Impact of drainage on raised bogs in Estonia

Jaanus Paal[1], Iti Jürjendal[2], Ave Suija[1], Ain Kull[3]

[1] Department of Botany, Institute of Ecology and Earth Sciences, University of Tartu, Estonia
[2] Department of Science and Education, Tallinn Botanic Garden, Estonia
[3] Department of Geography, Institute of Ecology and Earth Sciences, University of Tartu, Estonia

SUMMARY

Drainage is the most important single factor affecting mires globally but its effects vary depending on drainage type, climate and wetland ecosystem. Sixteen transects in fifteen drained raised bogs in the hemiboreal zone of Estonia were examined to determine the spatial effects of drainage on vegetation and environmental factors. We found that the effects of drainage along a hydrosequence depended on the drainage type; i.e., whether it took the form of a cutoff ditch intercepting surface and subsurface water flow around the perimeter of the bog massif, or the drainage ditch crossed the central part of the bog. Some drains of the latter type were still functioning whereas old hand-dug examples seemed to be derelict and inactive. For both of the active drainage types, maximum water levels stabilised within 25 m of the ditch but drawdown effects on minimum and average water levels extended to 450 m. The vegetation variables that were most sensitive to drainage were the number and the percentage of bog-specific species, the number of ground vegetation species, the total cover of *Sphagnum* species, and the height and canopy cover of trees. Trees were rare when the minimum water level was higher than -20 cm, and the number of bog-specific species increased rapidly as the minimum water level rose towards the surface from -90 cm. Total cover of the shrub layer decreased and total cover of *Sphagnum* species increased almost linearly with a rise of minimum water level up to -40 cm, whereas the total cover of field layer species stabilised when the minimum water level was at -100 cm. Total cover of *Sphagnum* species in the field layer increased over distances of up to 250–300 m from the drainage ditch and the percentage of bog-specific and fen-specific species stabilised 190–300 m from the ditches.

KEY WORDS: hydrosequence, indicator species, peatland, water level, vegetation change

INTRODUCTION

Mires are peatlands where the accumulation of organic matter (peat) from dead and decaying plant material occurs under conditions of permanent water saturation (Holden *et al*. 2004). Because of their dependence on water saturation of the peat matrix, mire ecosystems are highly sensitive to changes in hydrology, which may be caused by changes in climate or land use and in either case disturb the delicate balance between peat accumulation and decomposition. While climate change affects peatlands at global and regional scales (Swindles *et al*. 2019, Humphrey *et al*. 2021), the one anthropogenic factor that affects peatlands at all scales is drainage (Holden *et al*. 2004, Limpens *et al*. 2008, Leifeld & Menichetti 2018). Mires are important natural ecosystems with high value for climate regulation, biodiversity conservation, flood control and human welfare (Costanza *et al*. 1997, Erwin 2009) but the quality of these services will decline rapidly if peatlands are drained.

In Estonia the regular exploitation of mires for peat extraction and agriculture started in the 17th century. Large-scale drainage of mires, especially fens and transitional bogs, took place here between the 1950s and the 1980s. In the 1950s the total area of (ombrotrophic) raised bogs in Estonia was about 250,000 ha (Laasimer 1965) and, according to the mire inventory, almost 100,000 ha of bogs have been destroyed by man during the last 60 years (Paal 2011, Paal & Leibak 2013). Bog ecosystem degradation in Estonia is mainly a direct result of drainage associated with peat excavation and with land amelioration. Moreover, 30,000 ha of former bogs are currently abandoned or in use as industrial peat fields (Ramst & Orru 2009).

The extent of drainage effects varies depending not only on the size and type of the mire and the location of the drainage system within the mire (Ivanov 1953, Boelter 1972, Holden & Burt 2003, Landry & Rochefort 2012), but also on how the drainage system was established (Braekke 1983, Ingram & Bragg 1984). As many factors - such as

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climate, bog type, peat properties and drainage type - influence the spatial extent of drainage effects on the mire ecosystem, it is still highly uncertain which environmental or vegetation characteristics are the most sensitive and could serve as the best indicators of drainage impact. Although there is a long history of studies investigating the effects of drainage on bog ecosystems (Ivanov 1953, Tóth & Gillard 1988, Lundin & Bergquist 1990, Päivänen & Hånell 2012), these have usually focused on rather narrow topics (e.g., forestry drainage) or been based on only a few sites or on short time periods. Especially scarce are studies that simultaneously address the effects of drainage or other peatland management on both biotic and abiotic factors and their interactions (Braekke 1983, Laine *et al*. 1995, Paal *et al*. 2016). Relationships between biotic and abiotic characteristics can be used for the assessment of drainage impact as well as for prediction of the long-term efficiency of rewetting interventions. For nature conservation planning it is important not only to report mean values of certain variables, but also to consider their variability at site level and between areas (Päivänen & Hånell 2012).

The study reported here aimed to clarify the spatial extent of drainage effects on the most widely monitored environmental variables and characteristics of vegetation, in the raised bogs of Estonia. Our study sites were distributed across the whole of Estonia and observations in all sites were carried out simultaneously over a four-year period. Thus, our study representatively takes into account any regional variation in the vegetation-related factors that are affected by drainage. This could not be achieved with a smaller sample size or a more limited list of variables, even if they were studied simultaneously under the same climatic conditions.

METHODS

Study areas and field data

We studied 16 transects in 15 raised bogs located in different regions of the Estonian mainland (Figure 1). A stratified sampling method based on the Estonian mires inventory (Paal & Leibak 2011), the land amelioration information system (Register of Land Reclamation Systems 2022) and mire regions (Allikvee & Ilomets 1995) was used to select study areas. Specific criteria included: regional bedrock type (limestone or sandstone), landscape region, minimum diameter of the undrained part of the bog > 1.5 km, drainage type, and prevailing land use in the surroundings of the bog.

Most raised bog massifs in Estonia have been surrounded by a cutoff drainage ditch that intercepts surface and subsurface flow at the bog margin or at the foot of the marginal slope (rand) (Maastik *et al*. 2000). This is the most frequent drainage type amongst Estonian bogs (Type 1 in Figure 2). Bogs with drainage systems in this category are referred to hereafter as ‘bogs with drainage type 1’. The ages of these drains are highly variable (35–121 years in our study).

The other common drainage system (Type 2 in Figure 2) comprises one or several parallel ditches dug across the bog massif, dividing the bog into two parts of which one is used as a milled peat field or for silviculture and the other is left untouched. These ditches were dug 35–45 years ago; they are deep (> 1.5 m), filled with open water and still functioning. In the case of a neighbouring peat extraction site the unexcavated side of the bog has a second ditch, which is narrow and cuts through the acrotelm only (i.e., it is shallow), within 10–20 m of the first ditch and running parallel to it. Sites with drainage systems in this category are referred to hereafter as ‘bogs with drainage type 2’.

In ‘bogs with drainage type 3’, a single hand-dug ditch was established 88–131 years ago (Type 3 in Figure 2). The ditch is shallow, partly collapsed, and overgrown with *Sphagnum* mosses.

Our sample included eight bogs with drainage type 1, four with drainage type 2 and three with drainage type 3. In Kauru bog, both drainage type 1 and drainage type 3 were represented (in its opposite parts). All of the studied bogs had been affected by drainage for at least 35 years, and none had been grazed or subjected to tree removal. Therefore, in all cases we were dealing with almost stabilised ecosystems where most of the large changes caused by drainage had already become evident. According to Laine *et al*. (1995), the replacement of plant species assemblages following drainage typically takes about 30 years in Finnish bogs.

Sampling was performed along transects aligned perpendicular to either the cutoff ditch (in bogs with drainage type 1) or the ditch crossing the bog massif (in bogs with drainage type 2 or 3). In the case of bogs with drainage type 2 the transect was laid out across the unexcavated or unplanted half of the bog. The first sampling node (sampling area) was set 5 m from the ditch and the remaining nodes were spaced at successive intervals in the order of 10 m, 25 m, 50 m, 100 m and 250 m (Figure 3).

At each sampling node we installed a sampling gauge consisting of a 1.5 m long PVC tube of diameter 75 mm with the lowermost 1 m perforated

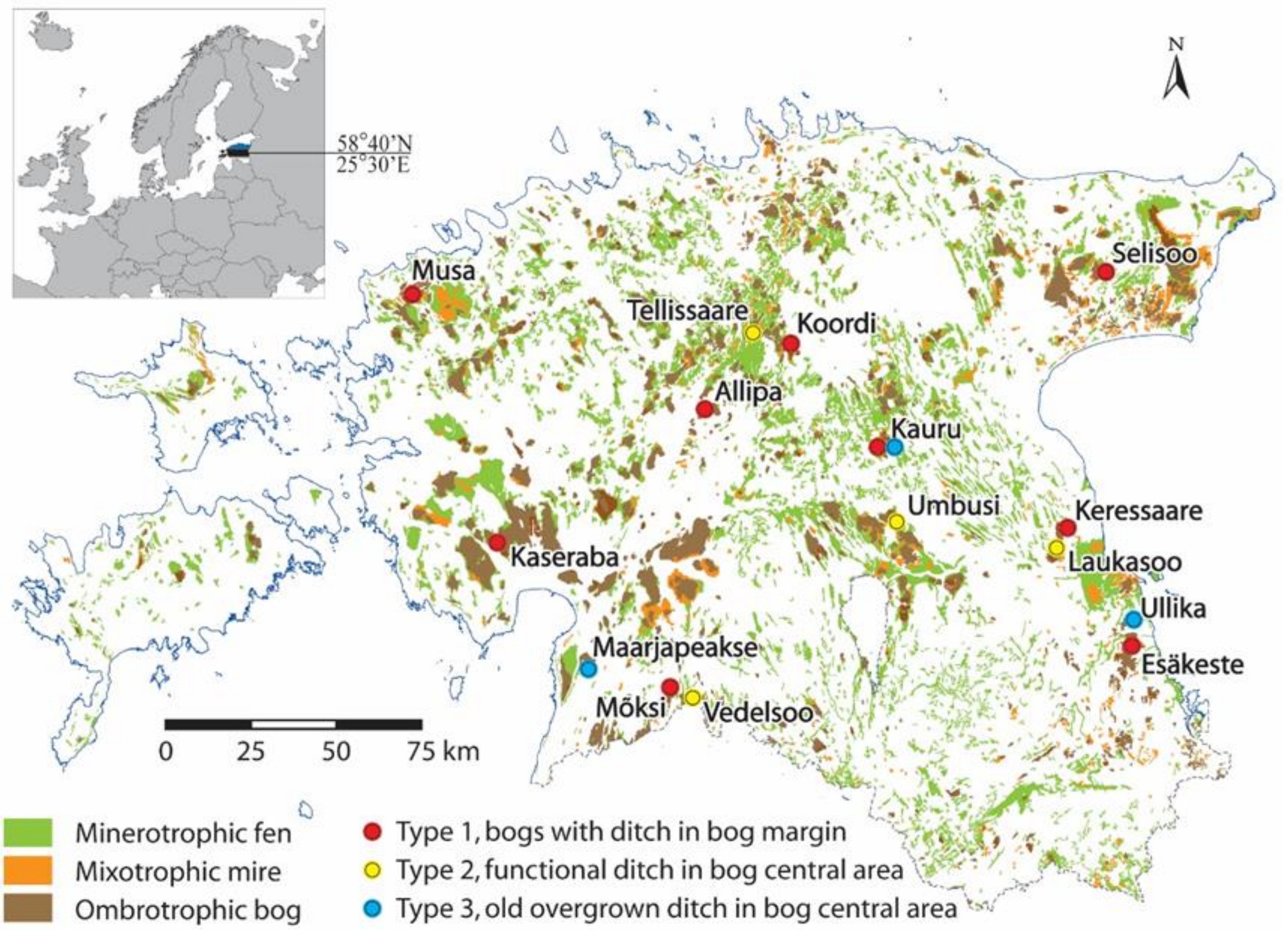

Figure 1. Locations of the study areas within Estonia.

Figure 2. Examples of three studied drainage types in bogs with detailed view of drainage ditch system (upper images, blue lines) and landscape level location of the transect (lower images, yellow dashed line).

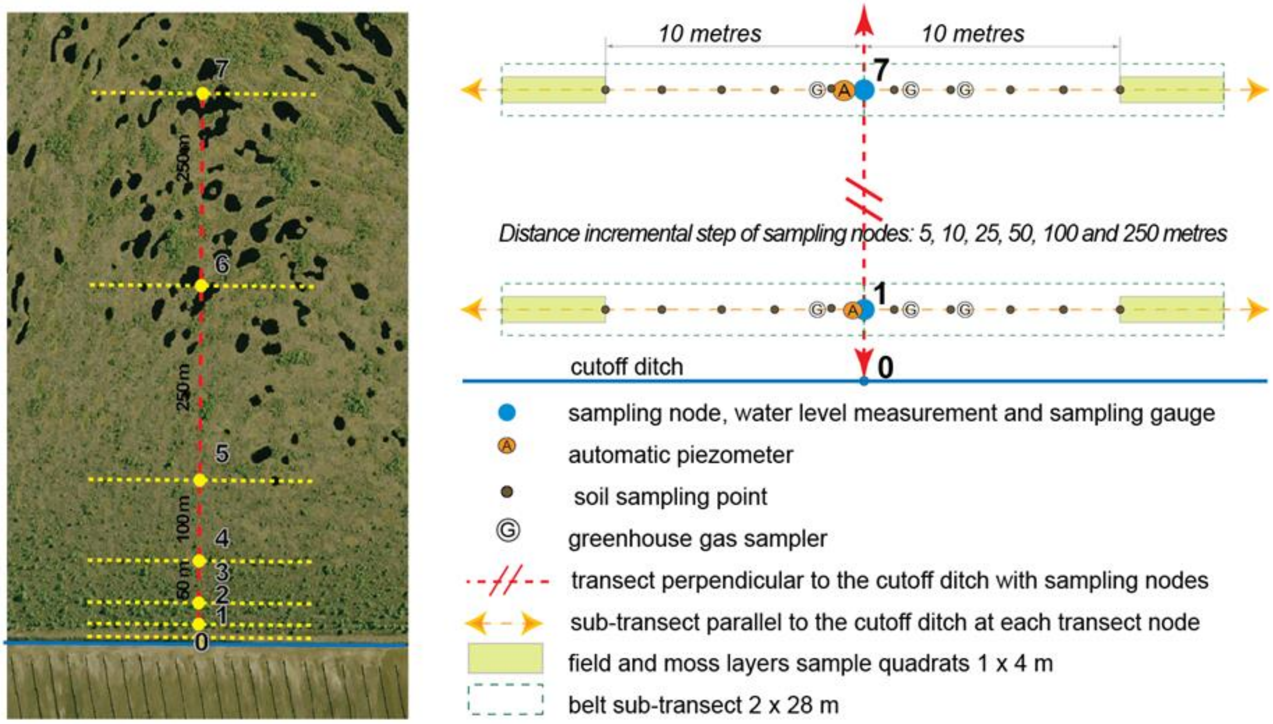

Figure 3. Study transect layout with sampling nodes and sample quadrats along the sub-transects.

and covered with DuPont Geoproma filtration fabric, which was set vertically in the peat and fitted with an automatic piezometer (GeotechAB). At the time of installation we used a peat corer to measure the thickness of the peat layers, determining peat types organoleptically. Every sampling gauge (Figure 3) was visited at monthly intervals throughout the year from June 2012 until August 2016 to measure peat water temperature, dissolved oxygen content, pH and electrical conductivity (EC) using a calibrated handheld YSI Professional Plus multimeter. Soil temperature was measured at 10, 20, 30 and 40 cm depth with a Comet System temperature logger S0110. Manual measurements of water properties were carried out at least once per month and automatic measurements were recorded daily. Mean values of water properties were calculated as averages for full years of the observation period, e.g., average water level (AveWL) as the average water level for each year and mean minimum water level (MinWL) as the average water level in the month of lowest water level during each year. Maximum water level (MaxWL) is the highest water level recorded during the measurement period and reflects the combined effects of seasonal snowmelt, microtopography and surface runoff.

At every sampling node ten sub-samples of soil were taken at 2 m intervals along a sub-transect running at 90 degrees to the main transect (Figure 3). The sub-samples were taken from 0–40 cm depth, considering the base of the living moss layer as zero level, and the volume of each sub-sample was 125 cm^3. These ten sub-samples were mixed and homogenised before analysis in the laboratory. The analyses were carried out at the Plant Biochemistry Laboratory of the Estonian University of Life Sciences. For a detailed description of the chemical analysis of soil samples, see Paal *et al*. (2016).

To describe the field (dwarf shrubs + grasses + forbs) and moss layers of the vegetation, quadrats (1 × 4 m) oriented perpendicular to the direction of the main transect were marked out at a distance of 10 m from both sides of each sampling node (see Figure 3). In these quadrats the percentage cover of lichens, bryophytes and vascular plant species, as well as the total cover of every vegetation layer, was estimated visually. Species that could not be identified in the field were collected and determined in the laboratory. The lichen specimens were deposited in the lichen collection of the University of Tartu Natural History Museum.

Shrub stems and tree saplings were counted, and their heights were measured, in circular plots of radius 2 m centred on two diagonally opposite corners of each 1 × 4 m quadrat as well as on the node. All trees of diameter < 4 cm at breast height (1.3 m) and/or of height < 4 m were regarded as saplings.

A Suunto PM-5 hand-held clinometer was used to measure tree heights in belt sub-transects (2 m wide, 28 m long) extending from the nodes of the main transect to the farthest ends of the 1 × 4 m quadrats (Figure 3). Tree girths at 1.3 m height were determined in the same sub-transect using a tape measure. Mean tree height and canopy coverage were additionally estimated (see Paal *et al*. 2016) using high resolution LIDAR (LIght Detection And Ranging) data provided in LAS format by the Estonian Land Board. The LIDAR measurements were obtained using a Leica ALS50-II scanner flown at an altitude of 2,400 m during the period 2009–2012. The illuminated footprint diameter of the measurement point on the ground was 54 cm, the vertical accuracy was 7–12 cm, and the scattered point density on the ground was 0.45 illuminated points per m^2.

Nomenclature follows Krall *et al*. (2010) for vascular plants and Ingerpuu *et al*. (1998) for bryophytes. Bog-specificity of species was estimated according to their distributions and autecological optima in natural mires (Botch & Smagin 1993, Vellak *et al.* 2013, Ingerpuu *et al.* 2014).

Data processing

Cover data for ground vegetation (field and moss layer) species were averaged from the two 1 × 4 m quadrats at every sampling node. The numbers and heights of shrub stems and saplings on the five circular plots were summed for every species. The girths and estimated heights of trees were summed by species over every sub-transect.

Tree layer height and canopy cover were estimated from the LIDAR data (Næsset & Økland 2002, Andersen *et al*. 2006) as average values for contiguous 1 m wide zones running parallel to the drainage ditch, moving from the ditch towards the bog centre. The area of each zone was 1,000 m^2 and its midpoint was located on the transect line. Tree height was calculated as the difference between digital surface model (DSM) and digital elevation model (DEM) altitude. The DSM was calculated as the maximum height value of LIDAR reflectances belonging to classes I, III, IV and V in 5 × 5 m rectangles (the average area of a single tree canopy in mires) with a 1 m step of the moving calculation cell. The bare earth surface (DEM) was calculated along the 1 m zone with a 1 m step of the moving calculation cell. Mean tree canopy cover was calculated using the same method and resolution but, to avoid occasional inclusion of reflectances from tall sedge hummocks, dwarf shrubs, etc., any reflectances belonging to vegetation classes were considered to be part of the tree canopy only if the reflectance height was ≥ 1.3 m above bare ground level. Mean tree canopy cover was then calculated as the canopy-covered area within the 1 m wide zone divided by the total area of the zone (1,000 m^2).

The importance of single vegetation variables was evaluated by factor analyses, including Varimax normalised rotation of factors. For visualisation of the overall correlation structure of variables, the main environmental gradients in the studied bogs and their effects on vegetation structure, we used ordination biplots generated by principal component analysis (StatSoft Inc. 2005). Correlation of vegetation structure and environmental variables with water level characteristics was evaluated as Spearman rank order correlation coefficients.

Relationships between the variables of vegetation structure and distance from the drainage ditch were demonstrated using box plots with the range of boxes corresponding to the standard error of the mean and the outer ends of whiskers at the minimum and maximum values. The significance level of differences in vegetation characteristics between sampling areas at increasing distances from the drainage ditch was estimated by univariate ANOVAs, nonparametric Kruskal-Wallis rank tests and Fisher LSD post-hoc tests (StatSoft Inc. 2005).

Generalised relationships between characteristics of the vegetation structure and environmental variables (distance from drainage ditch, minimum water level) were illustrated using scattergrams of empirical data with regression lines fitted by the distance-weighted least squares regression (DWLSR) method. Using this method, a second-order polynomial regression was calculated for each value on the X-variable scale to determine the corresponding Y-value such that the influence of the individual data points on the regression decreased with distance from the particular X-value (StatSoft Inc. 2005).

The indicator values of the species, along with their relative frequencies and relative abundances at sampling nodes at different distances from the ditch, were calculated by the Dufrêne & Legrendre (1997) method included in the package PC-ORD (McCune & Mefford 1999). The statistical significance of indicator values was evaluated using the Monte Carlo permutation test (N = 499).

RESULTS

According to the first-factor (F1) loadings of environmental variables for bogs with drainage type 1, the most important environmental variables in the general variation structure of the analysed data are minimum and average water level, distance from (the cutoff) ditch, thickness of bog peat and total thickness of peat (Table 1). These five variables are rather strongly intercorrelated (Spearman correlation coefficients 0.57–0.72) and they are prevalent in determining the vegetation characteristics. The last two (relating to peat thickness) are not direct results of human influence but, rather, reflect an inherent natural gradient for raised bogs. The vegetation variables with the highest first-factor (F1) loadings are number of bog-specific species, tree layer height from LIDAR data, tree layer canopy closure, the sums of tree girths and heights, and tree layer cover from LIDAR data (Table 1). The second-factor (F2) loadings highlight the importance of environmental variation induced by changes in peat water pH, which correlates most strongly with shrub layer characteristics; e.g., the Spearman correlation coefficient of water pH with shrub layer species number is 0.70, and with sum of shrub stems it is 0.54. Increasing peat water pH supports forest species such as *Picea abies*, *Oxalis acetosella*, *Dryopteris carthusiana*, *Rhytidiadelphus triquetrus*, *Brachythecium oedipodium*, etc., whereas increasing the gradient of the cutoff ditch promotes species of minerotrophic and mixotrophic mires like *Betula nana*, *Carex lasiocarpa*, *Menyanthes trifoliata* and *Equisetum fluviatile* (Figure 4).

Water level characteristics are also the most important factors connected with human influence in bogs with drainage type 2. However, compared to the situation in bogs with drainage type 1, the importance of distance from drainage ditch and peat water pH is considerably reduced while absolute altitude of the mire surface and drainage ditch depth gain importance (Table 1). The vegetation variables with the highest first-factor loadings are tree layer cover and height from LIDAR data, the sums of tree girths and heights, and the number of field and moss layer species. Total cover of lichens also has a relatively high F1 value. The most important F2 variables are total cover of moss layer and total cover of *Sphagnum* species, which are tightly intercorrelated.

In bogs with drainage type 2, the high factor loadings of water temperature and peat temperature are remarkable. These values are mainly dependent on the openness of the bog surface: the Spearman correlation coefficients of water temperature with tree layer cover from LIDAR data, and with total cover of the shrub layer, are -0.63 and -0.67, respectively; while correlating soil temperature at 20 cm depth with tree layer cover from LIDAR data returns a value of -0.74. These inverse relationships are well illustrated by the ordination biplot (Figure 5), where we can also identify a positive effect of increased drainage ditch depth on the number and abundance of lichen species. A rather high correlation also emerges between shrub layer characteristics and years since drainage began: the correlation coefficient of number of shrub stems and tree saplings with drainage age is 0.80; while comparing total cover of shrub layer with drainage age returns a value of 0.60.

In bogs with drainage type 3, distance from the drainage ditch no longer plays a substantial role in determining the environmental conditions. The variables with the highest factor loadings on the first (F1) ordination axis are thickness of peat, content of ash in soil and peat water pH. Absolute altitude of mire surface and drainage ditch depth, followed by the average and minimum water levels, total thickness of peat and thickness of bog peat have the highest factor loadings on the second (F2) ordination axis. Bogs with old (type 3) drainage have noticeably higher factor loadings than bogs with drainage types 1 and 2 for ash content in soil, peat water pH and EC and, especially, years since drainage began. Higher ash content can be partly explained by the age of drainage which has imposed longer exposure of the uppermost peat layer to aeration, leading to stronger decomposition. On the other hand, higher pH and EC reflect a greater importance of precipitation water and overland flow in bogs of this type, as long term drainage has resulted in peat compaction expressed as subsidence and increased bulk density. Variables that are positively correlated with drainage age are the numbers of moss layer species, field and moss layer species and bog-specific species (r_{Spearman} = 0.63, 0.57 and 0.43, respectively). The abundance and number of lichen species is also increased (Figure 6). Amongst the vegetation variables, the highest positive F1 factor loadings are still tree layer characteristics and the number of field and moss layer species, followed by the number of moss layer species and the sum of shrub stem heights (Table 1).

In bogs with drainage type 1 or 2, the vegetation variables that are most sensitive to distance from the ditch (according to the correlation coefficients) are tree layer height and tree canopy cover from LIDAR data, number and percentage of bog-specific species, sum of tree girths and sum of tree heights (Table 2).

In the context of large-scale mire restoration activities, questions that merit particular attention are how far the drainage effect of the (cutoff or central) ditch on water level extends, and how other (target) variables are related to water level in the peat layer. However, it is important to remember that bogs with drainage type 1 usually have an inherited natural gradient of decreasing water level from the central mire expanse towards the margin, which is enhanced

Table 1. Explained variation and factor loadings of habitat environmental variables and vegetation structure characteristics for the two first factors (F1, F2) of factor analysis.

Variable	Drainage type					
	1		2		3	
	F 1	F 2	F 1	F 2	F 1	F 2
Explained variation (%)	14.0	6.5	10.3	10.2	12.3	8.7
Variables of habitat and environment						
Distance from ditch (m)	0.748	-0.116	0.453	0.446	0.395	0.083
Thickness of bog peat (cm)	0.770	-0.212	0.919	0.004	0.835	-0.407
Thickness of transitional mire peat (cm)	0.146	-0.194	0.153	0.481	0.248	0.344
Thickness of fen peat (cm)	0.168	0.131	-0.337	0.362	0.750	-0.596
Total thickness of peat (cm)	0.662	-0.133	0.658	0.416	0.854	-0.405
Absolute altitude of mire surface (m)	-0.079	-0.486	-0.357	0.647	0.153	0.908
Drainage ditch depth (cm)	0.075	0.146	0.263	-0.601	-0.376	0.896
Gradient of drainage ditch (m/km)	-0.191	-0.390	0.245	-0.268	0.284	-0.925
Minimum water level (cm)	0.838	-0.265	0.466	0.823	0.275	0.856
Average water level (cm)	0.758	-0.350	0.316	0.888	0.228	0.896
Maximum water level (cm)	0.535	-0.287	0.197	0.829	0.186	0.570
Water temperature (ºC)	0.647	-0.334	0.775	0.273	0.638	-0.184
Soil temperature at 20 cm depth (ºC)	0.632	0.016	0.662	-0.034	0.579	-0.493
Saturation of peat water with dissolved O_2 (%)	-0.558	-0.015	-0.343	-0.560	0.501	-0.545
Peat water conductivity (μS/cm^2)	-0.346	0.440	-0.158	-0.475	-0.689	0.586
Peat water pH	-0.269	0.798	-0.085	0.148	0.695	-0.436
Content of ash in soil (%)	-0.475	0.212	-0.139	0.117	-0.717	-0.014
Years since drainage began	0.008	0.007	-0.448	0.030	0.486	0.707
Variables of vegetation						
Total number of species	0.581	0.387	0.572	0.422	0.615	-0.005
Number of shrub layer species	-0.363	0.768	0.030	-0.319	0.645	-0.093
Number of ground vegetation species	0.798	0.030	0.604	0.473	0.532	0.041
Number of field layer species	0.494	0.079	-0.160	0.669	-0.738	0.169
Number of bottom vegetation species	0.713	0.003	0.709	0.257	0.780	-0.036
Number of moss layer species	0.686	0.051	0.622	0.503	0.772	0.146
Number of bog-specific species	0.940	-0.197	0.646	0.617	0.507	0.548
Percentage of bog-specific species (%)	0.819	-0.363	0.324	0.525	-0.271	0.574
Number of fen-specific species	-0.303	0.841	0.055	-0.596	-0.139	0.505
Percentage of fen-specific species (%)	-0.404	0.754	-0.008	-0.760	-0.190	0.486
Sum of tree girths (cm)	-0.841	0.113	-0.851	0.079	-0.814	-0.093
Sum of tree heights (m)	-0.839	0.155	-0.787	-0.001	-0.800	-0.106
Tree layer height from LIDAR data (m)	-0.898	0.046	-0.857	0.136	-0.407	0.586
Tree layer cover from LIDAR data (m^2/m^2)	-0.828	0.030	-0.863	-0.009	-0.827	0.424
Canopy closure of tree layer	-0.898	-0.018	-0.423	-0.075	-0.425	-0.080
Number of shrub stems and tree saplings	0.080	0.817	-0.648	0.116	0.019	-0.050
Sum of shrub layer stem heights (m)	-0.083	0.826	-0.574	-0.584	-0.768	0.133
Total cover of shrub layer (%)	-0.077	0.793	-0.470	-0.752	-0.417	0.326
Total cover of field layer (%)	0.568	0.140	-0.183	0.641	-0.172	0.131
Total cover of moss layer (%)	0.565	-0.588	0.054	0.942	0.412	-0.188
Total cover of *Sphagnum* species (%)	0.755	-0.355	0.245	0.842	0.539	-0.067
Total cover of lichens (%)	0.364	-0.043	0.667	-0.039	0.471	0.084

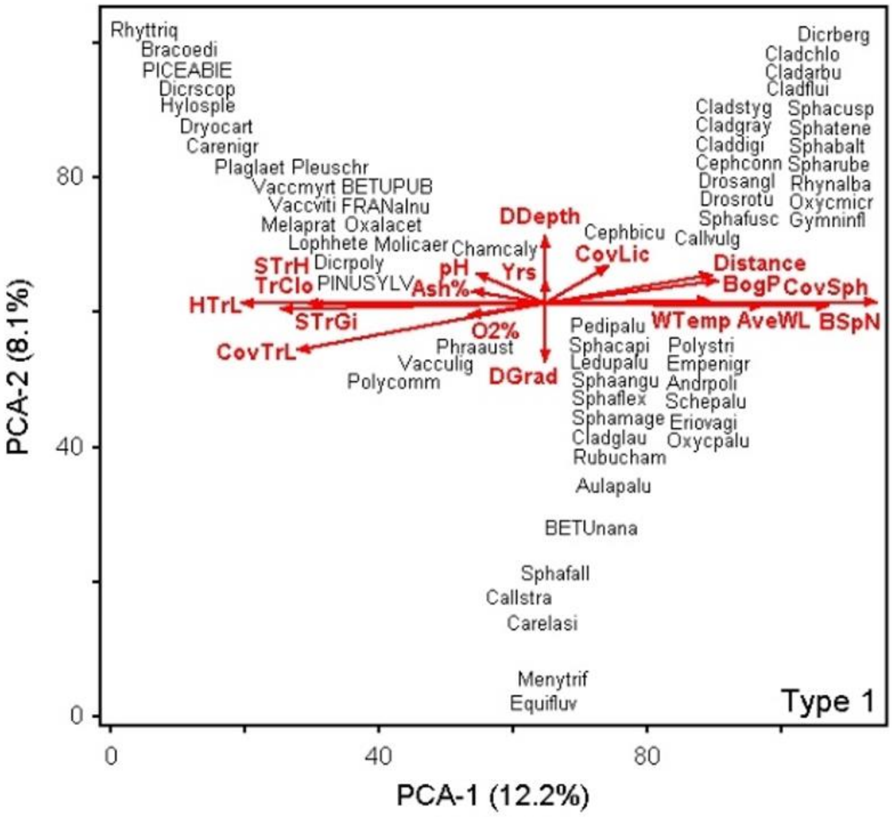

Figure 4. Ordination biplot of main vegetation structure and environmental variables in bogs with drainage type 1. Key to variables (in red): Dist = distance from the drainage ditch; DDepth = depth of drainage ditch (m); DGrad = gradient of drainage ditch (m km^{-1}), BotN = number of field and moss layer species; STrG = sum of tree girths, HTrL = tree layer average height (m) from LIDAR data, SShrH = sum of shrub stem heights (m); CovSph = total cover (%) of *Sphagnum* species; BSpN = number of bog-specific species; BogP, Peat = thickness of bog peat and total peat layer (m); pH = peat water pH; Cond = peat water conductivity (µS cm^{-2}); Ash% = percent of ash content in peat; MinWL, AveWL = minimum and average water level (cm). Full names of the plant species (in black) are presented in Table 4.

by drainage because of the location of the ditch. For this reason, the effects of cutoff ditches on the measured variables cannot be estimated directly. This problem could have been averted by including 3–4 undrained raised bogs in the study but, unfortunately, there are no longer any comparable undrained bogs of radius at least 400–500 metres in Estonia. Without undrained sites for comparison, it is still feasible to arrive at a useful assessment of the extent of drainage ditch impact in bogs with drainage type 2 by comparing results between bogs with drainage types 1 and 2, and we may thus also gain further insights about the type 1 situation.

In bogs with drainage types 1 and 2 the maximum water level has already stabilised 20–25 metres from the ditch, but the average and minimum water levels are affected up to distances of at least 440 metres (Figure 7). The similarity in extension of the drainage effect amongst bogs belonging to these two different drainage types could result from a strong drainage effect inducing subsidence which leads to development of a secondary bog slope, and thus suppresses the natural gradient. In bogs with old (type 3) drainage, the depth of the water level below the ground surface is no longer dependent on distance from the ditch.

In bogs with drainage type 2, dissolved oxygen content decreases rapidly over the first 200 metres of the transects but changes only very slowly thereafter. Peat water EC changes in a rather similar manner (Figure 8). This is clear evidence that precipitation water has only limited capacity to infiltrate in the near-ditch zone, due to the increased slope and peat bulk density, whereas infiltration can occur easily in more distant zones.

Water level drawdown and the associated changes in physicochemical factors have led to remarkable changes in vegetation. In bogs with drainage type 1,

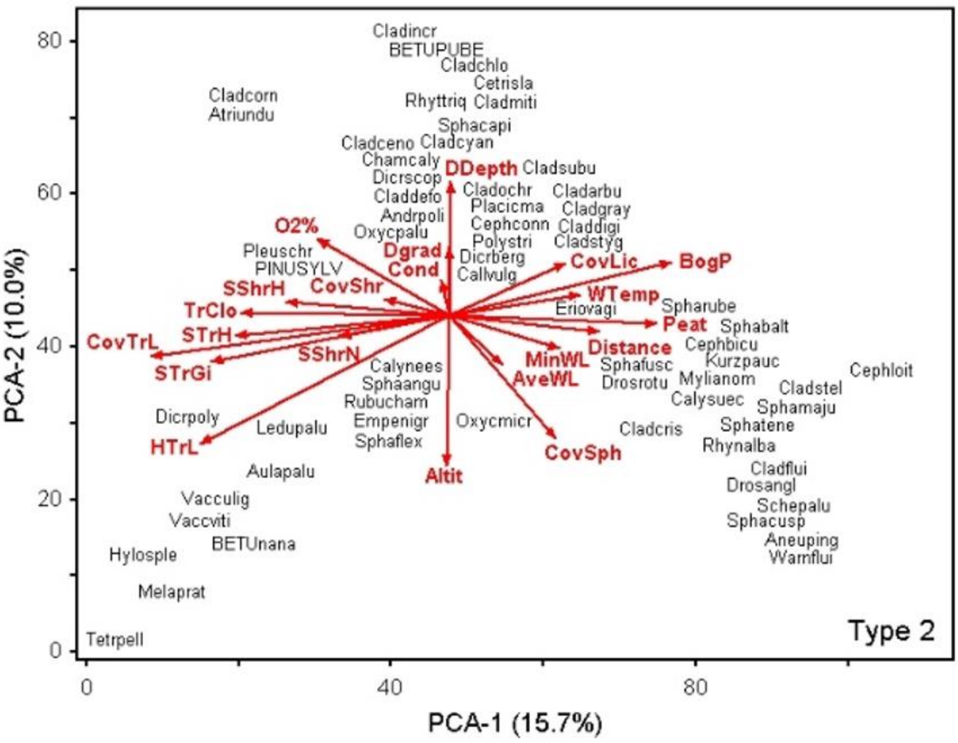

Figure 5. Ordination biplot of main vegetation structure and environmental variables in bogs with drainage type 2. Labels as in Figure 4.

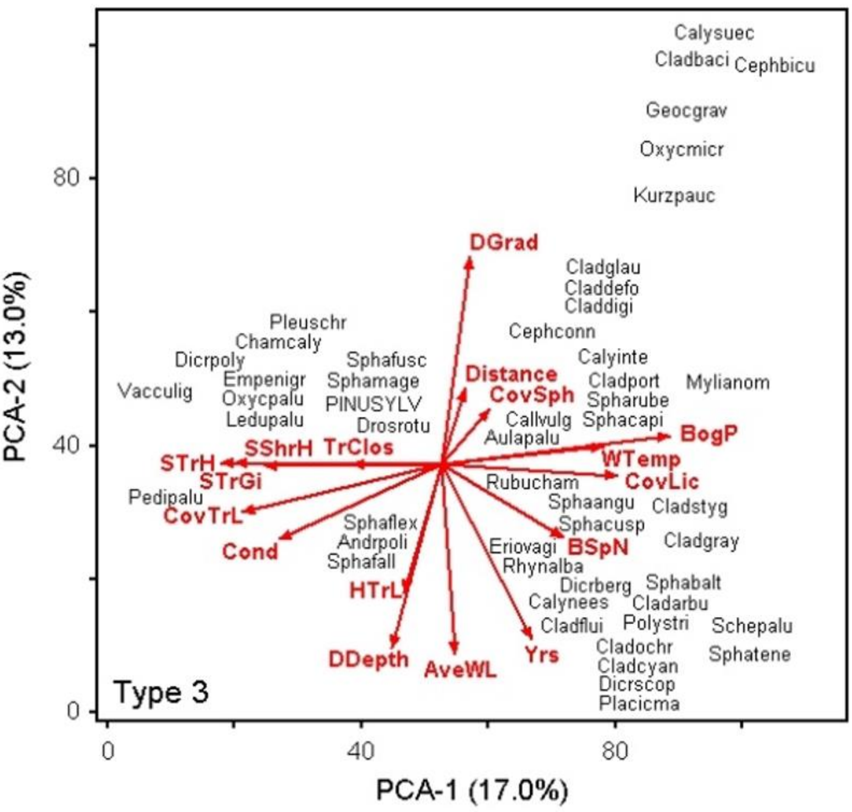

Figure 6. Ordination biplot of the main vegetation structure and environmental variables in bogs with drainage type 3. Labels as in Figure 4.

Table 2. Spearman rank order correlation coefficients of the distance from drainage ditch and water level characteristics with other variables. Notations: Dist = distance from drainage ditch; Min WL, Ave WL, Max WL = minimum, average and maximum water level, respectively.

Variable	Drainage type								
	1 ($p_{0.05} > 0.28$)			2 ($p_{0.05} > 0.38$)			3 ($p_{0.05} > 0.54$)		
	Dist	Min WL	Ave WL	Dist	Min WL	Ave WL	Dist	Min WL	Ave WL
Variables of habitats and environment									
Distance from ditch (m)	1.00	0.83	0.84	1.00	0.89	0.86	1.00	0.16	0.11
Thickness of bog peat (cm)	0.88	0.75	0.74	0.48	0.51	0.49	0.21	-0.25	-0.27
Thickness of transitional mire peat (cm)	0.18	0.25	0.18	0.36	0.42	0.47	0.35	0.46	0.50
Thickness of fen peat (cm)	0.10	0.07	0.04	0.25	0.16	0.08	0.38	-0.24	-0.31
Total thickness of peat (cm)	0.74	0.66	0.61	0.64	0.57	0.47	0.40	-0.25	-0.30
Absolute altitude of mire surface (m)	0.11	0.18	0.12	0.36	0.38	0.44	0.23	0.84	0.83
Drainage ditch depth (cm)	0.03	0.19	0.14	-0.06	-0.13	-0.21	0.00	0.84	0.84
Gradient of drainage ditch (m/km)	-0.12	-0.20	-0.17	0.00	0.17	0.23	0.00	-0.84	-0.84
Content of ash in soil (%)	-0.67	-0.60	-0.55	-0.09	0.04	0.11	-0.03	0.18	0.19
Minimum water level (cm)	0.83	1.00	0.91	0.89	1.00	0.96	0.16	1.00	0.95
Average water level (cm)	0.84	0.91	1.00	0.86	0.96	1.00	0.11	0.95	1.00
Maximum water level (cm)	0.63	0.64	0.79	0.60	0.74	0.85	0.34	0.60	0.67
Water temperature (ºC)	0.63	0.66	0.66	0.67	0.74	0.71	0.20	0.07	0.04
Saturation of peat water with dissolved O_2 (%)	-0.43	-0.68	-0.56	-0.80	-0.84	-0.83	-0.31	-0.25	-0.27
Peat water conductivity (µS/cm^2)	-0.31	-0.42	-0.36	-0.51	-0.54	-0.57	-0.12	0.34	0.40
Peat water pH	-0.15	-0.16	-0.20	0.26	0.22	0.24	-0.20	-0.21	-0.28
Soil temperature at 20 cm depth (ºC)	0.52	0.61	0.59	0.51	0.38	0.35	0.45	-0.34	-0.34
Years since drainage began	0.00	-0.12	-0.11	0.10	0.06	0.06	0.00	0.58	0.54
Variables of vegetation									
Total number of species	0.37	0.29	0.22	0.38	0.42	0.38	0.45	0.07	0.05
Number of shrub layer species	-0.41	-0.36	-0.37	-0.10	-0.08	-0.11	0.53	0.02	-0.07
Number of ground vegetation species	0.64	0.55	0.49	0.44	0.45	0.40	0.39	-0.01	0.00
Number of field layer species	0.29	0.28	0.25	0.23	0.41	0.39	0.03	-0.10	-0.07
Number of field and moss vegetation species	0.61	0.52	0.48	0.36	0.31	0.27	0.36	0.07	0.04
Number of moss layer species	0.59	0.49	0.46	0.49	0.50	0.47	0.40	0.31	0.27
Number of bog-specific species	0.86	0.80	0.80	0.79	0.77	0.69	0.34	0.45	0.51
Percentage of bog-specific species (%)	0.80	0.78	0.80	0.78	0.72	0.67	-0.12	0.51	0.60
Number of fen-specific species	-0.62	-0.53	-0.54	-0.19	-0.32	-0.36	0.20	0.25	0.39
Percentage of fen-specific species (%)	-0.68	-0.59	-0.59	-0.23	-0.36	-0.40	0.21	0.23	0.37
Sum of tree girths (cm)	-0.85	-0.69	-0.72	-0.68	-0.62	-0.50	-0.37	-0.11	-0.10
Sum of tree heights (m)	-0.87	-0.70	-0.73	-0.68	-0.63	-0.51	-0.40	-0.12	-0.10
Tree layer height from LIDAR data (m)	-0.87	-0.86	-0.81	-0.54	-0.42	-0.37	-0.48	0.37	0.38
Tree layer cover from LIDAR data (m^2/m^2)	-0.77	-0.78	-0.70	-0.74	-0.58	-0.50	-0.43	0.09	0.15
Canopy closure of tree layer	-0.81	-0.66	-0.69	-0.58	-0.37	-0.24	-0.33	-0.16	-0.14
Number of shrub stems and tree saplings	-0.14	-0.18	-0.17	-0.15	-0.14	-0.12	0.10	0.13	0.08
Sum of shrub layer stem heights (m)	-0.29	-0.32	-0.28	-0.45	-0.49	-0.48	-0.17	0.04	0.07
Total cover of shrub layer (%)	-0.16	-0.20	-0.19	-0.44	-0.54	-0.53	0.18	0.38	0.42
Total cover of field layer (%)	0.35	0.29	0.31	0.02	0.04	0.03	-0.12	-0.13	-0.12
Total cover of moss layer (%)	0.52	0.59	0.62	0.65	0.68	0.68	0.37	0.05	-0.02
Total cover of *Sphagnum* species (%)	0.60	0.69	0.72	0.79	0.77	0.72	0.43	0.21	0.18
Total cover of lichens (%)	0.55	0.44	0.41	0.39	0.29	0.23	0.37	-0.04	-0.06

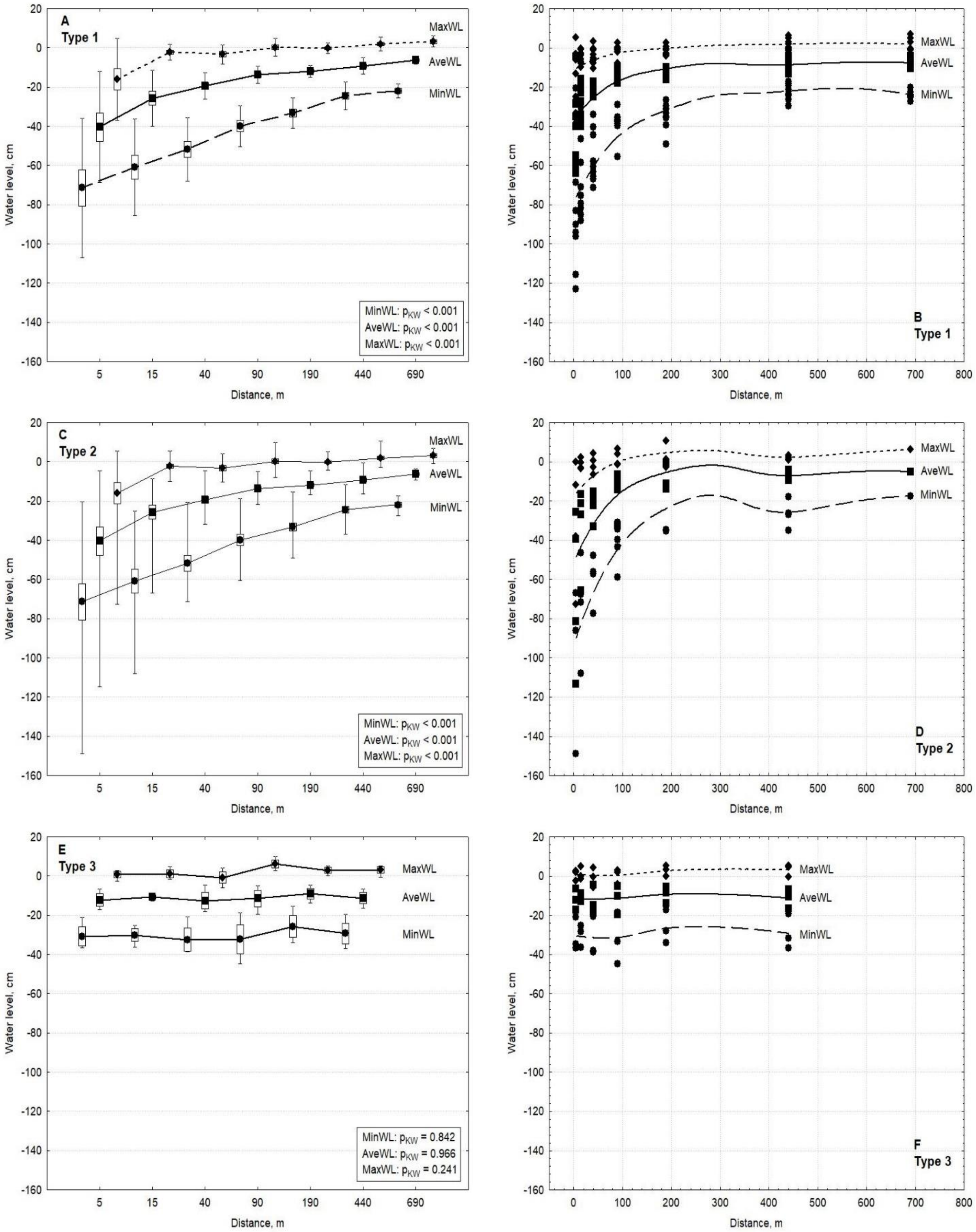

Figure 7. Relationships between distance from the drainage ditch and water level characteristics in bogs with different drainage types. Key to box and whisker graphs (left): MinWL, AveWL, MaxWL = minimum, average and maximum water level, respectively; black squares indicate mean values; boxes show standard error of mean; whiskers are minimum–maximum ranges; and p_{KW} is the significance level of the Kruskal-Wallis median test. The regression lines in the right-hand graphs are fitted by the distance-weighted least squares regression (DWLDR) method.

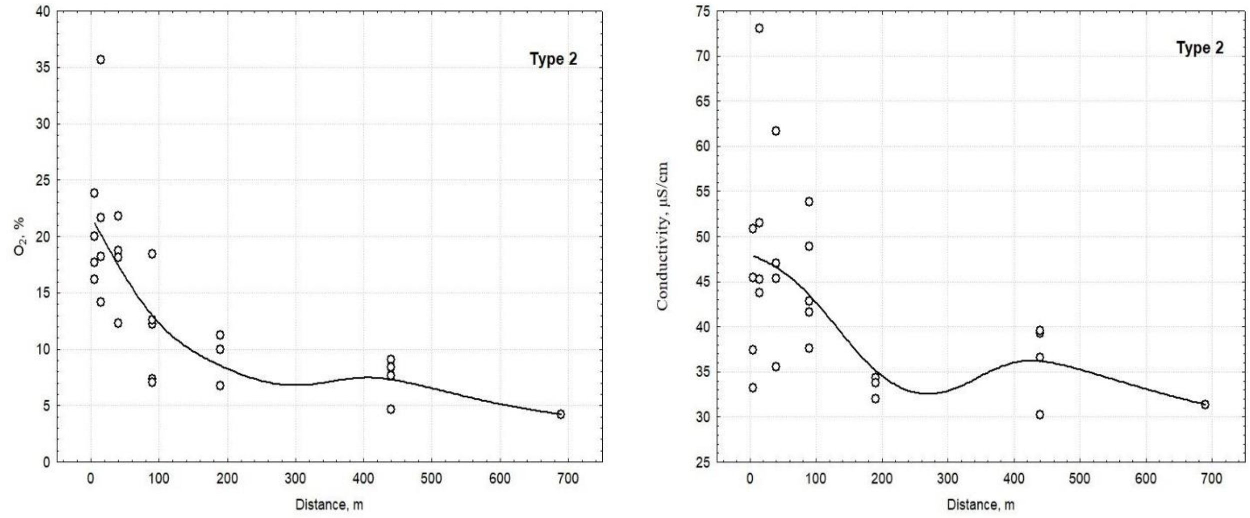

Figure 8. Change of dissolved oxygen content (A) and electrical conductivity (B) in peat water in bogs with drainage type 2. Regression lines are fitted by the DWLDR method.

total cover of the shrub layer is very low and depends only slightly on the minimum water level (MinWL), whereas total cover of the field layer increases from 0 % to almost 80 % in response to a rise of MinWL to -40 cm and total cover of *Sphagnum* mosses increases from 0 % to 90–100 % when MinWL rises to -20 cm (Figure 9A,B). In bogs with drainage type 2, total cover of the shrub layer decreases and total cover of *Sphagnum* species increases almost linearly as MinWL rises to -40 cm, while the total cover of field layer species stabilises at MinWL -100 cm (Figure 9D). In bogs with drainage type 3, only some single specimens of *Salix* sp. were recorded in the shrub layer, whereas total cover of the field layer and of *Sphagnum* species is 80–90 % everywhere (Figure 9E).

Trees almost disappear when MinWL is higher than -20 cm. The number of bog-specific species starts to increase rapidly if MinWL is closer to the surface than -90 cm, while the number of fen-specific species in these bogs is always low and, therefore, has a minute variance (Figure 10).

A detailed analysis of the drainage effect along the distance gradient reveals that a decrease of tree layer canopy cover based on LIDAR data is detectable up to 300 m from the ditch in bogs with drainage types 1 and 2 (Figure 11B,D). The other tree layer characteristics (tree layer height from LIDAR data, sum of tree girths, sum of tree heights, canopy closure of tree layer) follow the same pattern.

The extent of the drainage effect on other vegetation layers is of somewhat constrained magnitude, e.g., in bogs with drainage types 1 and 2, total cover of the field layer increases steeply over a distance of up to 250–300 metres from the drainage ditch while the total cover of *Sphagnum* species continues to increase until 300 metres from the drainage ditch (Figure 12A,B,C,D).

Comparison of the whole species complement at sample nodes along the transects using the multi-response permutation procedure ascertains that, in bogs with drainage type 1, the vegetation does not differ significantly between any neighbouring pairs of sample nodes up to 190 m from the beginning of the transect, whereas in nodes situated farther apart the species composition is reliably dissimilar (Table 3). In bogs with drainage type 2, only maximally separated sample nodes show any dissimilarity in species composition, while in bogs with drainage type 3 the species composition is already so homogeneous that no significant differences between sample nodes appear.

The indicator species analysis enables a good overview of how species composition and abundance changes along the hydrosequence. In bogs with drainage type 1, significant indicator species in the first sample node (5 m from the cutoff ditch) are common forest species such as: *Dicranum scoparium*, *D. polysetum*, *Brachythecium oedipodium* and *Lophocoelea heterophylla* in the moss layer; *Melampyrum pratense*, *Vaccinium vitis-idaea*, *V. myrtillus*, *Carex nigra*, *Molinea caerulea* and *Dryopteris carthusiana* in the field layer; *Betula pubescens* regrowth in the shrub layer; and *Betula pubescens*, *Pinus sylvestris* and *Picea abies* in the tree layer (Table 4). At the next sample node, 15 m from the drainage ditch, *Picea abies* regrowth has a significant indicator value. Other characteristic

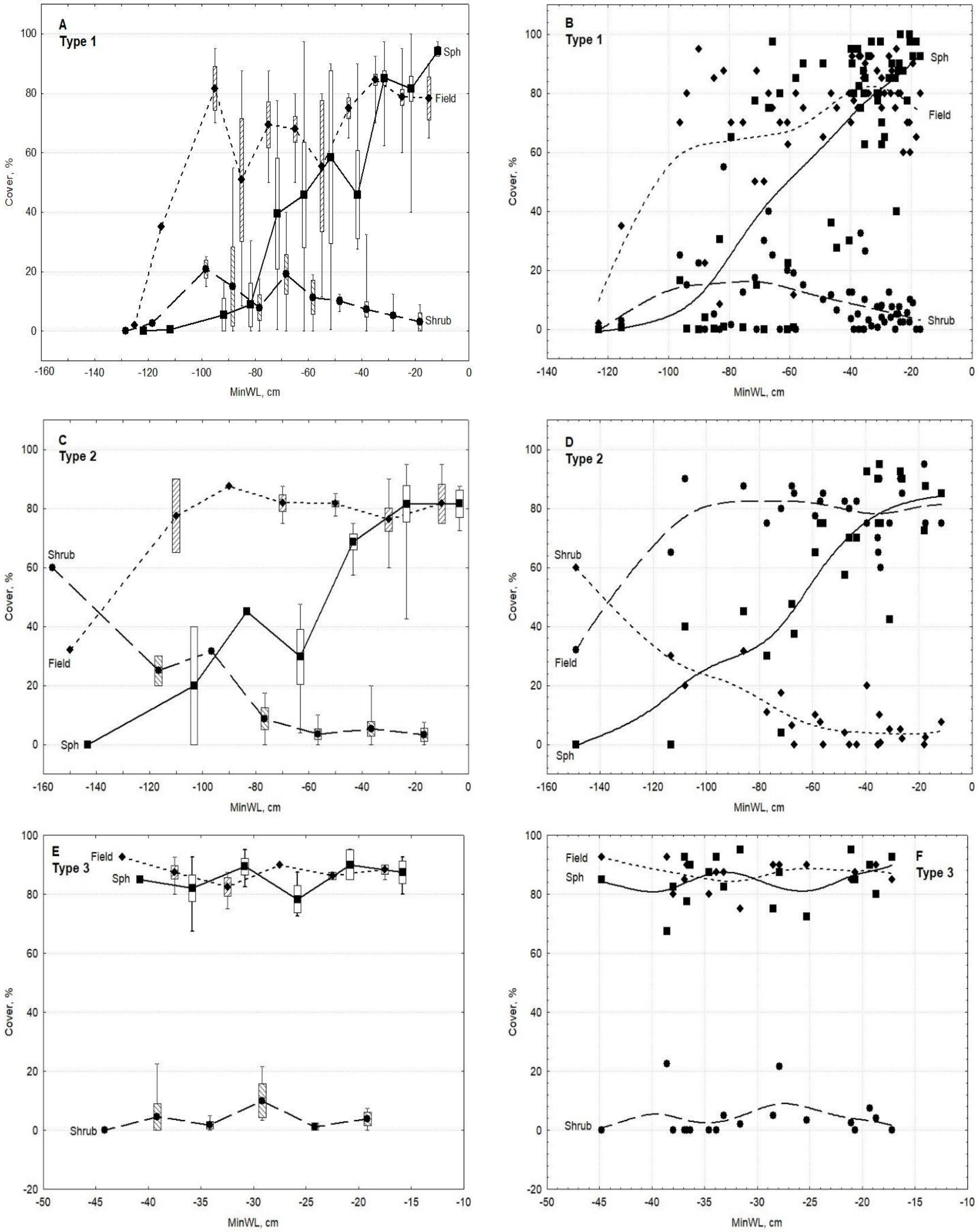

Figure 9. Dependency of the total percentage cover of the shrub and field layers, and *Sphagnum* (Sph) species, on the minimum water level (MinWL); merged data. Plotting methods as in Figure 7.

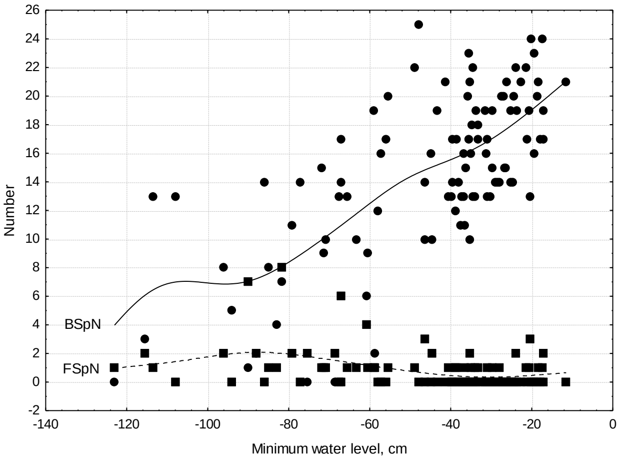

Figure 10. Dependency of the number of bog-specific species (BSpN) and the number of fen-specific species (FSpN) on the minimum water level. Merged data, DWLSR method.

species are: *Frangula alnus* in the shrub layer; *Phragmites australis* and *Oxalis acetosella* in the field layer; and *Hylocomium splendens*, *Pleurozium schreberi*, *Rhytidiadelphus triquetrus*, *Polytrichum commune* and *Calliergon stramineum* in the moss layer.

At the sample nodes 40 m and 90 m from the ditch the highest indicator values are already shown by typical mire species such as: *Carex lasiocarpa*, *Oxycoccus palustris*, *Ledum palustre*, *Rubus chamaemorus*, *Empetrum nigrum*, *Vaccinium uliginosum* in the field layer; and *Sphagnum angustifolium*, *S. flexuosum* and *S. magellanicum* in the moss layer. The lichen species *Cladonia glauca* also comes forward as an indicator species here.

On the mire expanse, 190 m and more from the cutoff ditch, a large part of the surface usually consists of low wet hollows where the field layer is dominated by *Equisetum fluviatile*, *Scheuchzeria palustris* and *Rhynchospora alba*, while *Sphagnum capillifolium*, *S. tenellum*, *S. balticum*, *S. cuspidatum* and *S. fallax* are characteristic in the moss layer. On hummocks *Sphagnum fuscum* becomes a typical species in the moss layer. At 440 m from the ditch, *Drosera rotundifolia*, *D. anglica* and the IUCN European Red List leafy liverwort *Mylia anomala* have significant indicator values (Table 4).

At the last sample node, 690 m from the ditch, the bryophytes *Cephalozia connivens*, *Sphagnum rubellum* and *Dicranum bergeri* emerge as significant indicator species; other typical species are *Cladopodiella fluitans*, *Kurzia pauciflora* and *Plagiothecium laetum*, the dwarf shrub *Calluna vulgaris*, and several lichens such as *Cladonia stygia*, *C. grayi*, *C. digitata* and *Cladina arbuscula* (Table 4). These species can be regarded as indicators of natural (undisturbed) mires.

The vegetation structure, characterised on the basis of percent bog-specific and fen-specific species, stabilises at a distance of 190–200 m from the ditch (Figure 13A,B).

In bogs with drainage type 2, although only *Dicranum polysetum* has a significant indicator value at distance 5 m from the drainage ditch, the relative abundance of species changes with increasing distance from the ditch. At 5–15 m, common bryophytes of forests such as *Dicranum polysetum*, *D. scoparium*, *Atrichum undulatum*, *Pleurozium schreberi*, *Hylocomium splendens* and *Rhytidiadelphus triquetrus* as well as the lichens *Cladonia cenotea* and *C. cornuta* are relatively abundant; and *Sphagnum capillifolium* is present at the second sample node (Table 4). At 40 m from the ditch, the vascular plants *Empetrum nigrum*, *Rubus chamaemoru*s, *Melampyrum pratense*, *Vaccinium vitis-idaea* and *Oxycoccus microcarpus*, along with the moss *Sphagnum flexuosum* and the lichens *Cladonia deformis*, *C. subulata*, *C. ochrochlora* and *Placynthiella icmalea* display their highest relative abundances. Particularly noteworthy are the high relative abundances of numerous lichens such as *Cladonia grayi*, *C. digitata*, *C. mitis*, *C. cyanipes*, *C. chlorophaea* and *Cetraria islandica* at distance 90 m from the ditch; and *Cladonia crispata*, *C. stygia*, *C. stellaris*, *C. arbuscula* and *C. floerkeana* at distance 190 m from the ditch and beyond. In these bogs the species content stabilises about 190 m from the drainage ditch (Figure 13C,D). At distance 440 m and farther from the ditch some bog hollows can occur and we associate with them the appearance of *Sphagnum cuspidatum*, *Rhynchospora alba* and *Scheuchzeria palustris* (Table 4).

As shown above, in (drainage type 3) bogs with an old collapsed ditch, the gradient caused by drainage has disappeared and we found no significant indicator species differentiating between sample nodes along the transect; i.e., most of the species recorded are represented along the whole length of the transect. This situation is well illustrated in Figure 13E,F which shows, moreover, that in these bogs we can no longer estimate the extent of the drainage effect in metres. Nevertheless, a gradual change in species indicator values is clear from the data in Table 4. At 5 m from the ditch, the species with the highest indicator values are the bryophytes *Sphaghum magellanicum*, *S. balticum* and *Pleurozium schreberi* along with the vascular plants *Oxycoccus palustris* and *Pinus sylvestris*. At 15 m from the ditch several other cryptogams (*Calypogeia*

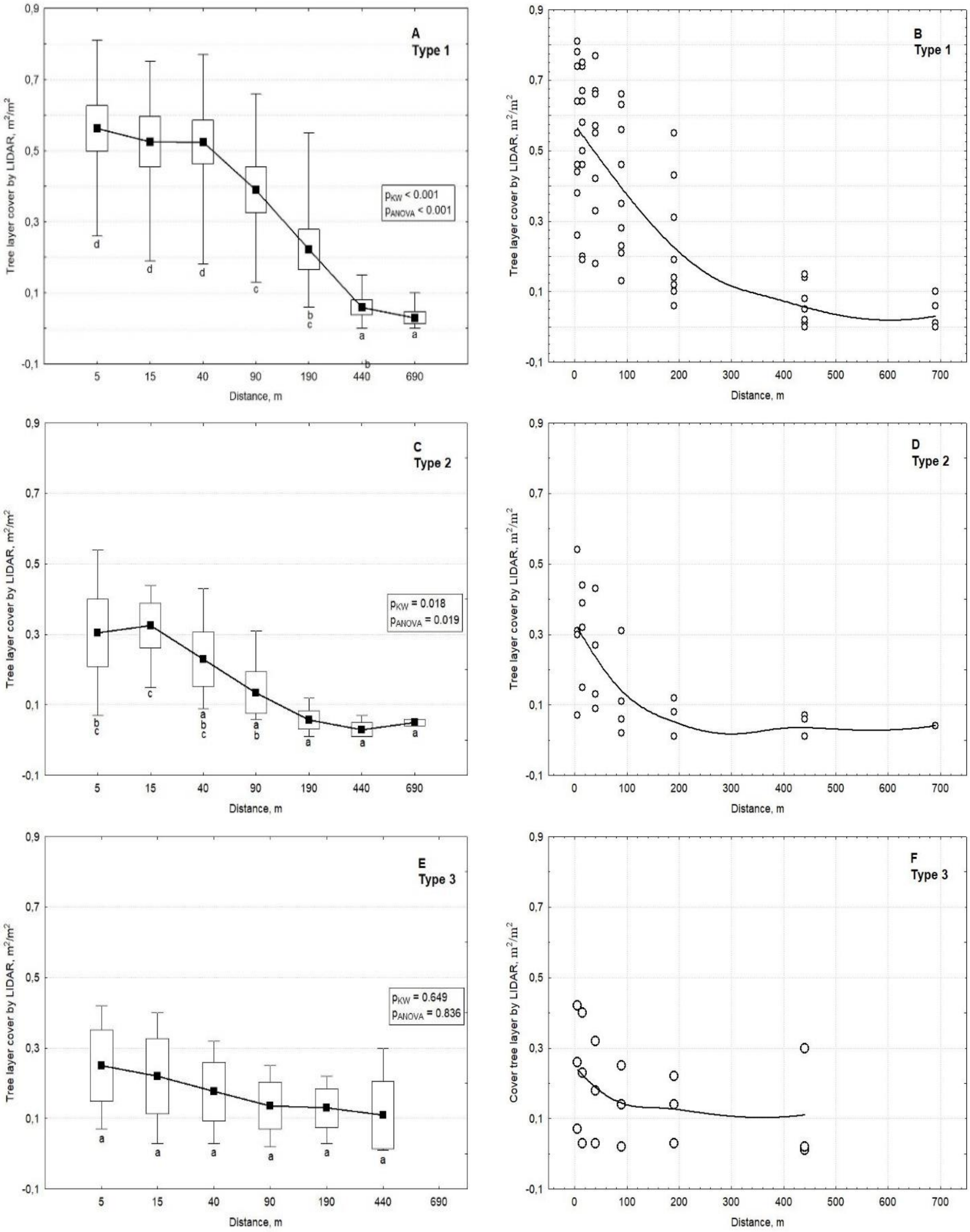

Figure 11. Dependency of tree layer canopy cover from LIDAR data on distance from the drainage ditch. Plotting methods as in Figure 7.

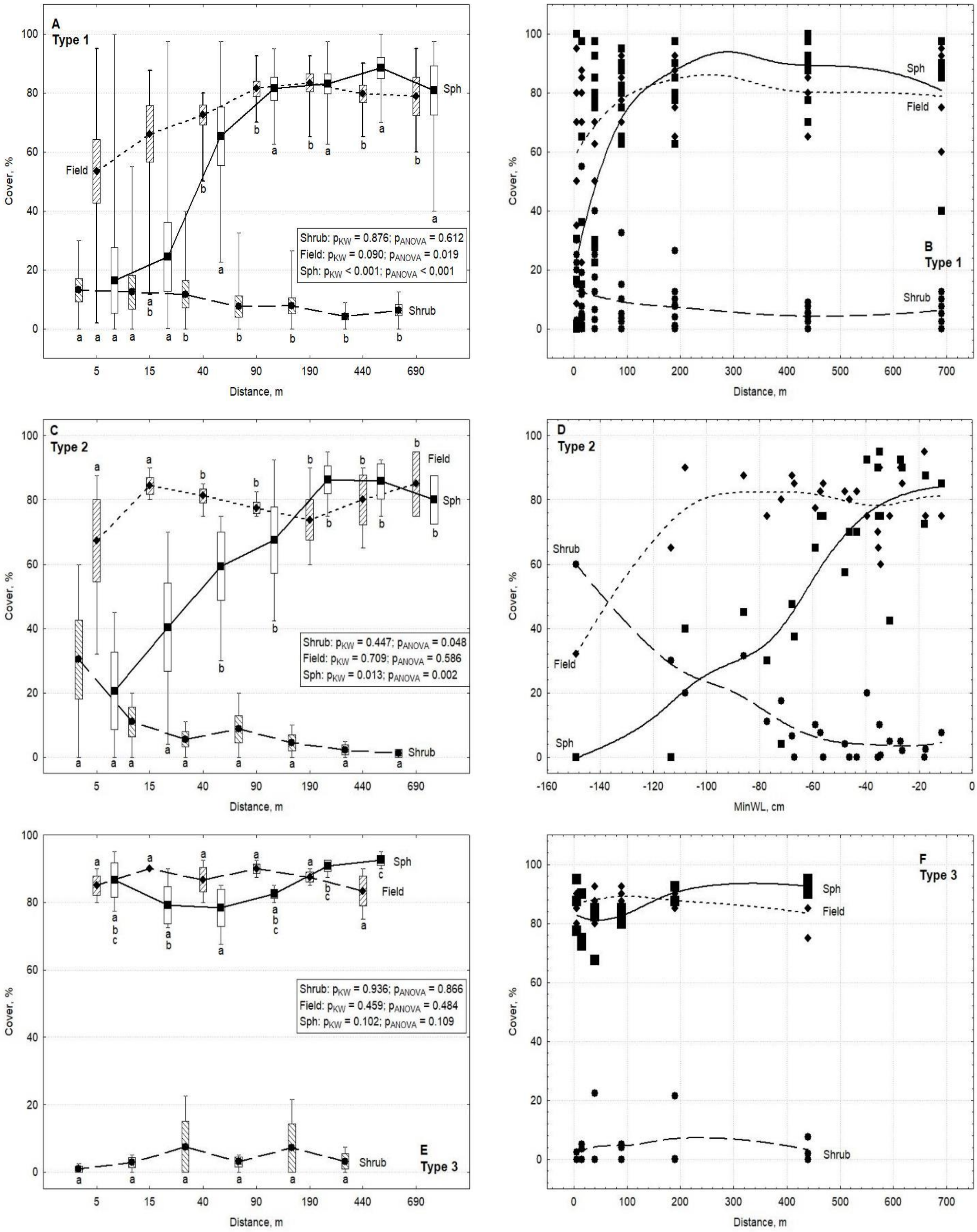

Figure 12. Dependency of the total cover of different vegetation layers on distance from the drainage ditch. Plotting methods as in Figure 7. Sph = *Sphagnum*.

Table 3. Significance level of species content similarity in sampling nodes determined by the multi-response permutations procedures.

Distances from ditch of compared sampling nodes (m)	Drainage type		
	1	2	3
5 *vs*. 15	0.979	0.801	0.576
5 *vs*. 40	0.041	0.400	0.413
5 *vs*. 90	0.002	0.143	0.596
5 *vs*. 190	0.001	0.075	0.385
5 *vs*. 440	0.001	0.013	0.157
5 *vs*. 690	0.001	0.030	-
15 *vs*. 40	0.195	0.744	0.797
15 *vs*. 90	0.006	0.427	0.842
15 *vs*. 190	< 0.000	0.278	0.870
15 *vs*. 440	< 0.000	0.088	0.872
15 *vs*. 690	< 0.000	0.222	-
40 *vs*. 90	0.756	0.500	0.873
40 *vs*. 190	0.003	0.404	0.515
40 *vs*. 440	< 0.001	0.296	0.680
40 *vs*. 690	0.001	0.396	-
90 *vs*. 190	0.335	0.883	0.741
90 *vs*. 440	0.061	0.428	0.846
90 *vs*. 690	0.060	0.855	-
190 *vs*. 440	0.431	0.897	0.827
190 *vs*. 690	0.831	0.975	-
440 *vs*. 690	0.903	0.905	-

integristipula, *C. neesiana*, *Dicranum polysetum*, *D. scoparium*, *Cladonia ochrochlora* and *Placynthiella icmalea*) have the highest relative abundance.

The lichens *Cladonia cyanipes* and *C. sulphurina* occur only at the third sample node, 40 m from the ditch. Here *Eriophorum vaginatum*, *Polytrichum strictum*, *Sphagnum capillifolium*, *Cladonia portentosa* and *Betula pubescens* regrowth have the highest abundance. *Scheuchzeria palustris* and *Pohlia* sp. appear 90 m from the ditch, while *Dicranum bergeri*, *Cladonia grayi*, *Cladina arbuscula*, *Cladina stygia*, *Sphagnum tenellum* and *Scheuchzeria palustris* are distinguished by their relative abundance.

Several raised bog species such as *Oxycoccus microcarpus*, *Andromeda polifolia*, *Ledum palustre*, *Empetrum nigrum*, *Sphagnum angustifolium*, *Cladonia deformis*, *C. digitata* and *C. glauca* are added to the species complement at the node located 190 m from the ditch, where the highest abundance of *Rhynchospora alba* is recorded in hollows (Table 4).

DISCUSSION

The extent of the effects of ditches on the physical and chemical properties - as well as on the biota - of drained bogs is a function of distance from the drains, but depends additionally on numerous collinear variables and circumstances. At landscape scale, essential factors are the mire type (Laiho & Laine 1994, Miller 2011), the slope of the mire surface (Stewart & Lance 1991) and its subsidence (Laine *et al*. 1995, Silins & Rothwell 1998), the slope/gradient and depth of drainage ditches (Pienimäki 1982, Brække 1983) and the distance between them (Ahti 1980, Belleau *et al*. 1992, Holden *et al*. 2004). The time since drainage commenced (Vasander 1987a, 1987b; Brække 1983, Minkkinen *et al*. 1999, Laiho *et al*. 2003) and properties of the peat - its thickness (Pikk 2003, Padari & Kiviste 2005), decomposition rate (Laine & Laiho 1992), nutrient level (Pakarinen & Ruuhijärvi 1978, Laine & Vanha-Majamaa 1992, Korpela 2004 and porosity (Boelter 1972, Price & Whitehead 2001, Holden *et al*. 2004) - are also of great importance. Therefore, data indicating the range of drainage effects on environmental variables or vegetation characteristics in different regions or in mires of different types are usually rather divergent (Miller 2011).

Even estimates of drainage effects on the water table level, which can be measured quite simply, are often difficult to define and generalise because water levels vary greatly from one site to another (Landry & Rochefort 2012) as well as through time. For example, in North American forested peatlands, Berry & Jeglum (1991) reported that water table level increased with distance from a ditch and approached a nearly constant level 5–10 m from the ditch edge in black spruce peatlands in Ontario, whereas drainage affected the water level in forested peatlands in Quebec up to a distance of 15 m (Prévost *et al*. 1997), 30 m (Belleau *et al*. 1992) or 60 m (Poulin *et al*. 1999, Roy *et al*. 2000) from the ditches. In Minnesota (USA), Boelter (1972) found that ditches in a forested peatland had little effect beyond 50 m and

Table 4. Indicator species at the sampling nodes. The names of tree layer species are capitalised, for shrub layer species and saplings only the genus name is capitalised. Notations: Type 1, Type 2, Type 3 = bog drainage types; Max node = node where the species indicator value was maximal (nodes: 1 = 5 m, 2 = 15 m, 3 = 40 m, 4 = 90 m, 5 = 190 m, 6 = 440 m, 7 = 690 m from drainage ditch); p = significance level.

Type 1			Type 2			Type 3		
Species	Max node	p	Species	Max node	p	Species	Max node	p
Dicranum scoparium	1	0.002	*Dicranum polysetum*	1	0.054	*PINUS SYLVESTRIS*	1	0.428
Vaccinium vits-idaea	1	0.003	*PINUS SYLVESTRIS*	1	0.411	*Sphagnum magellanicum*	1	0.851
BETULA pubescens	1	0.007	*Aulacomnium palustre*	1	0.561	*Pleurozium schreberi*	1	0.876
Vaccinium myrtillus	1	0.011	*BETULA nana*	1	0.805	*Oxycoccus palustris*	1	0.946
Carex niga	1	0.023	*PINUS sylvestris*	1	0.869	*Sphagnum balticum*	1	0.986
BETULA PUBESCENS	1	0.039	*Dicranum scoparium*	1	0.976	*BETULA PUBESCENS*	1	1.000
PICEA ABIES	1	0.039	*Andromeda polifolia*	1	0.986	*QUERCUS robur*	1	1.000
Melampyrum pratense	1	0.049	*Atrichum undulatum*	1	1.000	*Angelica sylvestris*	1	1.000
Brachythecium oedipodium	1	0.052	*Tetraphis pellucida*	1	1.000	*Carex canescens*	1	1.000
Pohlia sp.	1	0.065	*Cladonia cenotea*	1	1.000	*Chamaedaphne calyculata*	1	1.000
Lophocoelea heteroühylla	1	0.076	*Cladonia cornuta*	1	1.000	*Dryopteris carthusiana*	1	1.000
Dicranum polysetum	1	0.166	*Pleurozium schreberi*	2	0.176	*Filipendula ulmaria*	1	1.000
Molinia caerulea	1	0.220	*Ledum palustre*	2	0.221	*Pedicularis palustris*	1	1.000
PINUS SYLVESTRIS	1	0.243	*Vaccinium uliginosum*	2	0.522	*Rubus caesius*	1	1.000
Tetraphis pellucida	1	0.317	*Sphagnum capillifolium*	2	0.524	*Rubus idaeus*	1	1.000
Dryopteris carthusiana	1	0.494	*Dicranum bergeri*	2	0.567	*Vaccinium uliginosum*	1	1.000
PICEA abies	2	0.042	*Oxycoccus palustris*	2	0.660	*Cephalozia loitlesbergeri*	1	1.000
Hylocomium splendens	2	0.074	*BETULA PUBESCENS*	2	0.811	*Climacium dendroides*	1	1.000
Phragmites australis	2	0.132	*BETULA pubescens*	2	0.848	*Plagiochila asplenioides*	1	1.000
Pleurozium schreberi	2	0.153	*Hylocomium splendens*	2	0.859	*Ptilium crista-castrensis*	1	1.000
FRANGULA alnus	2	0.260	*Jungermannia* sp.	2	1.000	*Sphagnum cuspidatum*	1	1.000
Polytrichum commune	2	0.614	*Rhytidiadelphus triquetrus*	2	1.000	*Sphagnum fallax*	1	1.000
Calliergon stramineum	2	0.861	*Cladonia incrassata*	2	1.000	*Sphagnum majus*	1	1.000
Rhytidiadelphus triquetrus	2	0.912	*Empetrum nigrum*	3	0.049	*Sphagnum russowii*	1	1.000
Oxalis acetosella	2	1.000	*Cladonia deformis*	3	0.167	*Sphagnum teres*	1	1.000
Calypogeia suecica	3	0.090	*Rubus chamaemorus*	3	0.193	*Sphagnum flexuosum*	2	0.498
Cladonia glauca	3	0.173	*Cladonia subulata*	3	0.226	*Calypogeia integristipula*	2	1.000
Sphagnum angustifolium	3	0.180	*Sphagnum flexuosum*	3	0.296	*Calypogeia neesiana*	2	1.000
Bryum sp.	3	0.199	*Melampyrum pratense*	3	0.488	*Dicranum polysetum*	2	1.000
Oxycoccus palustris	3	0.224	*Cladonia ochrochlora*	3	0.564	*Dicranum scoparium*	2	1.000
Sphagnum flexuosum	3	0.255	*Placynthiella icmalea*	3	0.649	*Cladonia ochrochlora*	2	1.000
Ledum palustre	3	0.384	*Vaccinium vits-idaea*	3	0.721	*Placynthiella icmalea*	2	1.000
Sphagnum magellanicum	3	0.658	*Oxycoccus microcarpus*	3	0.796	*Cladonia cyanipes*	3	0.121
Carex lasiocarpa	3	0.846	*Polytrichum strictum*	4	0.131	*Eriophorum vaginatum*	3	0.302
Rubus chamaemorus	4	0.172	*Pohlia* sp.	4	0.245	*Sphagnum capillifolium*	3	0.914
Empetrum nigrum	4	0.242	*Cladonia grayi*	4	0.312	*Polytrichum strictum*	3	0.941

Type 1			Type 2			Type 3		
Species	Max node	p	Species	Max node	p	Species	Max node	p
Vaccinium uliginosum	4	0.245	*Cladonia digitata*	4	0.334	*BETULA pubescens*	3	1.000
BETULA nana	4	0.640	*Cladonia mitis*	4	0.456	*Cladopodiella fluitans*	3	1.000
Cladonia ochrochlora	4	0.688	*Cladonia cyanipes*	4	0.812	*Cladonia portentosa*	3	1.000
Menyanthes trifoliata	4	0.948	*Cladonia chlorophaea*	4	0.815	*Cladonia sulphurina*	3	1.000
Gymnocolea infnflata	4	0.991	*Calluna vulgaris*	4	0.908	*Dicranum bergeri*	4	0.051
Chamaedaphne calyculata	4	0.996	*Cetraria islandica*	4	1.000	*Mylia anomala*	4	0.358
PINUS sylvestris	5	0.198	*Cladonia crispata*	5	0.112	*Cladonia grayi*	4	0.359
Sphagnum capillifolium	5	0.336	*Cladonia stygia*	5	0.213	*Cladonia arbuscula*	4	0.609
Calypogeia neesiana	5	0.543	*Cephalozia bicuspidata*	5	0.239	*Cladonia stygia*	4	0.686
Equisetum fluviatile	5	0.710	*Sphagnum majus*	5	0.267	*Drosera rotundifolia*	4	0.725
Drosera rotundifolia	6	0.008	*Sphagnum magellanicum*	5	0.273	*Bryum* sp.	4	0.895
Polytrichum strictum	6	0.013	*Cladonia stellaris*	5	0.283	*Sphagnum tenellum*	4	0.900
Drosera anglica	6	0.015	*Cladonia arbuscula*	5	0.721	*Scheuchzeria palustris*	4	1.000
Sphagnum tenellum	6	0.023	*Cephalozia connivens*	5	0.806	*Pohlia* sp.	4	1.000
Sphagnum fuscum	6	0.056	*Bryum* sp.	5	0.809	*Sphagnum angustifolium*	5	0.117
Sphagnum balticum	6	0.078	*Cladonia floerkeana*	5	1.000	*Andromeda polifolia*	5	0.493
Rhynchospora alba	6	0.080	*Drosera rotundifolia*	6	0.074	*Ledum palustre*	5	0.733
Andromeda polifolia	6	0.090	*Eriophorum vaginatum*	6	0.077	*PINUS sylvestris*	5	0.944
Scheuchzeria palustris	6	0.125	*Sphagnum fuscum*	6	0.112	*Empetrum nigrum*	5	0.970
Eriophorum vaginatum	6	0.196	*Sphagnum cuspidatum*	6	0.217	*Oxycoccus microcarpus*	5	1.000
Cephalozia bicuspidata	6	0.257	*Sphagnum tenellum*	6	0.263	*Rhynchospora alba*	5	1.000
Sphagnum cuspidatum	6	0.292	*Kurzia pauciflora*	6	0.293	*Cladonia deformis*	5	1.000
Mylia anomala	6	0.367	*Sphagnum balticum*	6	0.374	*Cladonia digitata*	5	1.000
Cladonia chlorophaea	6	0.452	*Rhynchospora alba*	6	0.611	*Cladonia glauca*	5	1.000
Aulacomnium palustre	6	0.607	*Calypogeia suecica*	6	0.863	*Kurzia pauciflora*	6	0.017
Oxycoccus microcarpus	6	0.639	*Cephalozia loitlesbergeri*	6	1.000	*Calypogeia suecica*	6	0.320
Pedicularis palustris	6	0.688	*Aneura pinguis*	7	0.240	*Aulacomnium palustre*	6	0.399
Sphagnum fallax	6	0.963	*Warnstorfia fluitans*	7	0.240	*Rubus chamaemorus*	6	0.414
Cephalozia connivens	7	0.002	*Sphagnum rubellum*	7	0.244	*Sphagnum fuscum*	6	0.516
Sphagnum rubellum	7	0.024	*Mylia anomala*	7	0.411	*Cephalozia connivens*	6	0.570
Dicranum bergeri	7	0.038	*Scheuchzeria palustris*	7	0.483	*Calluna vulgaris*	6	0.824
Cladopodiella fluitans	7	0.076	*Drosera anglica*	7	0.566	*Sphagnum rubellum*	6	0.916
Cladonia stygia	7	0.076	*Cladopodiella fluitans*	7	0.574	*Barbilophozia attenuata*	6	1.000
Kurzia pauciflora	7	0.077	*Chamaedaphne calyculata*	7	0.643	*Cephalozia bicuspidata*	6	1.000
Cladonia arbuscula	7	0.147	*Calypogeia neesiana*	7	0.678	*Geocalyx graveolens*	6	1.000
Calluna vulgaris	7	0.209	*Sphagnum angustifolium*	7	0.982	*Cladonia bacillaris*	6	1.000
Cladonia grayi	7	0.415						
Plagiothecium laetum	7	0.521						
Cladonia digitata	7	0.562						

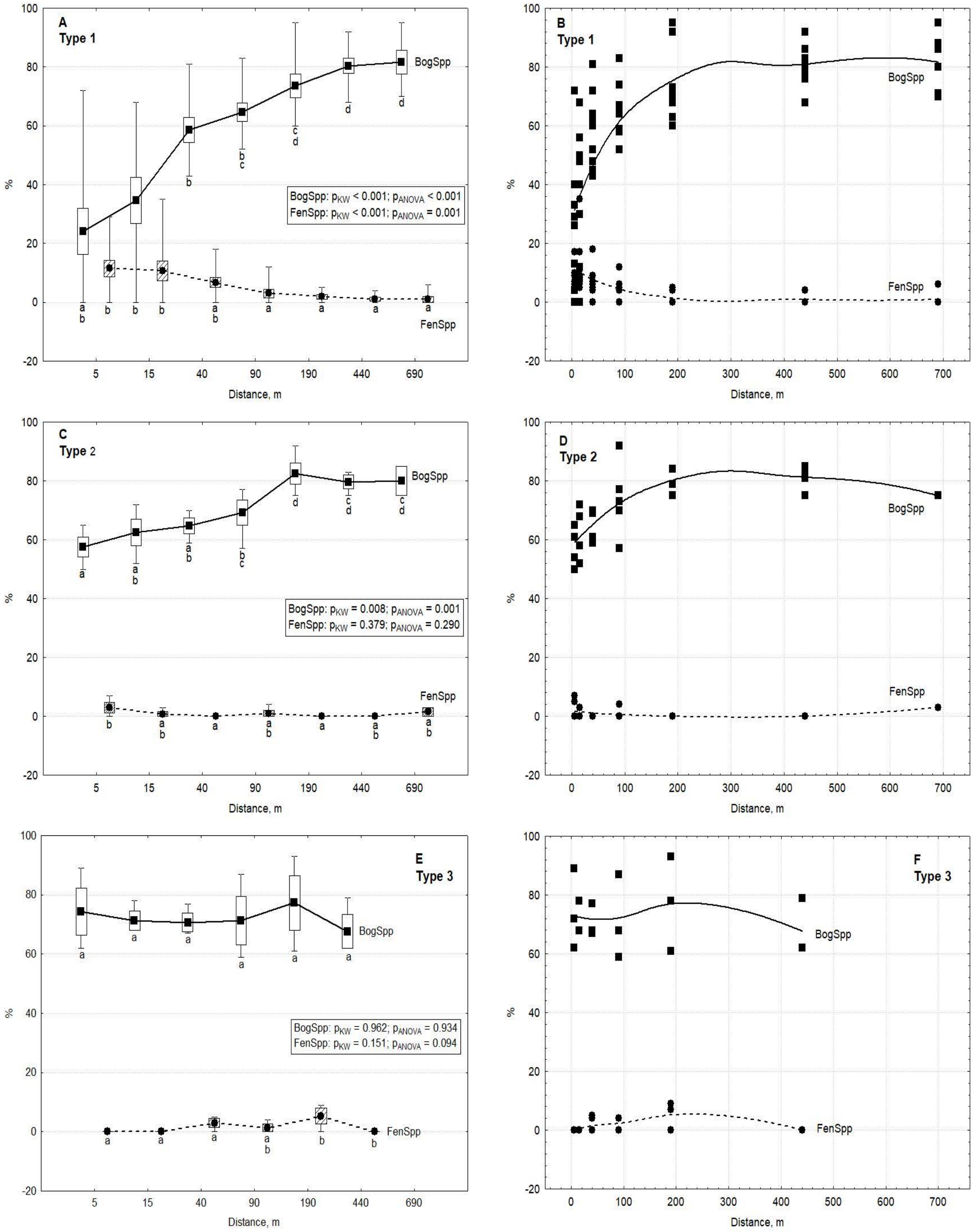

Figure 13. Dependency of the percent cover of bog-specific and fen-specific species (BogSpp and FenSpp, respectively) on distance from the drainage ditch. Plotting methods as in Figure 7.

the most effective drainage occurred within only 5 m of the ditch. For peatlands in Michigan (USA) which overlie sand deposits, drainage effects on hydrological characteristics were observed up to 150–200 m from drainage ditches (Trettin *et al*. 1991), whereas in UK blanket bogs (Pennine Hills, northern England) Stewart & Lance (1991) established that the average water table near drains was lower than at locations farther away but the lowering was slight and confined to a zone only a few metres wide on either side of the drain. Tomberg & Valk (1965) and Valk (1968, 2005) ascertained that the drainage effect on water level does not extend beyond 10–20 m from the drainage ditches in Estonian drained bog forests. On the other hand, Ilomets *et al*. (2006) recorded lowering of the water table at a distance of 100–120 m from a cutoff ditch at the foot of the marginal slope of a raised bog.

Our results for transitional mires, based on monthly recordings over a period of 2.5 years, confirmed a drainage effect on water level up to a distance of at least 250 m from the ditches (Paal *et al.* 2016). In raised bogs (as shown in this article) the maximum water level was affected by drainage only within 20–25 m of the ditches but drawdown of the average and minimum water levels was still detectable at distances of 450–500 m, which is noticeably farther than recorded by other researchers elsewhere. These discrepancies may arise from differences in the research methods, i.e., single records *versus* long-term averaged data as in our study, restricted number of studied bogs *versus* the larger sample analysed in our research; and perhaps also from climatic peculiarities at larger scale. For example, it has been asserted that Canadian peatlands are usually drier than peatlands in Finland (Vitt 2006, Miller 2011), where climatic conditions are approximately similar to those in Estonia, so the more extensive effect of drainage in Estonian bogs than elsewhere could be explained to some degree by this circumstance.

As indicated earlier in this article, a fundamental methodological problem in evaluation of the extent of drainage effects in (raised) bogs with drainage type 1 arises from the coincidence of the man-made drainage gradient with the natural gradient from mire expanse to margin. A rigorous partitioning of effects would be possible only on the basis of a parallel study of (i) bogs drained by a surrounding cutoff ditch and (ii) undrained bogs of sufficient diameter/size to accommodate the full range of the natural gradient. Unfortunately, bogs that fulfil the latter criterion are very rare in Estonia nowadays. In any case, because the cutoff ditch in each bog with drainage type 1 is located at a different distance from the bog margin, we still could not avoid the difficulty that placement of the starting point of a supposedly comparable transect in a bog with no cutoff ditch would be, essentially, arbitrary.

These considerations introduce a further issue around the comparability of different estimates of the drainage extent of ditches from other studies, relating to the type and state of the drainage system(s) in the bog(s) under study. As we have demonstrated in this article, the results of a drainage impact study along the hydrosequence depend crucially on the location within the bog massif of the drainage ditch whose effect is being assessed; i.e., did the analysed gradients commence at a cutoff ditch in the margin of the massif and proceed towards its centre, or did they start from a ditch dug across the centre and proceed towards the margin?

The range of water level fluctuations in response to precipitation events and long-lasting droughts is a very important factor for vegetation development and composition (Vasander 1984, Laitinen *et al*. 2008, Talbot *et al.* 2010). Vasander (1984) indicates that water level fluctuations may have a greater effect on plant species in hollows than on hummocks, and Strack *et al*. (2008) state that the older the drainage installations are, the greater the water level fluctuations become. According to our study, in bogs with functioning drainage systems the amplitude of water level fluctuations decreases with increasing distance from the drainage ditches in a rather regular manner; whereas in bogs with old drainage, where the ditches are usually overgrown with mosses and often partly collapsed, water level fluctuations are ubiquitously more modest.

The changes in bog vegetation associated with water level drawdown and accompanying changes in physicochemical factors have been addressed by numerous researchers in different countries (e.g., Sarasto 1957, Prévost *et al*. 1997, Pikk 2003, Korpela 2004). According to Price & Whitehead (2001) and Van Seters & Price (2002), the presence of *Sphagnum* in Canadian peatlands is strongly correlated with water level between -11 and -30 cm, which agrees well with our results indicating that raising MinWL will promote an increase of the total cover of *Sphagnum* mosses and achieve 90–100 % *Sphagnum* cover at MinWL -20 cm and higher. On the basis of our results we can also define critical MinWLs for some other components of the vegetation: the shrub and tree layers almost disappear when MinWL is higher than -30 cm and -20 cm, respectively; and a rapid increase of bog-specific species occurs if MinWL is closer to the surface than -90 cm.

The most conspicuous post-drainage changes in vegetation are connected with the increased growth of trees. Nevertheless, estimates of the actual extent of drainage effects on tree layer growth are rather scattered. In Canadian peatlands Prévost *et al*. (2005) recorded an increase in growth of small trees (height 1–4 m) within 25–30 m of ditches, whereas increase in trunk diameter of larger trees (height 8–12 m) was not supported by drainage. According to Valk (1968, 2005) the heights of trees in Estonian drained bog forests essentially increased only within 10–20 m of drainage ditches, but results of modelling suggest that drainage can affect bog forest growth up to a distance of 250 m from ditches under Estonian conditions (Padari & Kiviste 2005). Based on our data, the sum of tree girths and tree heights remains fairly constant over distances of up to 200 m from ditches. The objective results we obtained for tree canopy coverage and average height (using detailed LIDAR derived data) demonstrate a drainage effect extending up to 350–400 m beyond the drainage ditches. A taller tree layer with more continuous canopy coverage thus becomes a detectable indicator not only for drainage, but also for changes in species composition of the field and moss layers and the degree of shading by the tree layer (Reinikainen *et al*. 1984, Vasander 1987a, 1987b; Laine *et al*. 1995).

Drainage also leads to changes in the field layer. The abundance of dwarf shrubs characteristic for bogs such as *Oxycoccus palustris*, *O. microcarpus*, *Andromeda polifolia* and *Chamaedaphne calyculata* decreases considerably or they disappear, while the frequency and cover of dwarf shrubs typical of forest (*Vaccinium* species, *Ledum palustre*) increase dramatically (e.g., Masing & Valk 1968, Sarasto & Seppälä 1977, Korpela 2004). Species diversity is usually lower in drained than in undisturbed bogs (Vasander 1984, 1987a, 1987b; Vasander *et al*. 1993) yet sometimes, at least in the first stages of a post-drainage succession, species diversity in the moss layer increases because the original bog species survive for some time, growing alongside colonising forest mosses. An increase of species richness in the ground layer may also arise after drainage through decline of a formerly dominant (*Sphagnum*) species and its replacement by more than one new species (Vasander 1987a). Extensive increase in the abundance, proportion and complement of ericaceous species due to drainage has also been described in Canadian peatlands (Pellerin & Lavoie 2003, Pellerin *et al*. 2008, Talbot *et al.* 2010). In our study the total number of ground vegetation (field and moss layer) species continues to increase up to > 440 m from the drainage ditch.

Finally, it is pertinent to underline the importance and potential role of lichens as indicators of drainage impact. In Finland, Sarasto (1961) observed an increase of *Cladonia alpestris* (= *Cladina stellaris*), *Cladonia rangiferina* (= *Cladina rangiferina*) and *C. sylvatica* (= *Cladina arbuscula*) during the initial phases of raised bog drainage, followed by their later decline. Later, Vasander (1981, 1982) recorded *Cladonia arbuscula* (= *Cladina arbuscula*) and *Cladonia rangiferina* on hummocks, while Korpela (2004) affirmed an increase of *Cladina rangiferina* and *Cladonia cornuta* in drained bogs. In fact, the lichen flora of raised bogs is much richer than this, with at least 21 species identified in our study. Most of these lichens do not occur in the vicinity of drainage ditches but appear at distances of 90 m and more, i.e. they indicate a weakened or weak drainage effect.

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AUTHOR CONTRIBUTIONS

JP planned the research, undertook the vegetation analysis and data processing, prepared Figures 4–13, wrote the first draft, and is the lead author; IJ estimated the bryophytes; AS estimated the lichens; AK planned the work, undertook all environmental measurements and analysis, prepared Figures 1–3, and complemented the manuscript text.

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Author for correspondence:
Professor Emeritus Jaanus Paal, Department of Botany, Institute of Ecology and Earth Sciences, University of Tartu, Lai St 40, Tartu, 51005 Estonia. Tel: +372 737 5835; E-mail: jaanus.paal@ut.ee