overlapped (Figure 9). However, attention should be paid to two areas where the cluster of points representing relevés from the 1980s was slightly wider than that representing relevés from 2006–2008: brown moss - small sedge fen (Type 1) in the left part of the graph and *Sphagnum* - small sedge fen (Type 2) in the bottom part of the graph (Figure 10).

Water level measurements

In general, water levels seemed to be lower in 2016 than in 2007–2008. In *Sphagnum* - small sedge fen and in all of the forest communities at the edges of the valley, the water table at the end of June 2016 was below the lowest level recorded between 01 May and 31 August during the two years of observation 2007–

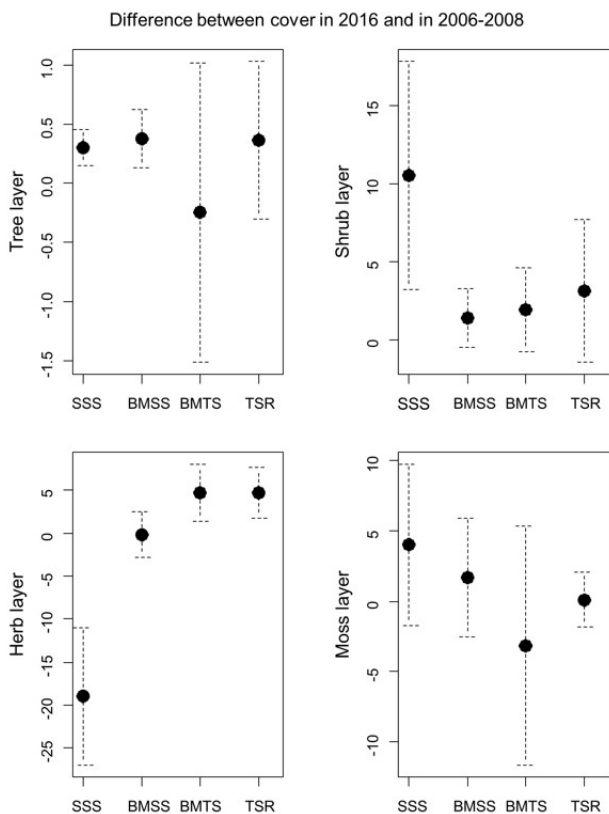


Figure 7. Means and 95 % confidence intervals for the differences in cover of tree, shrub, herb and moss layers between 2016 and 2006–2008, expressed in percentage points, in four open fen vegetation types: (SSS) *Sphagnum* - small sedge fen (Type 2), (BMSS) brown moss - small sedge fen (Type 1), (BMTS) brown moss - tall sedge fen (Type 3), (TSR) tall sedge -reed fen (Type 4); analysed jointly for Transects I, II, IIB, III and IV.

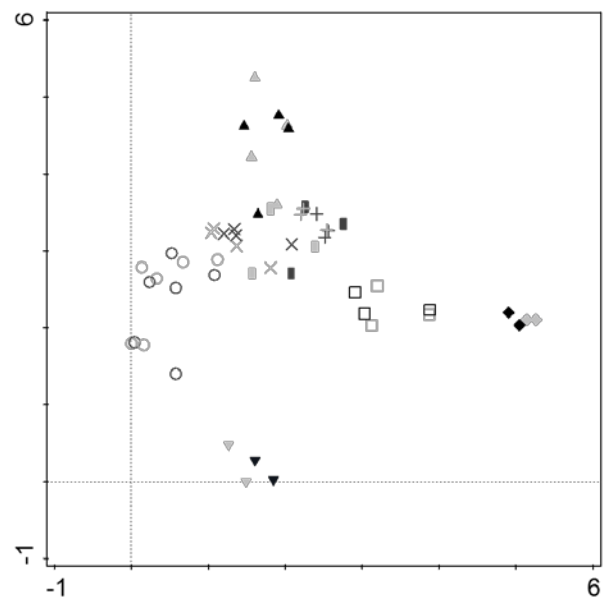


Figure 8. Detrended correspondence analysis of vegetation relevés from the selected sampling plots along the five transects in the Rospuda mire (Figure 2). Grey symbols: relevés recorded in 2006–2008 (presented by Jabłońska *et al.* 2011); black symbols: relevés recorded in 2016. For this analysis, vegetation layers were not combined. Eigenvalues: I – 0.7126; II – 0.4968; III – 0.2933; IV – 0.2015.

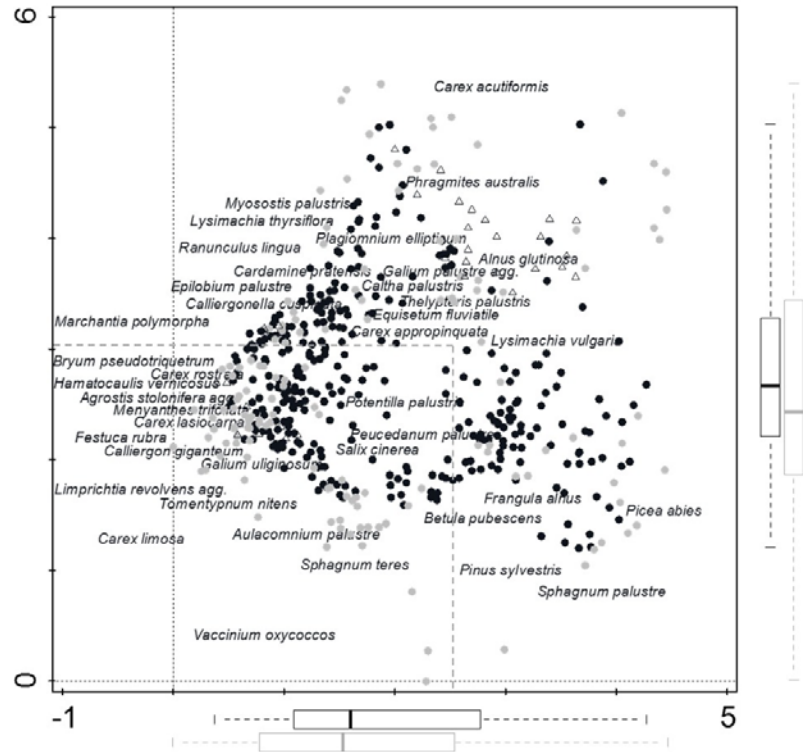


Figure 9. Detrended correspondence analysis of vegetation relevés from the Rospuda mire. Grey dots: relevés from the 1980s (from Sokołowski (1996); data for aquatic plant communities and vegetation on mineral soils discarded); black dots: relevés from 2006–2008; triangles: additional relevés from 2010–2013. All vegetation layers combined. Eigenvalues: I – 0.5503, II – 0.3699, III – 0.2317, IV – 0.1974. The most important 40 species (of the 405 recorded in total) are shown. The grey dashed lines delimit the part of this ordination that is shown (enlarged) in Figure 10. The DCA plot is supplemented with boxplots summarising the scores of samples along the first and second DCA axes (minimum, first quartile, median, third quartile and maximum values); grey boxplots represent 1980s relevés and black boxplots represent relevés recorded in 2006–2013.

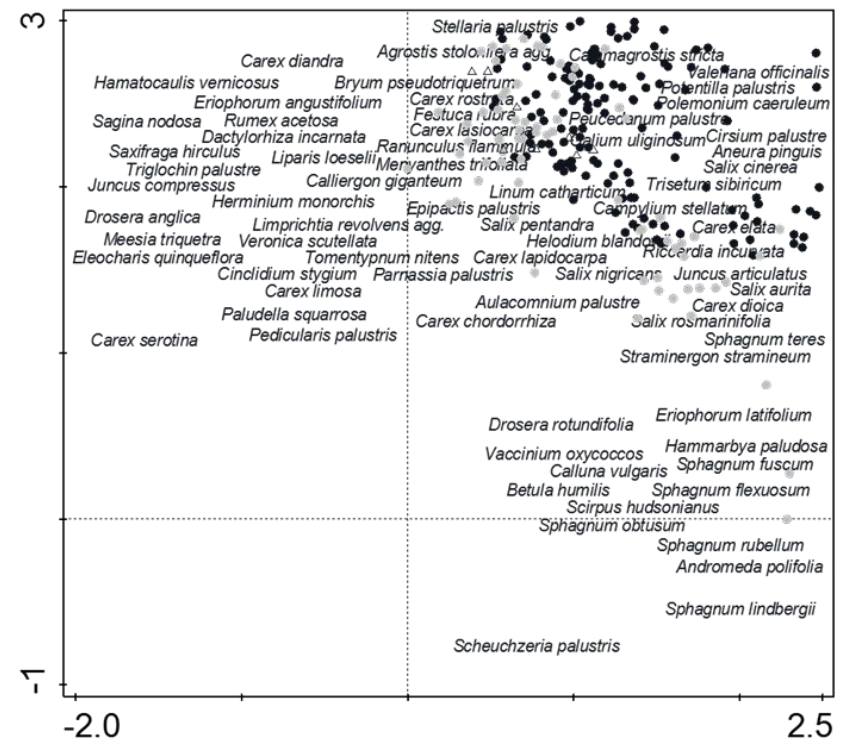


Figure 10. The part of the DCA of vegetation relevés from the Rospuda mire (Figure 9) that includes the brown moss - sedge vegetation type, showing all species. Grey dots: 1980s relevés from Sokołowski (1996); black dots: relevés from the transects recorded in 2006–2008; triangles: additional relevés recorded in 2010–2013. All vegetation layers combined.

2008 (Table 1). The 2016 water table level in brown moss - small sedge fen, brown moss - tall sedge fen and tall sedge - reed fen was close to the minimum levels observed during May–August in 2007 and 2008. The water table in inundated alder woodland was higher in 2016 than the minimum May–August levels observed in 2007–2008.

DISCUSSION

For undisturbed bogs and poor fens (i.e. mires supplied with base-poor water), several long-term vegetation studies have documented succession towards drier and more acidic habitats, indicated by an increasing representation of hummock-forming *Sphagnum* species and an expanding cover of trees and shrubs. Kollmann & Rasmussen (2012) described this tendency in a spectacularly long 160-year study (1844–2005) on a bog in Denmark that was left untouched after peat cutting ceased. The

same pattern has been documented in Sweden, over a 40-year interval (1954–1997) in a natural (almost pristine) mire (bog and poor fen) by Gunnarsson *et al.* (2002) and over 50 years (1954–2008) in a fen-bog mire complex by Kapfer *et al.* (2011). Hedwall *et al.* (2017) demonstrated a similar tendency in a 20-year study of Swedish peatland forests (1994–2013). These authors attributed the changes they observed to an autogenic succession, as well as to allogenic processes such as increased nitrogen deposition, lowered regional groundwater level or increase in temperature.

For natural rich fens (i.e. mires with base-rich water supplies and brown moss - sedge vegetation (Hájek *et al.* 2006, Joosten *et al.* 2017)), we found only three long-term vegetation studies (Fojt & Harding 1995, van Belle *et al.* 2006, Hájek *et al.* 2015). They revealed two successional trends: (1) towards drier and more acidic habitats and (2) towards wetter, reed-dominated habitats. The first tendency was revealed by van Belle *et al.* (2006) in a

Table 1. Minimum and maximum water table levels (relative to ground surface level; units: cm) measured in dipwells located in selected ‘permanent’ sampling plots located along the five transects on the Rospuda mire, grouped according to the eight vegetation types distinguished here (2–6 plots per vegetation type). Water table levels were measured at 15-day intervals for two years (January 2007 to December 2008) and once at the end of June 2016. For each set of plots, median values and ranges of the lowest and highest water table levels (of ten) recorded per plot in May–June and in July–August 2007–2008 are shown, along with the lowest and highest water table levels recorded in 2016.

Vegetation type	No. plots	2007–2008				2016	
		May–June		July–August		late June	
		lowest	highest	lowest	highest	lowest	highest
1 brown moss - small sedge fen	6	-2 (-9 to 0)	+7 (+3 to +12)	-3 (-7 to +4)	+10 (+3 to +16)	-8	-1
2 <i>Sphagnum</i> - small sedge fen	2	-12 (-14 to -11)	-2 (-3 to 0)	-10 (-10 to -10)	0 (-2 to +1)	-21	-17
3 brown moss - tall sedge fen	4	-10 (-14 to +3)	+2 (+2 to +13)	-3 (-6 to +9)	+6 (+3 to +22)	-12	+2
4 tall sedge - reed fen	4	-2 (-3 to 0)	+8 (+3 to +14)	+4 (0 to +21)	+19 (+11 to +37)	-5	+3
5 pine - birch fen woodland and shrubland	3	-11 (-12 to +10)	-1 (-2 to +6)	-14 (-16 to -10)	0 (-3 to +11)	-27	-25
6 spruce fen woodland	2	-15 (-17 to -13)	-4 (-5 to -3)	-13 (-16 to -11)	-3 (-7 to +2)	-30	-23
7 inundated alder woodland	3	-4 (-9 to -3)	+6 (+3 to +12)	0 (-6 to 0)	+15 (+13 to +19)	0	+5
8 alder spring fen woodland	3	-7 (-13 to -4)	2 (-2 to +2)	-9 (-11 to -4)	+1 (-1 to +3)	-25	-10

study carried out on a fen in a Dutch polder over 43 years (1944–1987). There were considerable changes in vegetation type and species composition, along with a decreasing input of minerotrophic surface water. Mesotrophic brown moss - sedge rich fen vegetation disappeared or decreased in abundance, whereas oligotrophic bog vegetation and mesotrophic to eutrophic semi-aquatic vegetation appeared and the cover of mesotrophic to eutrophic alder carr increased. Among the 39 species lost there were 19 fen specialists including *Scorpidium scorpioides*, *Campylium stellatum*, *Fissidens adianthoides* and *Hammarbya paludosa*, whereas the species gained were bog specialists, trees, shrubs and epixylic mosses (reflecting maturation of carr forests). A comparison of historical (1953–1967) and recent (2002–2013) vegetation records in rich fens in the Bohemian Massif (Czech Republic) by Hájek *et al.* (2015) similarly showed a decline of rich fen mosses (*Campylium stellatum*, *Limprichtia revolvens*, *Tomentypnum nitens*) and an expansion of *Sphagnum* spp. and *Calliergonella cuspidata*. The authors attributed these changes to increasing nutrient availability or lowered regional groundwater level because the fens had never been drained and there had not been a change in management. The second tendency was revealed by Fojt & Harding (1995) in an unmanaged valley fen in England where no changes in groundwater regime could be identified. During the 30 years between 1959 and 1991, they recorded a substantial increase of wet tall-herb fen with *Phragmites australis* at the expense of short vascular plants (*Carex panicea*, *Pinguicula vulgaris*, *Schoenus nigricans*, *Succisa pratensis*, *Valeriana dioica*) and bryophytes (*Fissidens adianthoides*, *Limprichtia revolvens*) typical of rich fen.

The vegetation of the mire in the Rospuda valley has remained generally unchanged over the last 30 years. Our comparison showed that the same or similar plant communities were present in historical and modern times, and these were more or less the same as those reconstructed from the peat deposit (Jabłońska *et al.* 2014), which formed over the last ca. 1200 years. Some discrepancies between our results and vegetation records from the 1980s (Sokołowski 1996; Figure 10) may have resulted from differences in plot locations. Random selection of plots, or their relocation close to rather than exactly coincident with previously sampled sites, generally results in greater deviation from previous survey results than would arise if sampling of the same plots was repeated (Chytrý *et al.* 2014). Sokołowski (1996) chose relevé locations subjectively, placing them to represent different plant

communities throughout the Rospuda valley, and some of his relevé locations must have been missed by our regular sampling (and even by our additional targeted relevés). Especially, this may be the case for the area around a small lake in the northern part of the valley which has a floating mat of poor fen vegetation (with *Scheuchzeria palustris* and *Andromeda polifolia* inter alia), as well as for a *Sphagnum fuscum* dominated side valley to the west of the river. The shift between the clusters of grey and black points in the lower part of the DCA plot in Figure 10 is explained by the lack of sampling in these areas. However, what cannot be explained by differences in sampling strategy are the changes in frequency and area occupied by the pioneer rich fen community *Eleocharitetum quinqueflorae* (left part of Figure 10). This community could also be assigned to the *Stygio-Caricion limosae* (Peterka *et al.* 2017), mainly due to the often abundant occurrence of two diagnostic species of this alliance, namely *Carex limosa* and *Cinclidium stygium*. We suppose that the extent of pioneer rich fen vegetation was very limited in the 1980s because the area of most of the relevés recorded in these communities by Sokołowski was 5 m², whereas he used 100 m² or even 200 m² relevés for the dominant brown moss - sedge communities. However, Sokołowski (1996) did not specify the part of the peatland in which he found this community, or the sizes of the areas it occupied. The patches dominated by *Eleocharis quinqueflora* have now almost disappeared; there is only one such relevé in our database, although early-succession species such as *C. limosa*, *C. stygium*, *Drosera anglica*, *E. quinqueflora* and *Meesia triquetra* still occur here without forming distinct assemblages. There is a possibility that we overlooked small scattered patches of pioneer rich fen vegetation. On the other hand, it is possible that they decreased over 30 years, similarly to the succession observed over 43 years by van Belle *et al.* (2006) who showed that pioneer rich fen vegetation disappeared or decreased in abundance and was displaced by other communities over the course of the succession.

Unlike van Belle *et al.* (2006) and Hájek *et al.* (2015), we did not observe acidification of mesotrophic brown moss - sedge vegetation in our 10-year study. There was no increase of *Sphagnum* species at our sampling points (Table 2) but, rather, a gradual increase of eutrophic and reedbed-related species (e.g. *Lysimachia thyrsiflora*, *Phragmites australis*, *Thelypteris palustris*, *Calliergonella cuspidata*) at the expense of rich fen mosses (*Calliergon giganteum*, *Campylium stellatum*, *Limprichtia cossonii*) similar to the trend reported by Fojt & Harding (1995). However, no tall sedges

entered the community (Table 2). This seems surprising given the rise in temperature and potential drop in regional water level. To illustrate the climatic conditions in NE Poland over the past 30 years we analysed total precipitation and average daily temperature data from the Suwałki meteorological station (54° 07' 51" N, 22° 56' 56" E) for the period 1973–2016. The data were compared quarterly, for autumn (September to November), winter (December–February), spring (March–May) and summer (June–August). There was a clear trend of increasing mean daily temperature, especially in summer (Figure 11). On the other hand, the amount of precipitation fluctuated but no trend was observed. These patterns are consistent with the results of past climate change analyses for the whole of Poland, which show: (1) increasing temperature leading to increased evapotranspiration; (2) shortening of the snow-lie season with reduced snowpack and earlier snowmelt, which results in lower water supply in spring and lower water level in summer; (3) no clear

change in annual precipitation total but a tendency for decreased summer precipitation in favour of winter precipitation and an increase in the number of days with heavy precipitation (Degirmendžić *et al.* 2004, Anders *et al.* 2014, Owczarek & Filipiak 2016). Such processes, operating through a decline in regional groundwater level especially in summer (i.e. during the growing season), ought to result in a shift towards drier rather than wetter habitats. However, even the water levels measured in brown moss - sedge vegetation during the very dry summer of 2016 were not very low (1–8 cm below the surface; Table 1), probably due to oscillation of the mire surface driven by fluctuations of the absolute water level. Nevertheless, a lowered groundwater supply could lead to surface water from the Rospuda River gaining influence in this area, bringing in extra plant nutrients and thus leading to the expansion of reedbed-related species (*Phragmites australis*, *Thelypteris palustris*) (and decrease of *Alnus*) in riparian inundated alder woodland

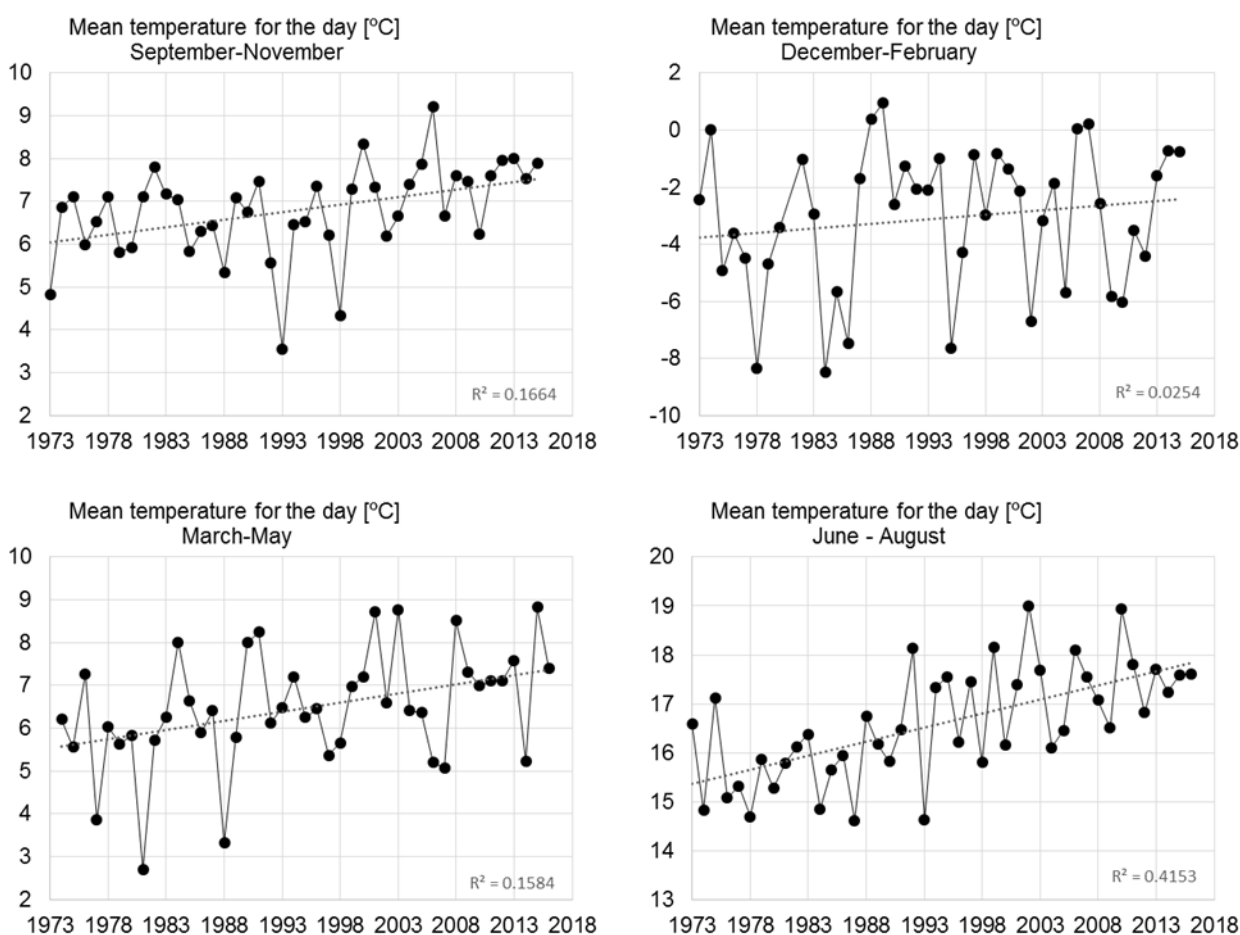


Figure 11. Mean daily temperature at Suwałki (calculated quarterly), 1973–2016. Based on online data provided by the National Climatic Data Center (US).

(Table A2) similarly points to an increased importance of flooding in the riverine zone. Vegetation changes within the forests on the edge of the mire confirm our expectations for potential effects of increased temperature and change in the pattern of precipitation incidence. A shift towards drier habitats was indicated by a decline of *Sphagnum* species and an increase of moss species typical of drier environments in pine-birch fen woodland, as well as by a decrease of fen herbs (*Caltha palustris*, *Menyanthes trifoliata*, *Thelypteris palustris*) in alder spring fen woodlands. Here, the groundwater level dropped considerably (from 10 cm to 30 cm below ground surface; Table 1), probably due to the high decomposition rate and consequent compaction of peat disabling mire surface oscillations, combined with relatively intense evapotranspiration; moreover, the long distance to the river and the inclined mire surface would prevent river water from reaching this habitat.

We also noticed a very low water level in *Sphagnum* - small sedge fen communities in 2016, along with a marked decline of *Vaccinium oxycoccos* and intense overgrowing of patches of this vegetation type by woody species (Table A2, Figure 5, increased cover of shrub layer in Figure 7). These are the only places within the mire where an expansion of trees and shrubs over open fen communities was clearly visible over the 10-year period. Again, we attribute this to the lack of significant mire surface oscillations in this zone, due to more compacted peat and a shallower layer of gyttja beneath the peat compared to the rest of the open mire (c.f. Jabłońska *et al.* 2014). The habitat has become drier and more eutrophic due to faster decomposition of the peat under aerobic conditions, fostering the growth of woody species. Facilitation of ectomycorrhizal fungi in aerated peat may also have contributed to tree and shrub expansion (Thormann *et al.* 1999). Finally, atmospheric nitrogen deposition could have affected vegetation by increasing the supply of nutrients; however, we do not consider this an important cause of the observed changes because it should not exceed 4–7 kg N ha⁻¹ year⁻¹ and has been relatively constant since the 1990s (based on data from a nearby environmental monitoring station in a similar landscape setting, in Wigry National Park; source: <http://zmsp.gios.gov.pl>).

Although some changes in mire vegetation were observed during the last decade, we consider them to be relatively small (the relative difference between relevés from 2016 and 2006–2008 reached, on average, 0.15 % of the whole vegetation variability; Figure 8) and we conclude that the mire as a whole remains very stable, with the presence of fen

vegetation indicating peat-forming processes over a large part of the mire and high biodiversity overall. Factors underpinning the stability of the Rospuda mire are its geomorphological landscape setting in a large catchment (allowing a constant groundwater supply) with a deep gyttja layer underlying the peat in the largest southern basin (c.f. Jabłońska *et al.* 2014), and the lack of local hydrological disturbance e.g. by drainage ditches or regulation of the adjacent river. As a result, the mire is resilient and there is no need for mowing management. This is a unique situation among percolation fens in Europe which are, overall, affected by drainage and internal as well as extrinsic eutrophication. Further development of the mire will depend on the future climatic and hydrological conditions. Due to the high spatial and temporal variability of precipitation, predicted changes in the amount of precipitation in central Europe are subject to considerable uncertainty (Anders *et al.* 2014). If precipitation increases, a rise of regional groundwater level can be expected, and this could trigger a change back towards wetter and less productive habitats. However, in a more probable climatic scenario, temperature will continue to increase and summer precipitation to decrease, perpetuating the lowering of regional groundwater level. In such a scenario the tipping point in braking resilience of the Rospuda mire might be reached. Nevertheless, in accordance with Mäkiranta *et al.* (2018), we suspect that moderate warming under wet conditions will have negligible effects on plant community composition; whereas changes are more likely to be observed in the case of drastic lowering of the water level, irrespective of temperature rise.

Post-scriptum: towards effective conservation of the Rospuda mire

In the last 10–15 years of the twentieth century, the Rospuda mire was threatened by the planned construction of an express road which would cut across the valley of the Rospuda river and the mire itself. After Poland joined the European Union (EU) in 2004 the Rospuda valley was included in the Special Area of Conservation (SAC) Ostoja Augustowska (PLH 200005), a newly designated Natura 2000 site under the European Habitats Directive (Council Directive 92/43/EEC). Although the European Commission evaluated the chosen route of the express road as being devastating for the Rospuda mire, its construction started, firstly outside the Natura 2000 site. In 2007 strong protests against the destruction of the Rospuda mire by road construction were raised by environmental scientists, NGOs and environmental activists, international mire specialists, artists and the general public. In July that

year the European Commission filed an injunction with the European Court of Justice to immediately stop the construction works. Polish courts also evaluated the previously issued decisions and environmental permissions and, in September 2008, the Main Administrative Court of Poland revoked the environmental case for construction of the road. Afterwards, the building permit was also revoked. A new Environmental Impact Assessment with an independent analysis of alternative routes was finished in 2009, and this recommended a new route passing around the Rospuda mire. The road, following the new route, was opened for vehicles in November 2014. In Poland the Rospuda mire case became a symbol of successful social cooperation to protect the non-material value of nature (Tygodnik Powszechny 2014).

We present our study as evidence of the natural character of the Rospuda mire and, following Sokołowski (1988, 1989, 1996), we again appeal for its legal protection through designation as a nature reserve; which is the appropriate nature conservation status according to Polish law. In our opinion the obstacle of partly private ownership of land could be overcome by allocating national funding for the purchase of land. The mire of Rospuda also warrants designation as a Ramsar site because it fulfils Ramsar Criteria 1, 2 and 3. According to Criterion 1, a wetland designated as a Ramsar site should contain a representative, rare or unique example of a natural or near-natural wetland type found within the appropriate biogeographic region. The Rospuda mire fully meets this condition, being one of the most natural large mires in temperate Europe - a typical, near-pristine percolation rich fen. Criterion 2 states that a designated wetland should support vulnerable, endangered or critically endangered species or threatened ecological communities. This is also fulfilled, as the Rospuda mire is a refuge for several plant species that are endangered in Poland and the rest of Europe. As many as 37 of its vascular plant, moss and liverwort species are listed in the Polish Red List of Plants (e.g. *Baeothryon alpinum*, *Carex chordorrhiza*, *Eriophorum gracile*, *Meesia triquetra*, *Paludella squarrosa*, *Tomentypnum nitens*) (Pawlikowski *et al.* 2010) and the Rospuda valley is the only Polish site for the musk orchid *Herminium monorchis*. The Rospuda mire also accommodates the most numerous and best-preserved Polish populations of two EU Habitats Directive species, namely *Liparis loeselii* and *Saxifraga hirculus*, thereby fulfilling Ramsar Criterion 3 - that a designated wetland should support populations of plant and/or animal species that are important for maintaining the biological diversity of a particular

biogeographical region. A proposal for Ramsar designation of the Rospuda mire was submitted to the National Secretariat of the Ramsar Convention in 2014 but has not been considered to date. On behalf of the large group of ecologists, conservationists and others who fought for preservation of the Rospuda mire's unique character, the authors express a sincere hope that this site will soon be granted the appropriate national and international conservation status.

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Supplementary material (available for separate download as a .zip file):

Supplement 1: Phytosociological tables for relevés recorded in 2006–2008 along Transects I–V (Excel file).

Supplement 2: Pairs of photographs taken in 2009 and 2016 at (the same) permanent sampling plots, selected to represent the distinct vegetation types occurring along Transects I–V (.pdf).

Appendix

Table A1. Synoptic table for the eight vegetation types along the five transects, prepared on the basis of relevés recorded in 2006–2008. Only species with frequency category II and higher are shown. Vegetation types: 1 = brown moss - small sedge fen, 2 = *Sphagnum* - small sedge fen, 3 = brown moss - tall sedge fen, 4 = tall sedge - reed fen, 5 = pine - birch fen woodland and shrubland, 6 = spruce fen woodland, 7 = inundated alder woodland, 8 = alder spring fen woodland.

Vegetation type	7	4	3	1	2	5	6	8
Number of relevés	8	19	38	90	30	68	47	8
ChCl., DCl. Alnetea glutinosae								
<i>Calamagrostis canescens</i>	III				II		II	
<i>Salix rosmarinifolia</i>				II	II	II		
<i>Salix cinerea</i>	II		II	II	III	III	II	III
<i>Alnus glutinosa</i>	V		III	II		V	IV	IV
<i>Lycopus europaeus</i>	III	II	III			III	II	IV
<i>Solanum dulcamara</i>	V	II					II	V
<i>Dryopteris cristata</i>	II					II		
<i>Sphagnum squarrosum</i>						III	II	
<i>Trichocolea tomentella</i>							II	
ChCl. Phragmitetea								
<i>Carex rostrata</i>		III	V	V	V	IV	II	
<i>Thelypteris palustris</i>	V	II	IV	IV	III	V	IV	IV
<i>Peucedanum palustre</i>	V	II	IV	III	II	V	II	II
<i>Equisetum fluviatile</i>	IV	V	V	IV	IV	V	III	V
<i>Galium palustre</i>	IV	III	IV	IV	IV	V	III	IV
<i>Carex appropinquata</i>	IV	II	V	IV	II	V	III	IV
<i>Ranunculus lingua</i>	III	II	IV	II	IV			II
<i>Lysimachia thyrsoiflora</i>	II	IV	III	IV	III			III
<i>Phragmites australis</i>	V	V	V	II		III	II	II
<i>Scutellaria galericulata</i>	III	II	II			II	II	III
<i>Carex acutiformis</i>	V	V	II			II		V
<i>Carex elata</i>	II					II		
<i>Glyceria maxima</i>	II							II
<i>Acorus calamus</i>	II							
<i>Typha latifolia</i>		II	III	II				II
<i>Phalaris arundinacea</i>		III						II
<i>Cicuta virosa</i>		III	III					
<i>Iris pseudacorus</i>		II	II					
<i>Rorippa amphibia</i>		II						
<i>Sparganium erectum</i>		II						
<i>Rumex hydrolapathum</i>			III					

Vegetation type	7	4	3	1	2	5	6	8
Number of relevés	8	19	38	90	30	68	47	8
ChCl., DCl. Molinio-Arrhenatheretea								
<i>Lysimachia vulgaris</i>	V	II	V	III	II	V	V	IV
<i>Epilobium palustre</i>	IV	IV	V	V	V	II		
<i>Myosotis palustris</i>	II	III	IV	III	II			IV
<i>Caltha palustris</i>		II	III	IV	III	III		IV
<i>Galium uliginosum</i>	II		III	V	V	III	II	II
<i>Festuca rubra</i>	II		III	IV	V	III		II
<i>Cardamine pratensis</i>	II	II	IV	IV		III	II	II
<i>Lythrum salicaria</i>	II	III	III					
<i>Poa trivialis</i>	IV		II	III			II	V
<i>Carex cespitosa</i>	IV					III	III	II
<i>Climacium dendroides</i>	IV					IV	II	
<i>Filipendula ulmaria</i>	V					III		II
<i>Fissidens adianthoides</i>	II					II		
<i>Lathyrus palustris</i>	II							
<i>Rumex acetosa</i>				II	III			
<i>Lychnis flos-cuculi</i>			II	IV	IV			IV
<i>Poa pratensis</i>			II	II	II			II
<i>Agrostis stolonifera</i>			IV	IV	IV	II		
<i>Cirsium palustre</i>			II	II		III	III	II
<i>Equisetum palustre</i>						II		II
<i>Angelica sylvestris</i>						II	II	V
<i>Crepis paludosa</i>						II	II	III
<i>Molinia caerulea</i>						IV	II	
<i>Carex panicea</i>						II		
<i>Polygonum bistorta</i>						II		
<i>Veronica longifolia</i>			II					
<i>Cirsium oleraceum</i>								II
ChCl., DCl. Oxycocco-Sphagnetea								
<i>Drosera rotundifolia</i>					V	II		
<i>Aulacomnium palustre</i>			II	III	V	IV	III	
<i>Vaccinium oxycoccos</i>					V	IV	II	
<i>Sphagnum capillifolium</i>						IV	III	
<i>Calypogeia sphagnicola</i>						III	II	
<i>Polytrichum strictum</i>						II	II	
<i>Sphagnum fallax</i>						II	II	
<i>Sphagnum fuscum</i>						II		
<i>Sphagnum magellanicum</i>							II	
ChCl., DCl. Querco-Fagetea								
<i>Plagiomnium undulatum</i>						II	II	II
<i>Eurhynchium angustirete</i>							II	II

Vegetation type	7	4	3	1	2	5	6	8
Number of releves	8	19	38	90	30	68	47	8
<i>Paris quadrifolia</i>							III	II
<i>Luzula pilosa</i>							II	
<i>Corylus avellana</i>							II	
<i>Chrysosplenium alternifolium</i>								IV
<i>Impatiens noli-tangere</i>								II
<i>Prunus padus</i>								II
<i>Ribes spicatum</i>								II
ChCl., DCI. Artemisietea vulgaris								
<i>Urtica dioica</i>	IV							IV
<i>Eupatorium cannabinum</i>							II	IV
<i>Geum rivale</i>							II	II
<i>Galium aparine</i>								II
ChCl. Scheuchzerio-Caricetea nigrae								
<i>Carex lepidocarpa</i>				II				
<i>Drepanocladus aduncus</i>			II	II				II
<i>Carex lasiocarpa</i>			IV	IV		III		
<i>Campyllum stellatum</i>			II	II		IV	II	
<i>Menyanthes trifoliata</i>	II	III	IV	V	V	V	II	II
<i>Potentilla palustris</i>		IV	IV	II	III	III	II	II
<i>Carex dioica</i>				II	IV	IV	II	
<i>Calliergon giganteum</i>			II	III	II	II		
<i>Stellaria palustris</i>	III		III	II	IV			II
<i>Eriophorum angustifolium</i>			II	IV	IV			
<i>Calamagrostis stricta</i>			IV		III			
<i>Epipactis palustris</i>				III	III			
<i>Carex diandra</i>				III	II			
<i>Carex limosa</i>				II	IV			
<i>Hamatocaulis vernicosus</i>				II	II			
<i>Sphagnum teres</i>					V	V	III	
<i>Carex chordorrhiza</i>					III	II		
<i>Parnassia palustris</i>					III			
<i>Carex curta</i>						II	II	
<i>Carex flava</i>						III	II	
<i>Viola epipsila</i>						II	II	
<i>Carex nigra</i>							II	
ChCl., DCI. Vaccinio-Piceetea								
<i>Pinus sylvestris</i>				II	III	V	IV	
<i>Picea abies</i>						V	V	II
<i>Pleurozium schreberi</i>						IV	IV	
<i>Vaccinium myrtillus</i>						III	V	
<i>Hylocomium splendens</i>						III	III	

Vegetation type	7	4	3	1	2	5	6	8
Number of relevés	8	19	38	90	30	68	47	8
<i>Trientalis europaea</i>						II	III	
<i>Vaccinium vitis-idaea</i>						II	III	
<i>Dicranum scoparium</i>						III	II	
<i>Dicranum polysetum</i>						II		
<i>Lycopodium annotinum</i>							III	
<i>Orthilia secunda</i>							II	
<i>Pyrola rotundifolia</i>							II	
<i>Sphagnum girgensohnii</i>							II	
Others:								
<i>Brachythecium mildeanum</i>				II				
<i>Leptodictyum humile</i>		II						
<i>Lemna minor</i>		III	III					
<i>Rumex aquaticus</i>			II					
<i>Utricularia intermedia</i>			II					
<i>Utricularia minor</i>			II					
<i>Marchantia polymorpha</i>			III	IV	III			
<i>Betula pubescens</i>			II	III	IV	V	V	III
<i>Calliergonella cuspidata</i>	V		V	V	III	V	III	IV
<i>Plagiomnium ellipticum</i>	IV		V	III		IV	II	IV
<i>Bryum pseudotriquetrum</i>	IV		III	V	III	III		
<i>Frangula alnus</i>	II					IV	V	III
<i>Brachythecium rutabulum</i>	IV		III			IV	III	IV
<i>Galium elongatum</i>	IV	IV						II
<i>Plagiomnium cuspidatum</i>	III					II		II
<i>Viola palustris</i>	II					III	III	II
<i>Plagiothecium laetum</i>	II					III	II	
<i>Plagiomnium elatum</i>	II					II	II	
<i>Plagiothecium denticulatum</i>	II							II
<i>Angelica archangelica ssp. litoralis</i>	II							
<i>Stachys palustris</i>	II							
<i>Rhizomnium punctatum</i>						IV	II	II
<i>Maianthemum bifolium</i>						III	IV	II
<i>Sorbus aucuparia</i>						II	IV	II
<i>Lepidozia reptans</i>						II	II	II
<i>Sphagnum palustre</i>						IV	V	
<i>Juniperus communis</i>						IV	II	
<i>Potentilla erecta</i>						IV	II	
<i>Viburnum opulus</i>						III	III	
<i>Pohlia nutans</i>						III	II	
<i>Rhytidiadelphus triquetrus</i>						II	II	
<i>Rubus saxatilis</i>						II	II	

Vegetation type	7	4	3	1	2	5	6	8
Number of releves	8	19	38	90	30	68	47	8
<i>Sphagnum fimbriatum</i>						II	II	
<i>Tetraxis pellucida</i>						II	II	
<i>Cephalozia bicuspidata</i>						II		
<i>Cephalozia pleniceps</i>						II		
<i>Chiloscyphus pallescens</i>						II		
<i>Dicranum bonjeanii</i>						II		
<i>Tomentypnum nitens</i>				III	IV	III		
<i>Helodium blandowii</i>				II	IV	II		
<i>Dactylorhiza incarnata</i>				III	II			II
<i>Aneura pinguis</i>				II		II		II
<i>Limprichtia cossonii</i>				II		II		
<i>Sphagnum warnstorffii</i>						II		
<i>Lophocolea heterophylla</i>						II		II
<i>Oxalis acetosella</i>							IV	II
<i>Dryopteris carthusiana</i>							III	II
<i>Rubus idaeus</i>							II	II
<i>Athyrium filix-femina</i>							II	II
<i>Quercus robur</i>							II	
<i>Thuidium tamariscinum</i>							II	
<i>Anthriscus sylvestris</i>								II
<i>Cardamine amara</i>								II
<i>Elymus caninus</i>								II
<i>Fragaria vesca</i>								II
<i>Geranium robertianum</i>								II
<i>Glechoma hederacea</i>								II
<i>Humulus lupulus</i>								II
<i>Mycelis muralis</i>								II
<i>Polytrichastrum formosum</i>								II
<i>Rhamnus catharticus</i>								II

Table A2. Change in species composition between 2006–2008 and 2016, in the same sampling plots located in eight vegetation types. A change (increase or decrease) was recorded if the cover of a species increased (or decreased) by at least two points on the Braun-Blanquet scale if only two relevés were available to represent the vegetation type, or by at least one point on the Braun-Blanquet scale if data from more than two relevés were available for comparison. Letters in parentheses indicate the vegetation layer in which a shift in cover of the species occurred, where alternatives are possible: (a) = tree layer; (b) = shrub layer; (c) = herb layer.

Vegetation type	No. plots	Dominant species in vegetation type (as observed in 2006–2008)	Increasing species in sampling plots (newly appearing in bold)	Decreasing species in sampling plots (disappearing in bold)
1. brown moss - small sedge fen	6	<i>Carex appropinquata</i> <i>Carex chordorrhiza</i> <i>Carex diandra</i> <i>Carex dioica</i> <i>Carex lasiocarpa</i> <i>Carex rostrata</i> <i>Festuca rubra</i> <i>Menyanthes trifoliata</i> <i>Thelypteris palustris</i> <i>Calliergonella cuspidata</i> <i>Campylium stellatum</i> <i>Hamatocaulis vernicosus</i> <i>Limprichtia cossonii</i> <i>Tomentypnum nitens</i>	<i>Alnus glutinosa</i> (c) <i>Betula pubescens</i> (b) <i>Salix aurita</i> (c) <i>Agrostis stolonifera</i> <i>Carex chordorrhiza</i> <i>Carex diandra</i> <i>Carex lepidocarpa</i> <i>Carex rostrata</i> <i>Festuca rubra</i> <i>Lysimachia thyrsoiflora</i> <i>Mentha arvensis</i> <i>Myosotis palustris</i> <i>Phragmites australis</i> <i>Poa pratensis</i> <i>Thelypteris palustris</i> <i>Calliergonella cuspidata</i> <i>Plagiomnium cuspidatum</i>	<i>Alnus glutinosa</i> (b) <i>Calamagrostis canescens</i> <i>Carex elata</i> <i>Valeriana officinalis</i> <i>Aulacomnium palustre</i> <i>Calliergon giganteum</i> <i>Campylium stellatum</i> <i>Marchantia polymorpha</i>
2. <i>Sphagnum</i> - small sedge fen	2	<i>Carex chordorrhiza</i> <i>Carex dioica</i> <i>Carex limosa</i> <i>Menyanthes trifoliata</i> <i>Vaccinium oxycoccus</i> <i>Sphagnum teres</i> <i>Sphagnum angustifolium</i>	<i>Salix aurita</i> (c) <i>Salix aurita</i> (b) <i>Betula pubescens</i> (c)	<i>Vaccinium oxycoccus</i>
3. brown moss - tall sedge fen	4	<i>Carex appropinquata</i> <i>Carex rostrata</i> <i>Carex lasiocarpa</i> <i>Menyanthes trifoliata</i> <i>Thelypteris palustris</i> <i>Phragmites australis</i> <i>Calliergonella cuspidata</i> <i>Plagiomnium sp.</i>	<i>Alnus glutinosa</i> (a) <i>Salix cinerea</i> (c) <i>Calamagrostis stricta</i> <i>Carex acutiformis</i> <i>Epipactis palustris</i> <i>Peucedanum palustre</i> <i>Stellaria palustris</i> <i>Thelypteris palustris</i> <i>Valeriana officinalis</i> <i>Calliergonella cuspidata</i> <i>Fissidens adianthoides</i>	<i>Salix cinerea</i> (b) <i>Poa trivialis</i> <i>Utricularia intermedia</i> <i>Aulacomnium palustre</i> <i>Limprichtia cossonii</i> <i>Sphagnum capillifolium</i>
4. tall sedge - reed fen	4	<i>Carex acutiformis</i> <i>Phragmites australis</i> <i>Phalaris arundinacea</i>	<i>Alnus glutinosa</i> (c) <i>Carex rostrata</i> <i>Lythrum salicaria</i> <i>Phragmites australis</i> <i>Ranunculus lingua</i> <i>Amblystegium sp.</i>	<i>Alnus glutinosa</i> (a) <i>Carex acutiformis</i> <i>Equisetum fluviatile</i> <i>Lemna minor</i> <i>Phalaris arundinacea</i>

Vegetation type	No. plots	Dominant species in vegetation type (as observed in 2006–2008)	Increasing species in sampling plots (newly appearing in bold)	Decreasing species in sampling plots (disappearing in bold)
5. pine – birch fen woodland and shrubland	3	<i>Betula pubescens</i> <i>Betula humilis</i> <i>Pinus sylvestris</i> <i>Salix rosmarinifolia</i> <i>Salix cinerea</i> <i>Carex acutiformis</i> , <i>Carex appropinquata</i> <i>Equisetum fluviatile</i> <i>Menyanthes trifoliata</i> <i>Phragmites australis</i> <i>Thelypteris palustris</i> <i>Vaccinium oxycoccos</i> <i>Calliergonella cuspidata</i> <i>Pleurozium schreberi</i> <i>Hylocomnium splendens</i> <i>Mnium sp./Plagiomnium sp.</i> <i>Sphagnum capillifolium</i> <i>Sphagnum palustre</i> <i>Sphagnum squarrosum</i> <i>Sphagnum teres</i>	<i>Alnus glutinosa</i> (a) <i>Betula pubescens</i> (c) <i>Picea abies</i> (b, c) <i>Caltha palustris</i> <i>Crepis paludosa</i> <i>Galium uliginosum</i> <i>Menyanthes trifoliata</i> <i>Orthilia secunda</i> <i>Stellaria palustris</i> <i>Brachythecium rutabulum</i> <i>Dicranum scoparium</i> <i>Hylocomium splendens</i> <i>Plagiomnium cuspidatum</i>	<i>Alnus glutinosa</i> (b) <i>Betula pubescens</i> (a) <i>Pinus sylvestris</i> (a) <i>Viburnum opulus</i> (c) <i>Cardamine pratensis</i> <i>Dryopteris carthusiana</i> <i>Epilobium palustre</i> <i>Fissidens adianthoides</i> <i>Mnium hornum</i> <i>Rhizomnium punctatum</i> <i>Sphagnum palustre</i>
6. spruce fen woodland	2	<i>Picea abies</i> <i>Lycopodium annotinum</i> <i>Vaccinium myrtillus</i> <i>Hylocomium splendens</i> <i>Pleurozium schreberi</i> <i>Sphagnum palustre</i>	<i>Betula pubescens</i> (b) <i>Molinia caerulea</i> <i>Lycopodium annotinum</i> <i>Climacium dendroides</i>	<i>Betula pubescens</i> (a) <i>Vaccinium myrtillus</i>
7. inundated alder woodland	3	<i>Alnus glutinosa</i> <i>Carex acutiformis</i> <i>Carex cespitosa</i> <i>Phragmites australis</i>	<i>Cirsium palustre</i> <i>Phragmites australis</i> <i>Potentilla palustris</i> <i>Thelypteris palustris</i> <i>Plagiomnium cuspidatum</i>	<i>Alnus glutinosa</i> (b) <i>Carex acutiformis</i> <i>Calliergonella cuspidata</i> <i>Plagiomnium ellipticum</i>
8. alder spring fen woodland	3	<i>Alnus glutinosa</i> <i>Carex acutiformis</i> <i>Chrysosplenium alternifolium</i> <i>Crepis paludosa</i> <i>Poa trivialis</i> <i>Thelypteris palustris</i> <i>Plagiomnium undulatum</i>	<i>Alnus glutinosa</i> (b) <i>Chaerophyllum hirsutum</i> <i>Epilobium palustre</i> <i>Eupatorium cannabinum</i> <i>Glyceria maxima</i> <i>Impatiens noli-tangere</i> <i>Lysimachia vulgaris</i>	<i>Alnus glutinosa</i> (a) <i>Frangula alnus</i> (c) <i>Salix cinerea</i> (b) <i>Angelica sylvestris</i> <i>Calamagrostis canescens</i> <i>Caltha palustris</i> <i>Cardamine pratensis</i> <i>Cirsium oleraceum</i> <i>Equisetum fluviatile</i> <i>Menyanthes trifoliata</i> <i>Poa trivialis</i> <i>Thelypteris palustris</i> <i>Calliergonella cuspidata</i> <i>Plagiomnium ellipticum</i> <i>Plagiomnium undulatum</i>