Impact of drainage on vegetation of transitional mires in Estonia

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SUMMARY

The extent of drainage impact was studied in five transitional mires along a hydrosequence. The principal environmental variables driven by drainage are the minimum water level in the peat layer, together with the dry matter and total-N contents of peat. The drawdown effect of a cutoff ditch (intercepting surface and subsurface flow) on the minimum water level extends to a distance of 250–320 m. Peat water levels above -50 cm are associated with a sharp increase in *Sphagnum* cover, and the percentage of bog-specific species increases markedly when the minimum water level is higher than -25 cm. The girths and heights of trees and canopy closure of the tree layer decrease rapidly up to a distance of 200 m from the cutoff ditch. Negative impacts of the cutoff ditch on the canopy cover and average height of trees, estimated using LIDAR data, can be followed for distances up to 400 m and 350 m, respectively. The density and height of shrub stems start to increase at a distance of 16 m and continue to increase up to 400 m from the cutoff ditch. The percentage of bog-specific species increases up to a distance of 100 m, whilst the percentage of fen-specific species begins to decrease remarkably at a distance of about 200 m from the cutoff ditch.

KEY WORDS: hydrosequence, indicator species, soil nitrogen content, vegetation change, water level

INTRODUCTION

Drainage is still one of the major causes of loss and degradation of mire ecosystems resulting from human activities. All prevailing modes of mire resource utilisation (including peat excavation, agriculture, forestry, urban and industrial developments) require drainage of the mire before exploitation. Soon after drainage, the acrotelm degrades and only the catotelm remains (Ingram 1978, Landry & Rochefort 2012). Besides the direct effect of drainage ditches on the proximate surroundings, lowering of the groundwater level also affects the water regime, microclimate, vegetation and fauna of the neighbouring territory. The extent of this impact varies, depending on the size and type of the mire and the location of the drainage system within the mire. In Estonian mires, the area affected by drainage ranges from 20 % to 150 % of the area of the drainage system (Paal 2011). Therefore, the extent of drainage impact in mires that have been subjected to drainage, and the nature of the impact on different components of mire ecosystems, are important issues for both drainage engineers and nature conservationists.

Transitional or mixotrophic mires represent an intermediate succession stage between minerotrophic and ombrotrophic mires. They are situated on flat or slightly sloping areas at the margins of raised bogs or in depressions with poor runoff. The rooting zones of some of their plant species are influenced by groundwater, but several other species form hummocks and become relatively isolated from groundwater due to the thick peat layer; these plants acquire nutrients mainly from precipitation. Transitional mires are distributed unevenly in Estonia. The larger and more important examples are concentrated in the western and easternmost parts of the country (Paal & Leibak 2011).

Large-scale drainage of mires took place in Estonia between the 1950s and the 1980s. In the 1950s the total area of the country's open transitional mires was estimated at 76,200 ha (Laasimer 1965), but according to the recent mire inventory (Paal & Leibak 2011) this area has since decreased to 35,000 ha, i.e. it has more than halved. The main reason is the direct or indirect impact of drainage.

The aim of the present study was to clarify the spatial extent of drainage impact on the vegetation of Estonia's rather vulnerable transitional mires, and to identify the main environmental factors determining the change of vegetation structure under Estonian conditions. The results could be relevant to other boreonemoral areas of similar nature.

METHODS

Sample areas and field data

We studied five transitional mires situated in different regions of the Estonian mainland (Figure 1). A stratified sampling method was used to select study areas on the basis of data compiled for the Estonian mires inventory (Paal & Leibak 2011). Specific criteria included: bedrock type of the region (limestone or sandstone); landscape region; minimum diameter of the undrained part of the mire >1.5 km; drainage type; and neighbouring land use type. To eliminate additional effects on environment or vegetation, we studied mires that had only one drainage ditch (cutoff ditch, intercepting surface and subsurface flow; Maastik *et al*. 2000), creating two separately functioning hydrological units on the two sides of the ditch. These mires do not have any additional drainage ditches perpendicular or parallel to the studied cutoff ditch within the internal area of the mire. Moreover, they have not been grazed or subject to tree removal. The ditches in the mires that we studied were dug 37–53 years ago, so we were dealing with almost stabilised ecosystems where the noticeable changes caused by drainage had already occurred.

At each site, sampling was undertaken along a straight line transect aligned perpendicular to the ditch. The first sampling point was 5 m from the ditch and the others were spaced at successive intervals in the order of 10, 25, 50, 100 and 250 m. If the mire centre or an undisturbed mire area was not reached, additional sampling nodes were placed at repeated 250 m intervals (Figure 2). In the very large Tuhu mire complex two separate mire massifs (Tuhu and Tuudi) were studied. The Tuhu 1 and Hindaste transects were in transitional mires bordered by maintained deep cutoff ditches and large agricultural areas. In Tuhu 2 the ditch was old and almost overgrown by vegetation, whereas in the Kassisaare mire the cutoff ditch was moderately deep and water flow was only partly obstructed by vegetation.

At every transect node, the full peat profile was described in terms of peat type, the state of peat decomposition according to the von Post scale, and bulk density. Water level and water properties

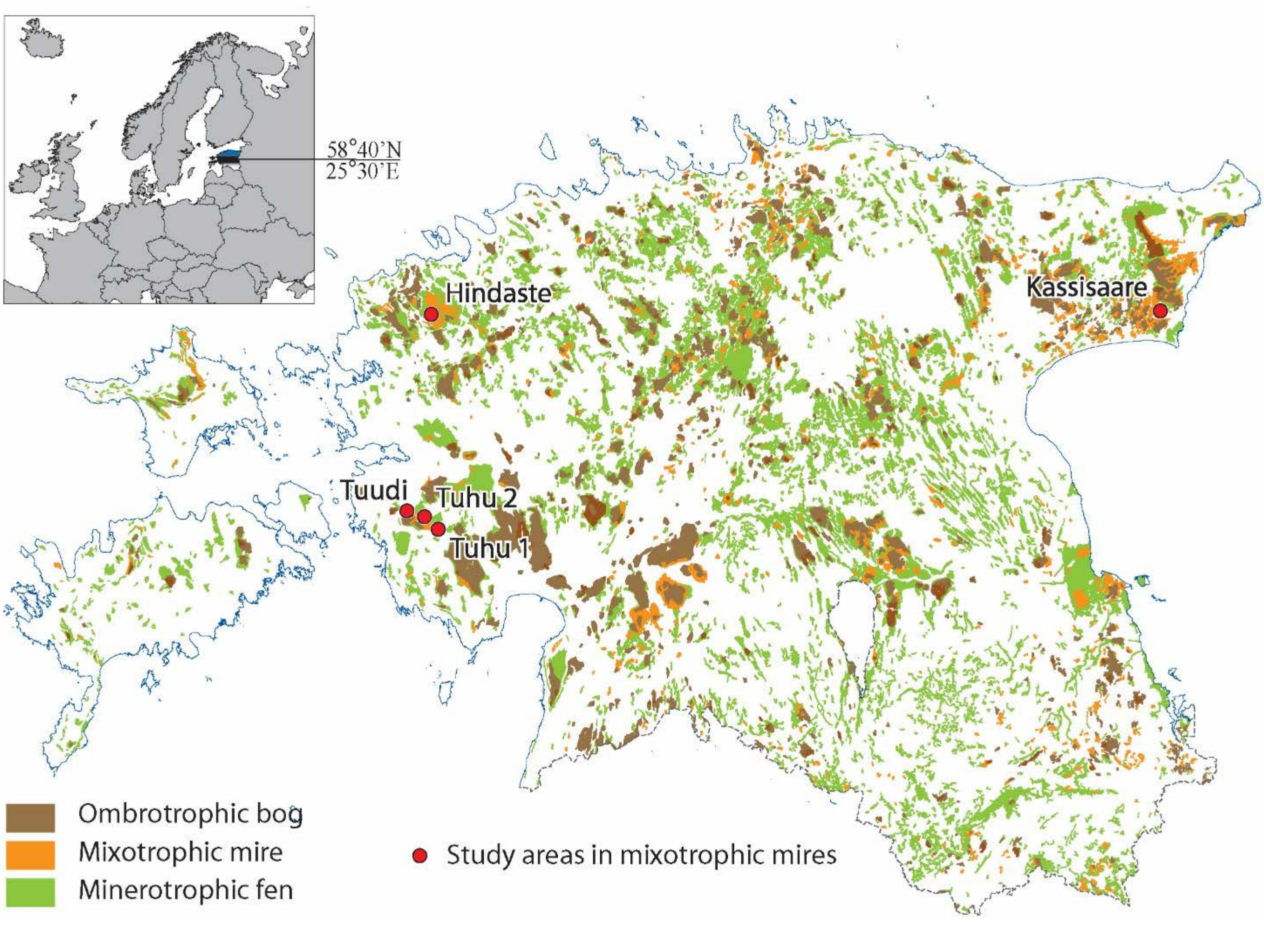

Figure 1. Locations of the study areas within Estonia.

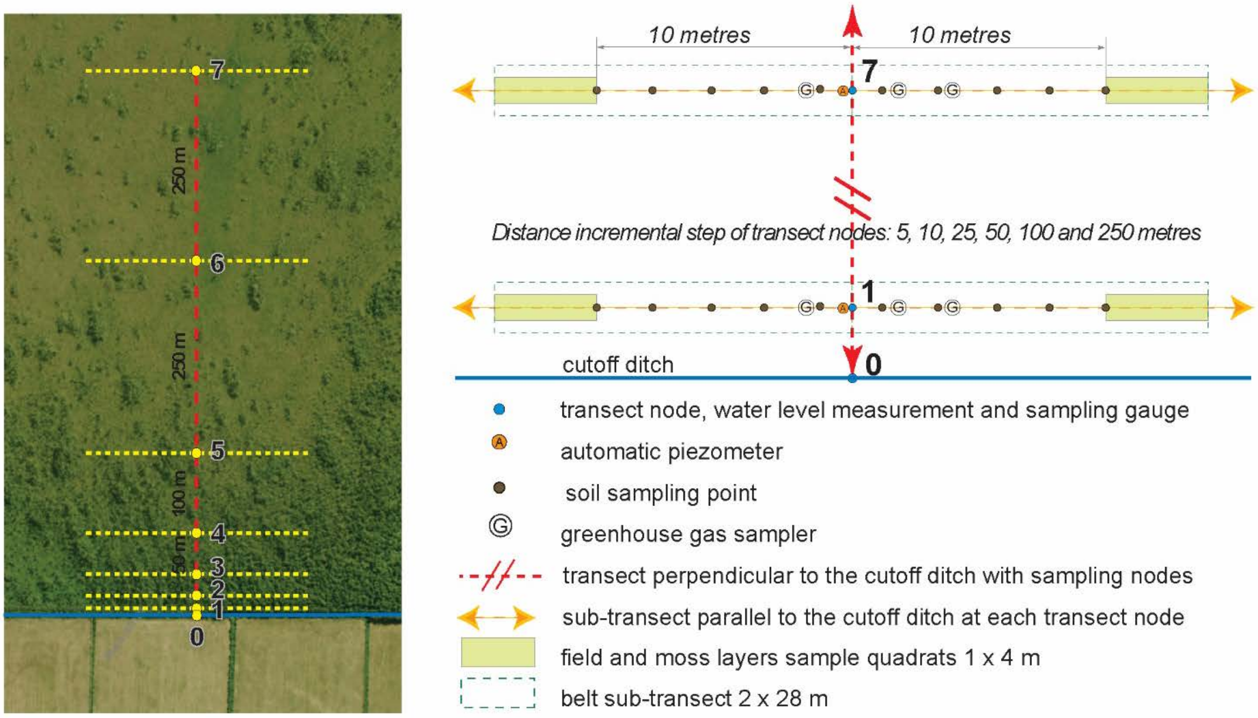

Figure 2. Study transect and layout of sampling areas with nodes and sampling plots along the sub-transects.

measurements were conducted in a sampling gauge (1.5 m long PVC tube, Ø 75 mm, lowermost 1 m perforated and covered with DuPont Geoproma filtration fabric). In every sampling gauge a calibrated handheld YSI Professional Plus meter was used to measure dissolved oxygen content, pH, electric conductivity, redox potential and temperature at monthly intervals throughout the year from June 2012. Water pressure and temperature were measured daily by automatic piezometers (Geotech AB). Data collected during the period June 2012 to December 2014 were used in the analyses presented here.

Soil and water samples for chemical analysis were collected during the period with the lowest water level, at the end of August. At every transect node ten sub-samples of soil were taken at 2 m intervals along a sub-transect (Figure 2) running at 90 degrees to the main transect. The volume of each sub-sample was 125 cm^3 and it was taken from depth 0–40 cm, where the zero level corresponded to the base of the living moss layer. These ten sub-samples were mixed and homogenised before analysis in the laboratory. The contents of dry matter, ash (3 hours at 550 °C) and total-C of the homogenised soil samples were determined using a dry combustion method on a varioMAX CNS elemental analyser. The soil samples were also analysed for total nitrogen (N) according to Kjeldahl (Tecator ASN3313), NH_4-N (Tecator ASN 65-32/84) and NO_3-N (Tecator ASN 65-31/84). Available (ammonium lactate extractable) phosphorus (P) was measured by flow injection analysis (Tecator ASTN 9/84). The same solution was analysed for available K, Ca and Mg content using the flame photometric method. These analyses were carried out at the Plant Biochemistry Laboratory of the Estonian University of Life Sciences. Water samples were analysed for total-N (ISO 11905-1), NH_4-N (ISO 11732), NO_3-N (ISO 10304-1), NO_2-N (ISO 13395), total-P (ISO 15681-2), PO_4-P (ISO 15681-2) and SO_4-S (ISO 10304-1) at the Tartu Laboratory of the Estonian Environmental Research Centre.

To describe the field (dwarf shrubs + grasses + forbs) and moss layers of the vegetation, sample quadrats measuring 1 m × 4 m were marked out at a distance of 10 m perpendicular to the transect direction from both sides of the node. In the sample quadrats the percentage cover of lichen, bryophyte 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 at the Natural History Museum of the University of Tartu.

Tree trunk girth was measured using a Bitterlich relascope at two diagonally opposite corners of every sample quadrat as well as at the node. At the same five points, the number of shrub stems and tree saplings was counted and their height was measured, in circular sample plots with a radius of 2 m. All trees of diameter less than 4 cm at breast height (1.3 m) and/or of height less than 4 m were regarded as saplings.

A Suunto PM-5 hand-held clinometer was used to measure tree height in belt sub-transects 2 m wide × 28 m long extending from the nodes of the base transect, at 90 degrees, to the farthest ends of the 1 × 4 m sample quadrats (Figure 2). In the following, we refer to an area near a node on the main transect where the water level and water chemistry measurements were carried out, together with the associated sub-transect where the vegetation data were recorded, as a sampling area.

Mean tree height and canopy cover were estimated 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. Recorded plant species were divided into raised bog and transitional mire groups according to their distributions and autecological optima in natural mires (Botch & Smagin 1993, Krall *et al.* 2010, Vellak *et al.* 2013, Ingerpuu *et al.* 2014).

Data processing

Tree height and canopy cover were estimated from LIDAR data (Næsset & Økland 2002, Andersen *et al*. 2006) as average values for 1 m wide zones running parallel to the cutoff ditch, moving from the ditch to the mire centre, the area of every zone being 1,000 m^2 and its centerpoint at 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 single tree canopy area in mires) with a 1 m step of the moving calculation cell. The bare earth surface (DEM) was calculated along the 1 m wide 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 the 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 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).

Cover data for ground vegetation species were averaged from the two 1 × 4 m sample quadrats at every sampling area. The numbers of shrub stems and saplings on the five circular subplots, as well as their heights, were summed for every species. The values for girth and estimated height of trees were summed by species over every sub-transect, and the respective average values calculated.

Detrended correspondence analysis (DCA) (McCune & Mefford 1999) was used for ordination of the vegetation data on sampling areas and environmental variables. The importance of environmental factors and variables of community structure was estimated by the correlation of variables with ordination axes (McCune & Mefford 1999) and by their loadings according to factor analysis (FA) with varimax rotation (StatSoft Inc. 2005). The mutual correlation between the variables considered was evaluated on the basis of non-parametric Spearman correlation coefficients.

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

The dependency of different vegetation structure variables on environmental variables was analysed by multiple regression analysis, for which the models were built by backward stepwise removal of variables (StatSoft Inc. 2005).

Relationships between the various characteristics of the plant cover and the main environmental variables (distance from the drainage ditch, bog water pH, minimum water level) were demonstrated on scattergrams of empirical data; the respective regression lines were fitted using the distance-weighted least squares regression method. Using this method, a polynomial (second-order) 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 their distance from the particular X-value (StatSoft Inc. 2005).

RESULTS

Factor analysis (FA) and detrended correspondence analysis (DCA) enabled identification of the principal variables determining the vegetation structure and environmental conditions. The results of both analyses were in concordance, differences appearing mainly because some variables (cover of moss layer and *Sphagnum* species, number of bog-specific species, average height of tree layer, minimum and average water level, dry matter content of peat) had the highest loading by the second factor in factor analysis, but by the first ordination axis according to DCA. In interpreting the results presented in Table 1, it is also important to consider the mutually high correlation (multicollinearity) of several groups of variables. For example, the number of species (total, ground and bottom vegetation, field and moss layer species), tree layer characteristics (sums of girth and height of trees, tree layer canopy closure), water level variables (minimum, average and maximum water level), peat chemistry properties (peat water pH and conductivity, content of dry matter, ash and Ca), *etc*.

The ordination analysis biplot (Figure 3) of the sampling areas and most of the principal variables determining vegetation structure and environmental conditions demonstrates a striking gradient driven by the minimum water level in peat and tightly correlated variables, namely dry matter content of peat ($r_{Spearman} = 0.73$; Figure 4) and total-N content of soil ($r_{Spearman} = 0.72$). Minimum water level and other variables associated with it have a significant impact on vegetation structure; e.g. when the minimum water level is higher than -50 cm, a rapid increase of *Sphagnum* spp. ($r_{Spearman} = 0.88$) and moss cover ($r_{Spearman} = 0.86$) (Figure 5) is noted. The same can be observed from the percentage of bog-specific species ($r_{Spearman} = 0.70$), which increases sharply when the minimum water level is above -25 cm (Figure 6).

Table 1. Factor loadings of vegetation structural characteristics and habitat environmental variables by first two factors (FA1, FA2) of the factor analysis.

Variable	FA1	FA2
Log-transformed distance from cutoff ditch	0.078	-0.856
Variables of vegetation structure		
Total number of species	0.863	0.104
Number of shrub layer species	0.753	0.274
Number of ground vegetation species	0.816	-0.080
Number of field layer species	0.539	-0.292
Number of bottom vegetation species	0.785	0.149
Number of moss layer species	0.811	0.099
Sum of tree girths (cm)	-0.240	0.716
Sum of tree heights (m)	-0.245	0.791
Canopy closure of tree layer	-0.171	0.776
Average height of tree layer (m)	-0.044	0.924
Tree layer cover from LIDAR data	0.196	0.764
Number of shrub stems and tree saplings	0.569	-0.536
Sum of shrub layer stem heights (m)	0.432	-0.335
Total cover of shrub layer (%)	0.485	-0.405
Total cover of field layer (%)	0.074	-0.151
Total cover of moss layer (%)	-0.393	-0.776
Total cover of *Sphagnum* species (%)	-0.523	-0.726
Total cover of lichen species (%)	-0.023	0.037
Number of bog-specific species	-0.252	-0.673
Percentage of bog-specific species (%)	-0.551	-0.638
Number of fen-specific species	0.699	-0.051
Percentage of fen-specific species (%)	0.396	-0.085

Variable	FA1	FA2
Variables of habitat and envrironment		
Thickness of bog peat (cm)	-0.567	-0.419
Thickness of transitional mire peat (cm)	-0.484	-0.292
Thickness of fen peat (cm)	0.520	0.002
Total thickness of peat (cm)	0.272	-0.284
Absolute altitude of mire surface(m)	-0.779	-0.263
Depth of cutoff ditch (cm)	0.083	0.161
Incline of cutoff ditch (m km^{-1})	0.493	0.049
Minimum water level (cm)	-0.301	-0.795
Average water level (cm)	-0.276	-0.740
Maximum water level (cm)	-0.158	-0.225
Water temperature (°C)	0.571	-0.179
Saturation of peat water with dissolved O_2 (%)	0.467	0.351
Peat water conductivity (μS cm^{-2})	0.588	-0.024
Peat water pH	0.799	0.191
Peat water redox potential (mV)	-0.488	0.004
Content of dry matter in peat (%)	0.414	0.819
Content of NH_4-N in soil (mg kg^{-1})	0.281	0.559
Content of NO_3-N in soil (mg kg^{-1})	0.129	0.123
Content of total-N in soil (%)	0.615	0.564
Content of total-P in soil (mg kg^{-1})	0.338	0.206
Content of total-K in soil (mg kg^{-1})	-0.559	-0.391
Content of total-Ca in soil (mg kg^{-1})	0.681	0.327
Content of total-Mg in soil (mg kg^{-1})	0.719	0.145
Content of C (organic matter) in soil (%)	-0.520	-0.474
Content of ash in soil (%)	0.498	0.451
Years since drainage began	0.527	0.165

Another obvious gradient on the ordination analysis biplot reflects distance of the sample from the cutoff ditch, with sampling areas situated near the cutoff ditch occupying the lower left triangle of the ordination biplot (Figure 3), compared with areas located in the central parts of the mires occupying the upper right triangle of the biplot. The minimum water level is modestly correlated with log-distance ($r_{Spearman} = 0.41$; Figure 7) and the drawdown effect of the cutoff ditch subsides at a log-distance of 2.4–2.5, corresponding to 250–320 metres on the ground. Several other ecologically important variables are well correlated with the distance factor, e.g. the dry matter content of peat decreases continuously when moving farther from the cutoff ditch ($r_{Spearman} = -0.72$; Figure 8); and the dissolved O_2 saturation of peat water ($r_{Spearman} = -0.34$; Figure 9) and the total-N content of peat ($r_{Spearman} = -0.40$; Figure 9) start to decline about 40 m (log-distance 1.6) from the ditch.

For vegetation structure characteristics, the tree layer variables such as sum of girths ($r_{Spearman} = -0.87$; Figure 10) and sum of heights ($r_{Spearman} = -0.87$) of trees, tree layer crown closure ($r_{Spearman} = -0.81$; Figure 11) and tree layer canopy cover derived from LIDAR data ($r_{Spearman} = -0.75$; Figure 12) are most strongly correlated with the distance factor. The girths and heights of trees, as well as canopy closure of the tree layer, decrease rather steeply up to the log-distance value 2.3, i.e. up to a distance of ~ 200 m from the cutoff ditch. This trend continues with increasing distance from the ditch even though there are relatively few data points.

The canopy cover of the tree layer estimated up to the mire centre from LIDAR data provides complementary information. This variable decreases rapidly in the first 260–270 metres, after which it continues to decrease moderately up to 400 metres where it achieves an average value of 0.1 m^2 m^{-2} (Figure 12). The average tree height derived from LIDAR shows a more pronounced steep decrease in

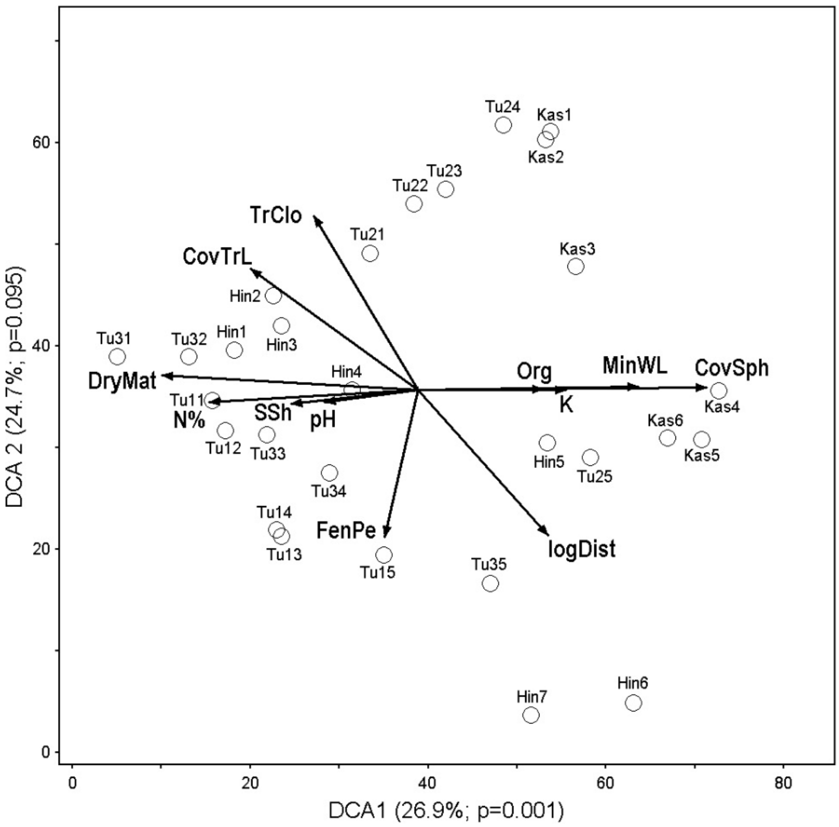

Figure 3. DCA biplot of sampling areas, main variables determining the vegetation structure and environmental conditions. Abbreviations: DryMat = content of dry matter in peat; CovTrL = tree layer cover from LIDAR data; TrClo = canopy closure of tree layer; Org = content of C (organic matter) in soil; K = content of total-K in soil; MinWL = minimum water level; CovSph = total cover of *Sphagnum* species; logDist = log-transformed distance from cutoff ditch; FenPe = thickness of fen peat; pH = peat water pH; SSh = number of shrub layer species; N% = total-N content of soil. For the Tuhu (Tu1, Tu2) and Tuudi (Tu3) mires, the first number indicates the transect number, and the second number the sampling area starting from the cutoff ditch; for the other mires – Hindaste (Hin) and Kassissare (Kas) only the sampling area number is shown.

the first 150 m from the cutoff ditch and slowly fades thereafter until 350 m distance, where it fluctuates around the mean value of 2.1 m (Figure 12).

Simultaneously with the weakening of tree layer growth, development of the shrub layer is favoured. The number of shrub stems and their height starts to increase as early as log-distance 1.2 (16 m) and the latter variable continues to increase up to log-distance 2.0–2.1 (100–130 m) (Figure 10). The percentage of bog-specific species increases when moving away from the cutoff ditch up to log-distance 2.0 (100 m), whilst the percentage of fen-specific species begins to decline after log-distance 2.3 (200 m) (Figure 13). The cover values for both *Sphagnum* spp. and the whole moss layer begin to increase rapidly at log-distance 1.2–1.6 (16–40 m) from the cutoff ditch and this trend continues up to log-distance 2.0 (100 m) (Figure 14).

The distribution of species on the ordination biplot also strongly reflects the gradients of minimum water level and distance from the cutoff ditch (Figure 15). Deeper (lower) water level and the complex of factors connected with it supports forest species such as *Picea abies*, *Fragaria vesca*, *Rubus saxatilis*, *Dicranum scoparium*, *Tetraphis pellucida* and *Calypogeia integristipula*. On the other hand, high water level is associated with mire species such as *Betula nana*, *Equisetum fluviatile*, *Sphagnum fallax* and *Andromeda polifolia*. In habitats farther from the cutoff ditch (i.e. in the central parts of the mires) *Drosera rotundifolia*, *Menyanthes trifoliata*, *Sphagnum fuscum*, *S. angustifolium*, *Polytrichum strictum* and stunted *Pinus sylvestris* are typical.

The indicator species analysis presents a detailed overview of change in species composition and relative abundance of species with increasing distance from the cutoff ditch (Table 2). Although single species are not statistically significant and

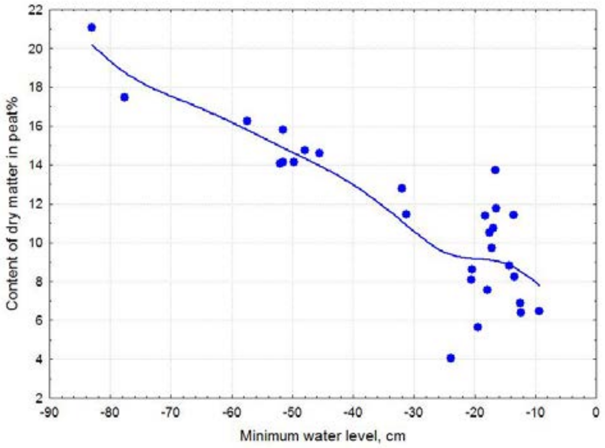

Figure 4. Relationship between the dry matter content of peat and minimum water level.

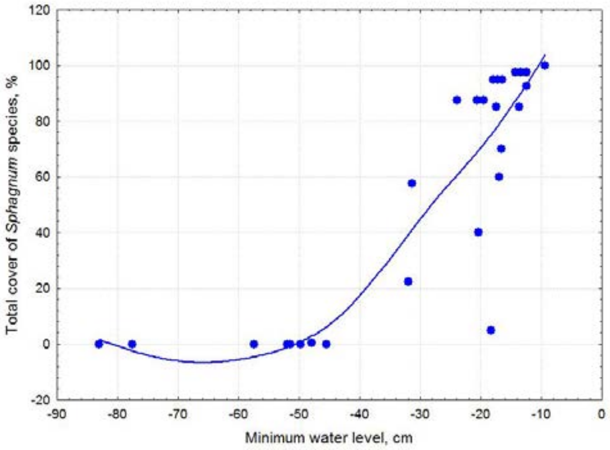

Figure 5. Relationship between the total cover of *Sphagnum* species and minimum water level.

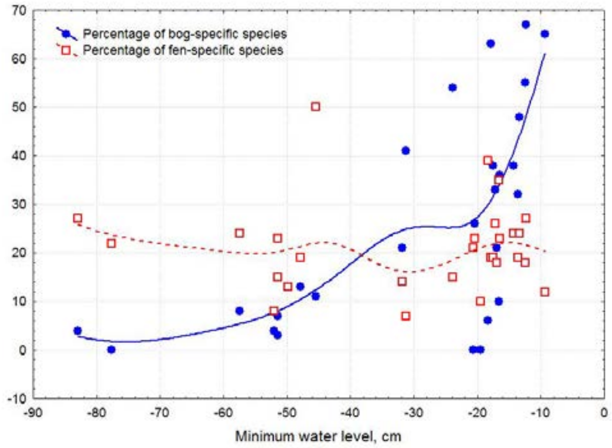

Figure 6. Relationships between the representation of bog-specific and fen-specific species, and minimum water level.

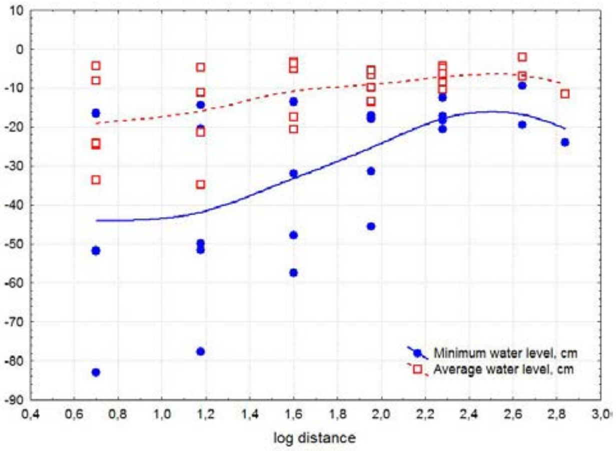

Figure 7. Relationships between the minimum and average water level, and log-distance from the cutoff ditch.

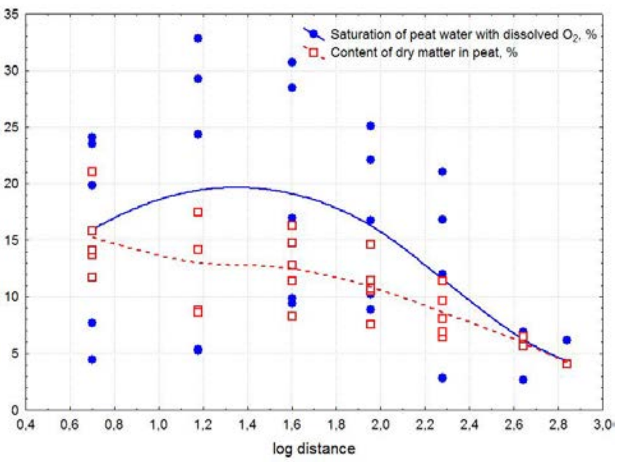

Figure 8. Relationships between saturation of peat water with dissolved O_2 and content of dry matter in peat, and log-distance from the cutoff ditch.

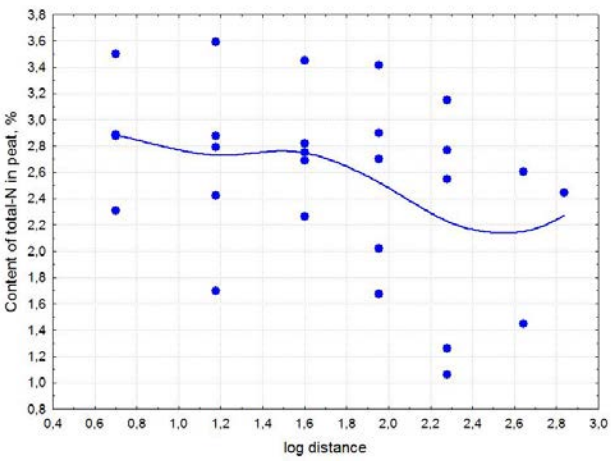

Figure 9. Relationship between the total-N content in soil and log-distance from the cutoff ditch.

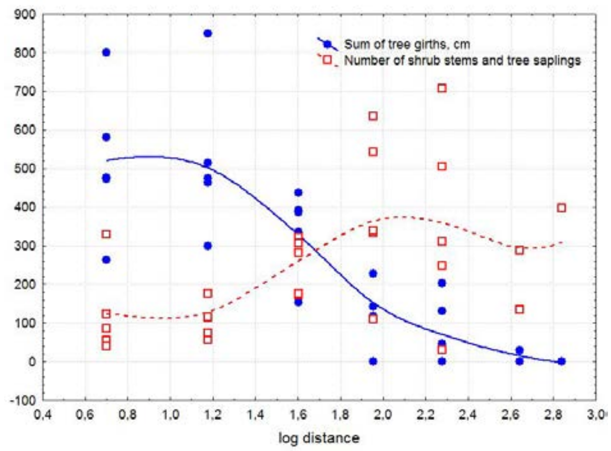

Figure 10. Relationships between the sum of tree girths and number of shrub stems and tree saplings, and log-distance from the cutoff ditch.

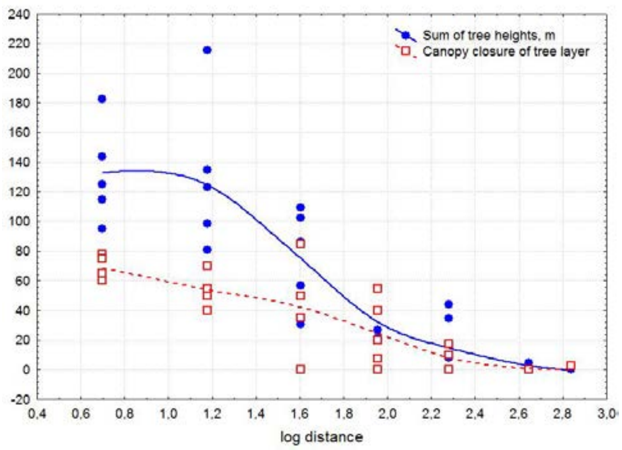

Figure 11. Relationships between the sum of tree heights and tree layer canopy closure, and log-distance from the cutoff ditch.

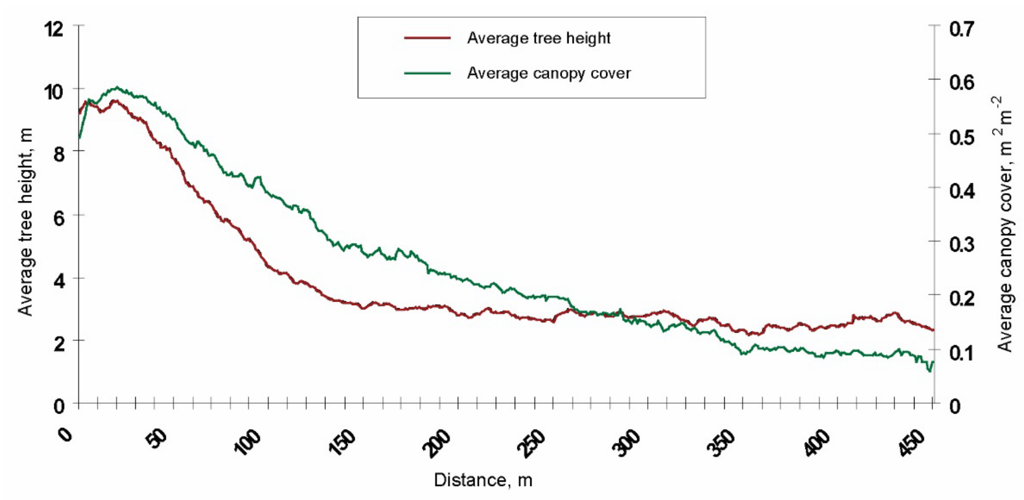

Figure 12. Relationships between the tree layer canopy cover (derived from LIDAR data) and average tree height, and distance from the cutoff ditch.

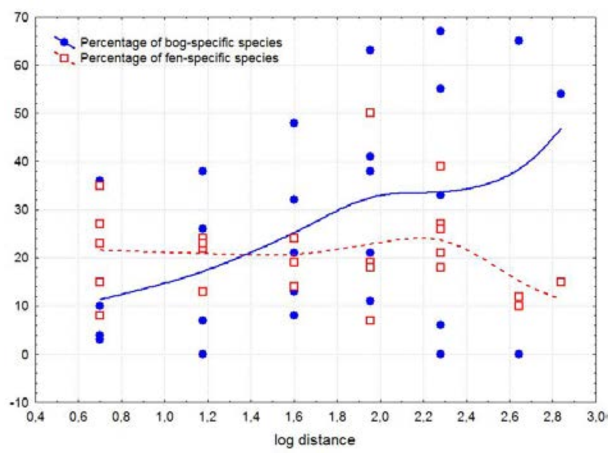

Figure 13. Relationships between percentages of bog-specific and fen-specific species, and log-distance from the cutoff ditch.

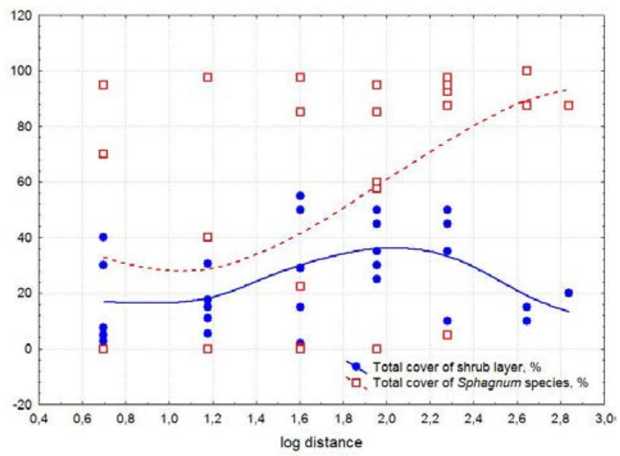

Figure 14. Relationships between total cover of shrub layer and total cover of *Sphagnum* species, and log-distance from the cutoff ditch.

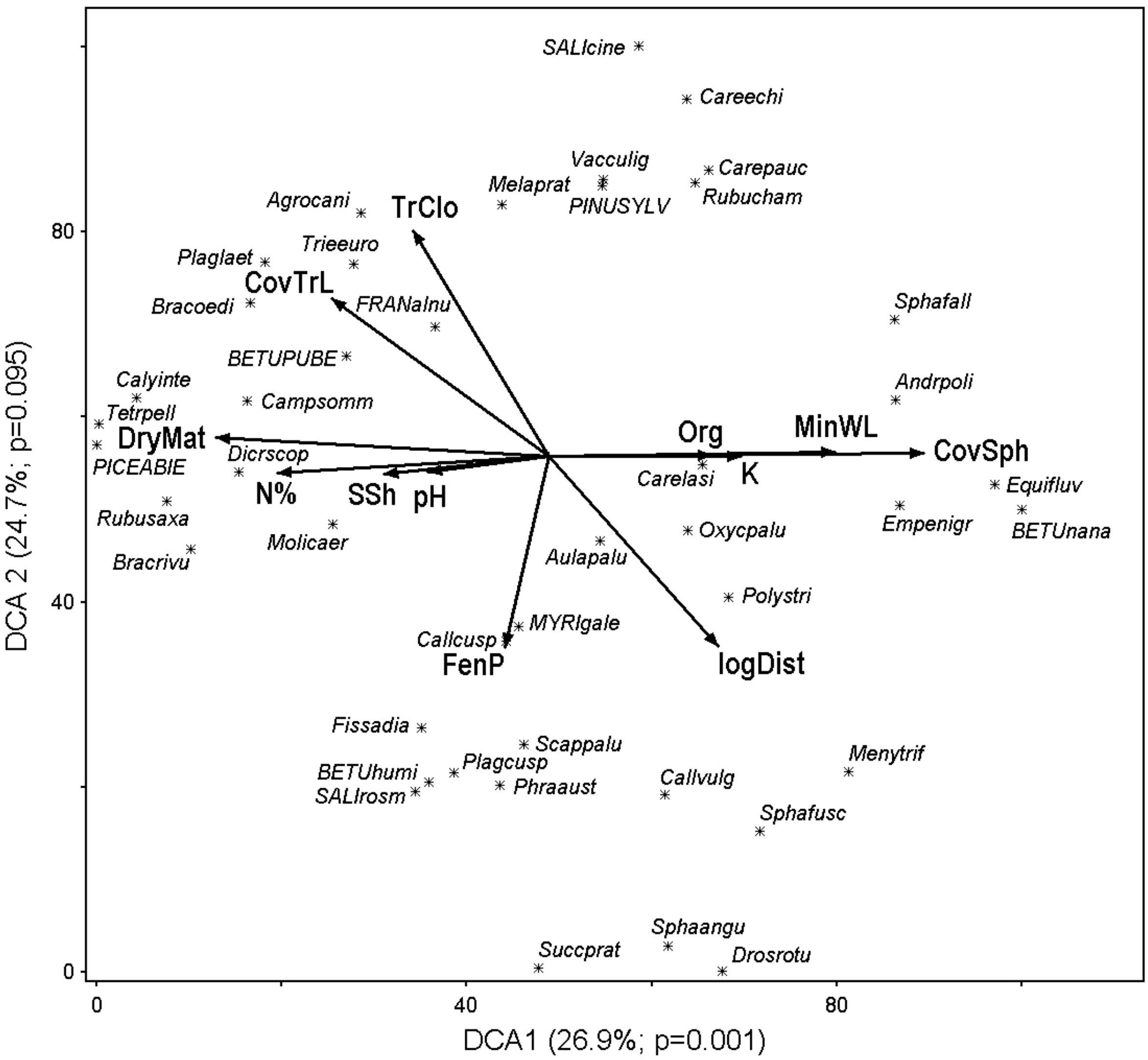

Figure 15. DCA biplot of the most indicative species and main variables determining the vegetation structure and environmental conditions. Abbreviations: DryMat = content of dry matter in peat; CovTrL = tree layer cover derived from LIDAR data; TrClo = tree layer canopy closure; Org = content of C (organic matter) in soil; K = total-K content of soil; MinWL = minimum water level; CovSph = total cover of *Sphagnum* species; logDist = log-transformed distance from cutoff ditch; FenPe = thickness of fen peat; pH = pH of peat water; SSh = number of shrub layer species; N% = total-N content of soil. Tree species: *BETUPUBE = Betula pubescens, PICEABIE = Picea abies, PINUSYLV = Pinus sylvestris*; shrubs: *BETUhumi = Betula humilis, BETUnana = Betula nana, FRANalnu = Frangula alnus, MYRIgale = Myrica gale, SALIcine = Salix cinerea, SALIrosm = S. rosmarinifolia*; field layer species: *Agrocani = Agrostis canina, Andrpoli = Andromeda polifolia, Callvulg = Calluna vulgaris, Careechi = Carex echinata, Carelasi = C. lasiocarpa, Carepauc = C. pauciflora, Drosrotu = Drosera rotundifolia, Empenigr = Empetrum nigrum, Equifluv = Equisetum fluviatile, Melaprat = Melampyrum pratense, Menytrif = Menyanthes trifoliata, Molicaer = Molinea caerulea, Oxycpalu = Oxycoccus palustris, Phraaust = Phragmites australis, Rubucham = Rubus chamaemorus, Rubusaxa = R. saxatilis, Succprat = Succisa pratensis, Trieeuro = Trientalis europaea, Vacculig = Vaccinium uliginosum*; moss layer species: *Aulapalu = Aulacomnium palustre, Bracoedi = Brachythecium oedipodium, Bryum_sp = Bryum* sp., *Callcusp = Calliergonella cuspidata, Calyinte = Calypogeia integristipula, Campsomm = Campylium sommerfeltii, Dicrscop =Dicranum scoparium, Fissadia = Fissidens adianthoides, Plagcusp = Plagiomnium cuspidatum, Plaglaet = Plagiothecium laetum, Polystri = Polytrichum strictum, Scappalu = Scapania paludicola, Sphaangu = Sphagnum angustifolium, Sphafall = S. fallax, Sphafusc = S. fuscum, Tetrpell = Tetraphis pellucida.*

Table 2. Indicator values, relative frequency and relative abundance of transitional mire species in relation to distance from the cutoff ditch. Abbreviations: D = distance step from the cutoff ditch (1 = 5 m, 2 = 15 m, 3 = 40 m, 4 = 90 m, 5 = 190 m, 6 = 440 m), p = significance level.

Species	D	p	Indicator value						Relative frequency						Relative abundance					
			Distance step																	
			1	2	3	4	5	6	1	2	3	4	5	6	**1**	2	3	4	5	6
Juniperus communis	1	0.248	**38**	1	0	0	0	0	**40**	20	20	0	0	0	**95**	5	0	0	0	0
Sorbus aucuparia	1	0.249	**27**	7	0	0	0	0	**40**	20	0	0	0	0	**67**	33	0	0	0	0
Fragaria vesca	1	0.255	**30**	5	0	0	0	0	**40**	20	0	0	0	0	**75**	25	0	0	0	0
Tetraphis pellucida	1	0.264	**27**	6	0	0	0	0	**40**	20	0	0	0	0	**68**	32	0	0	0	0
Calypogeia integristipula	1	0.352	**32**	7	0	1	0	0	**40**	40	0	20	0	0	**79**	18	0	3	0	0
Carex canescens	1	0.536	**21**	5	4	2	1	0	**40**	40	20	20	20	0	**53**	12	18	12	6	0
Brachythecium oedipodium	1	0.638	**16**	9	16	0	0	0	**40**	40	40	0	0	0	**39**	22	39	0	0	0
Vaccinium vitis-idaea	1	0.902	**12**	6	1	1	0	0	**20**	20	20	20	0	0	**61**	30	6	3	0	0
Plagiothecium laetum	2	0.225	1	**27**	11	0	0	0	20	**40**	40	0	0	0	5	**67**	28	0	0	0
Lophocolea heterophylla	2	0.295	6	**23**	6	9	2	0	40	**60**	40	40	20	0	15	**38**	15	23	8	0
Cephalozia connivens	2	0.296	0	**20**	3	0	7	0	0	**40**	20	0	20	0	0	**50**	17	0	33	0
Potentilla palustris	2	0.446	1	**25**	5	1	3	0	20	**40**	20	60	40	0	3	**64**	23	2	9	0
Campylium sommerfeltii	2	0.476	8	**18**	2	2	0	0	20	**40**	20	20	0	0	38	**46**	8	8	0	0
Trientalis europaea	2	0.519	13	**29**	17	0	1	0	40	**80**	60	40	40	0	33	**36**	28	1	2	0
Melampyrum pratense	2	0.646	6	**15**	6	0	0	0	20	**40**	20	20	0	0	30	**37**	31	1	0	0
Potentilla erecta	2	0.861	0	**13**	1	2	12	0	0	**40**	40	40	20	0	0	**32**	2	5	61	0
Brachythecium rivulare	2	0.921	6	**10**	0	4	0	0	20	**20**	0	20	0	0	32	**48**	0	19	0	0
Carex pauciflora	2	0.923	0	**11**	8	0	0	0	20	**20**	20	0	0	0	1	**56**	42	0	0	0
Carex echinata	2	0.928	8	**11**	2	0	0	0	20	**20**	20	0	0	0	39	**53**	8	0	0	0

continued overleaf

Table 2 continued

Species	D	p	Indicator value						Relative frequency						Relative abundance					
			Distance step																	
			1	2	3	4	5	6	1	2	3	4	5	6	**1**	2	3	4	5	6
Fissidens adianthoides	2	0.934	0	**11**	5	3	6	0	20	**40**	20	20	20	0	1	**27**	26	13	32	0
Dactylorhiza sp.	3	0.233	3	0	**34**	0	0	0	20	0	**40**	0	0	0	14	0	**86**	0	0	0
Dicranum scoparium	3	0.245	9	17	**26**	1	0	0	40	60	**60**	20	0	0	21	29	**43**	7	0	0
Agrostis sp.	3	0.919	0	7	**13**	0	0	0	20	20	**20**	0	0	0	1	33	**66**	0	0	0
Scapania paludicola	4	0.259	0	0	1	**27**	6	0	0	0	20	**40**	20	0	0	0	6	**67**	28	0
Carex nigra	4	0.409	2	4	0	**20**	4	5	20	20	0	**60**	20	33	12	20	0	**33**	20	14
Aulacomnium palustre	4	0.655	0	6	12	**22**	16	21	20	60	80	**100**	80	67	2	10	14	**22**	20	32
Sphagnum capillifolium	4	0.674	0	0	8	**16**	4	5	20	0	40	**40**	20	33	2	0	20	**41**	21	16
Polytrichum commune	4	0.766	2	12	11	**14**	0	0	40	40	40	**40**	0	0	6	31	27	**36**	0	0
Calliergon stramineum	4	0.990	5	1	6	**7**	6	1	20	20	40	**20**	40	33	25	5	15	**37**	15	4
Salix rosmarinifolia	4	1.000	0	0	7	**9**	4	0	0	0	20	**20**	20	0	0	0	33	**44**	22	0
Epilobium sp.	4	1.000	0	3	3	**7**	7	0	0	20	20	**20**	20	0	0	17	17	**33**	33	0
Galium palustre	4	1.000	5	0	5	**10**	0	0	20	0	20	**20**	0	0	25	0	25	**50**	0	0
Bryum sp.	5	0.054	5	0	0	0	**45**	0	20	0	0	0	**60**	0	25	0	0	0	**75**	0
Peucedanum palustre	5	0.246	4	0	4	13	**34**	0	40	0	40	60	**60**	0	10	0	11	22	**57**	0
Succisa pratensis	5	0.353	0	0	2	7	**22**	0	0	0	20	20	**40**	0	0	0	9	36	**55**	0
Rubus chamaemorus	5	0.811	0	5	0	8	**17**	0	20	40	20	20	**40**	0	2	12	0	42	**43**	0
Plagiomnium cuspidatum	5	0.941	3	0	5	5	**8**	0	20	0	20	20	**20**	0	13	0	25	25	**38**	0
Equisetum fluviatile	5	0.969	0	1	6	5	**10**	2	0	20	40	20	**20**	33	0	3	15	27	**48**	7
Drosera rotundifolia	6	0.001	0	0	2	2	7	**84**	0	0	40	40	80	**100**	0	0	4	4	8	**84**

reliable indicators, the diagonal structure of Table 2 is striking; i.e. a certain assemblage of species is characteristic for every distance step, having there the highest relative frequency and cover values. Specific to the central parts of transitional mires, unaffected by drainage, is the simultaneous occurrence of typical raised bog species such as *Drosera rotundifolia*, *Rubus chamaemorus* and *Aulacomnium paluste* growing on hummocks with fen species such as *Equisetum fluviatile*, *Succisa pratensis*, *Peucedanum palustre*, *Carex nigra etc*. in hollows.

The results of the multiple regression analyses (Table A1, Appendix) confirm that different characteristics of vegetation structure usually depend on different environmental factors; or if an environmental factor that affects several vegetation characteristics is examined, its effects may have different signs. For example, absolute height of the mire surface has a negative effect on the total number of species, the number of shrub layer species, and the percentage of fen-specific species; but a positive impact on the number of bog-specific species. Higher O_2 content in peat water is associated with increases in the number of field layer species and the number of bottom vegetation and bog-specific species; whereas low O_2 content, which is characteristic of stagnant peat water, is associated with reduced tree layer canopy closure and a lower percentage of fen-specific species. The girths and heights of trees, as well as tree layer canopy closure, are negatively related to log-distance from the cutoff ditch; while the number of shrub layer stems and percentage of bog-specific species increases with distance from the cutoff ditch. The impact of peat water pH on the vegetation characteristics is negative in all models where it was included.

When interpreting the outcome of the multiple regression analyses, we have to consider that the results are not always unambiguous due to the collinearity of variables, i.e. some variables could be replaced by others which are strongly correlated with them without noticeable diminution of model quality statistics. In the current analyses we tried to mitigate this problem by selecting variables from tightly intercorrelated groups for the regression models on the basis of highest loading according to the factor analysis (Table 1).

DISCUSSION

The main effects induced by the drainage of mire ecosystems are well documented by several researchers. The extent of the impact is a function of distance from the drainage ditch(es), but depends additionally on numerous other variables which are more or less correlated with this factor (Reinikainen *et al*. 1984, Laine & Vanha-Majamaa 1992, Holden *et al.* 2004). The time since commencement of drainage (Brække 1983, Vasander 1987a,b, Minkkinen *et al*. 1999, Laiho *et al*. 2003) and properties of the peat such as 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) are also of great importance. At landscape scale, essential factors are the type of mire (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 and depth of drainage ditches (Pienimäki 1982, Brække 1983) and the distance between them (Ahti 1980, Belleau *et al.* 1992, Holden *et al*. 2004). Therefore, results expressing the range of the drainage effect on various environmental variables or vegetation characteristics in different regions or in mires of different types are usually rather divergent (Miller 2011). For example, concerning the extent of drainage impacts on the water table, Hainla (1957) pointed out that the groundwater level in Estonian transitional mire forests is unaffected at a distance of 50 m from a ditch. In Estonian drained bog forests the water level in the peat layer decreases rapidly in the zone closest to the ditch, but the drainage impact is already hardly noticeable at a distance of 10–20 m (Valk 2005). In Minnesota (USA), Boelter (1972) found that when the drainage ditch was 2 m deep and 2.5 m wide, the water table was lowered as far as 50 m from the ditch in an organic soil with less decomposed fibric peat, but when the ditch was 1.5 m deep and 2 m wide and the peat was highly decomposed and compacted, the water level was influenced only within 5 m of the ditch. According to different researchers in Québec (Canada), drainage of forested peatlands affected the water level up to a distance of 15 m (Prévost *et al*. 1997), 30 m (Belleau *et al*. 1992) or 60 m (Roy *et al*. 2000) from the drainage ditches.

Our results, showing a drainage effect of the cutoff ditch on the transitional mire water level up to a distance of at least 250 m, seem to be rather different from the cited studies. The reasons may be as follows: (i) our sites were open or sparsely wooded transitional mires, rather than mire forests where the tree layer consumes and transpires much water and has a considerable impact on the water level; and (ii) our study was carried out using transects encompassing the full hydrosequence from the cutoff ditch up to the central part of the mire massif.

Moreover, we did not rely on short-term or seasonal measurements of the water table, but followed its dynamics throughout the year in already stabilised ecosystems where the initially fast peat surface subsidence had already taken place.

Water level drawdown and associated physicochemical factors derived from peat drainage lead to significant changes in mire vegetation. The most obvious is the increased growth of tree layer species noticed by several investigators (e.g. Vasander 1987a,b, Prévost *et al*. 1997, Laiho *et al*. 2003). Nevertheless, estimates of the actual extent of the drainage impact on tree layer growth are rather scattered. According to Hainla (1957), tree height in Estonian drained transitional mire was still double that in undrained stands at a distance of 150–170 m from the ditch; and in Belarussian transitional mire forests the drainage impact on the tree layer was weakly observable even at a distance of 400 m (Leivikov 1926). Our results indicate that the magnitudes of the increases in tree layer canopy closure, tree girth and height are about the same within distances of up to 200 m from the cutoff ditch, especially taking into account that we did not deal with mire forests but only treed mires. Results based on modelling suggest that drainage can have an impact on bog forest growth parameters up to a distance of 250 m from the ditch (Padari & Kiviste 2005). The results we obtained for changes in canopy cover and average height of the tree layer (using detailed data derived from LIDAR) demonstrate objectively a drainage impact extending up to 350–400 m from the cutoff ditch. The enhanced growth of trees in transitional mires influenced by drainage can be attributed mainly to lowered water level which improves the aeration of peat water, especially in the growing season, but also to increased pH and nutrient availability due to peat mineralisation.

Drainage and increased shading by the tree layer (Reinikainen *et al*. 1984, Vasander 1987a,b, Laine *et al*. 1995) stimulate significant changes in the lower vegetation layers, especially in terms of species composition. In raised bogs and transitional mires, typical mire plant species are replaced by forest species (Sarasto 1957, Laine & Vanha-Majamaa 1992, Korpela 2004, *etc*.). The most dramatic changes are in the ground vegetation (moss layer), where *Sphagnum* species are replaced by other mosses like *Pleurozium schreberi*, *Hylocomium splendens*, *Dicranum polysetum* and *D. scoparium* (Hainla 1957, Reinikainen *et al*. 1984, Laine *et al*. 1995, Korpela 2004). In Estonian transitional mires eleven years after drainage, *Andromeda polifolia*, *Chamaedaphne calyculata*, *Drosera rotundifolia*, *Equisetum fluviatile*, *Lysimachia thyrsiflora* and *Malaxis paludosa* all disappeared from the field layer and species such as *Fragaria vesca*, *Valeriana officinalis*, *Solidago virgaurea*, *Poa compressa*, *Galium verum*, *Epilobium montanum*, *Mycelis muralis*, *Linnaea borealis*, *Gymnocarpium dryopteris, etc*. were recorded as new species (Kollist 1987). The most conspicuous change in the shrub layer is the increased density of *Frangula alnus* near ditches and the disappearance of species such as *Betula nana* and *Salix rosmarinifolia* (Kollist 1957). Although Kollist (1957) only compared data from vegetation analyses conducted at 5–30 m and 120–145 m from the drainage ditch, he underlined the continuous change in species composition with distance from the ditch.

The results of the indicator species analysis enabled an explicit overview of how the drainage-induced changes in vegetation composition come about not only in Estonian transitional mires but also in other regions with similar conditions. Comparing our results with the scarce data published by other researchers, it turns out that drainage has a considerably larger effect on the ground vegetation of transitional mires than previously stated. According to Poulin *et al*. (1999), drainage had an impact on *Sphagnum* cover up to 60 m from drainage ditches on peatlands in Québec and New Brunswick (Canada), while Trettin *et al*. (1991) reported a drainage impact at 150–200 m from ditches for peatlands situated on top of sand deposits. These estimates are rather modest in comparison with the extent of approximately 400 m for the effects on shrub height, *Sphagnum* species and moss layer cover found in this study. However, this accords well with the higher vulnerability of transitional mires, where a deep cutoff ditch effectively drains not only water from precipitation (as in ombrotrophic bogs) with habitat-scale repercussions; but also groundwater, which affects water level on a landscape scale.

CONCLUSIONS

1. The principal environmental variables driven by drainage in Estonian transitional mires and determining the vegetation structure are the minimum water level in the peat layer, and the dry matter and total-N contents of peat. These variables are closely correlated.

2. The drawdown effect of a cutoff ditch on the minimum water level extends up to a distance of 250–320 m.

3. Minimum water levels higher than -50 cm are associated with increased cover of *Sphagnum*

species and total cover of the moss layer; the percentage of bog-specific species increases when the minimum water level is higher than -25 cm.

4. For variables reflecting vegetation structure, distance from the cutoff ditch is most strongly correlated with tree layer characteristics (sum of tree girths, sum of tree heights, tree layer canopy closure and tree layer canopy cover as determined by LIDAR data). The values of the first three variables decrease sharply up to a distance of 200 m from the cutoff ditch, whereas the tree layer canopy cover estimated using LIDAR data decreases rapidly in the first 260–270 m; after that it continues to decrease slowly up to 400 m. The LIDAR-derived average tree height decreases considerably in the first 150 m from the cutoff ditch, after which it decreases slowly up to 350 m.

5. The number of shrub stems and their height starts to increase 16 m from the cutoff ditch, continuing up to 100–130 m.

6. The percentage of bog-specific species increases up to a distance of 100 m from the cutoff ditch, whilst the percentage of fen-specific species begins to decrease sharply at a distance of about 200 m from the cutoff ditch.

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Appendix

Table A1. Environmental factors affecting vegetation structure according to the multiple regression analyses by stepwise backward removal of variables. Notations: B = non-standardised regression coefficient (slope); SE_B = its standard error; t = value of t-criterion; p = significance level; β = standardised regression coefficient; $SE_β$ = its standard error.

Variable	B	SE_B	t_B	p_B	β	$SE_β$
Total number of species						
Intercept	31.91	4.45	7.17	<0.001		
Absolute height of mire surface	-0.50	0.10	-4.78	<0.001	-0.69	0.14
Minimum water level	0.22	0.08	2.59	0.016	0.64	0.25
Dry matter content of peat	1.13	0.43	2.60	0.016	0.64	0.25
Number of shrub layer species						
Intercept	8.78	0.72	12.13	<0.001		
Thickness of bog peat	-3.60	1.66	-2.17	0.040	-0.34	0.16
Absolute height of mire surface	-0.12	0.04	-3.29	0.003	-0.52	0.16
Number of field layer species						
Intercept	60.17	17.83	3.37	0.003		
Tree canopy cover derived from LIDAR data	-11.25	3.96	-2.84	0.010	-0.74	0.26
Average water level	0.25	0.09	2.84	0.010	0.72	0.25
O_2 content of peat water	3.18	1.02	3.13	0.005	1.31	0.42
pH of peat water	-7.97	3.18	-2.50	0.021	-1.31	0.52
Redox potential of peat water	-0.11	0.03	-3.57	0.002	-1.37	0.38
NH_4-N content of soil	0.29	0.10	2.79	0.011	0.67	0.24
Total-N content of soil	4.10	1.46	2.82	0.011	0.86	0.31
Number of bottom vegetation species						
Intercept	-1.48	2.59	-0.57	0.574		
Depth of cutoff ditch (cm)	2.84	0.88	3.21	0.004	0.79	0.24
Average water level	0.27	0.10	2.66	0.014	0.74	0.28
O_2 content of peat water	2.42	0.58	4.15	0.001	0.94	0.23
Dry matter content of peat	0.45	0.20	2.26	0.003	0.54	0.24
Sum of tree girths						
Intercept	786.55	74.93	10.50	<0.001		
Log-distance from cutoff ditch	-302.39	41.98	-7.20	<0.001	-0.82	0.11
Tree layer canopy closure						
Intercept	146.69	28.36	5.17	<0.001		
Log-distance from cutoff ditch	-34.83	4.65	-7.49	<0.001	-0.78	0.10
Slope of cutoff ditch	47.86	14.95	3.20	0.004	0.49	0.15
O_2 content of peat water	-7.02	3.32	-2.12	0.046	-0.31	0.15
pH of peat water	-26.75	8.75	-3.06	0.006	-0.47	0.15
Ash content of soil	10.89	4.39	2.48	0.021	0.36	0.15

continued overleaf

Table A1 continued

Variable	B	SE_B	t_B	p_B	β	$SE_β$
Sum of tree heights						
Intercept	198.15	17.82	11.12	<0.001		
Log-distance from cutoff ditch	-77.97	9.98	-7.80	<0.001	-0.84	0.11
Sum of shrub layer stem numbers						
Intercept	-662.19	185.18	-3.58	0.002		
Log-distance from cutoff ditch	164.33	57.13	2.88	0.009	0.59	0.20
Depth of cutoff ditch	171.52	46.15	3.72	0.001	0.86	0.23
Minimum water level	12.90	2.89	4.47	<0.001	1.46	0.33
Saturation of peat water with dissolved O_2	13.95	4.04	3.45	0.002	0.74	0.21
Dry matter content of peat	46.65	14.04	3.32	0.003	1.03	0.31
Cover of *Sphagnum* species						
Intercept	65.25	19.95	3.27	0.003		
Thickness of bog peat	41.56	19.67	2.11	0.046	0.22	0.10
Minimum water level	1.54	0.21	7.34	<0.001	0.74	0.10
Redox potential of peat water	0.21	0.09	2.35	0.028	0.20	0.08
NO_3-N content of soil	-0.47	0.22	-2.13	0.044	-0.18	0.09
Number of bog-specific species						
Intercept	5.32	13.97	0.38	0.707		
Thickness of fen peat	4.38	1.72	2.55	0.019	0.83	0.32
Absolute height of mire surface	0.63	0.19	3.23	0.004	1.36	0.42
Slope of cutoff ditch	11.22	4.51	2.49	0.022	0.74	0.30
Tree layer coverage by the LIDAR data	-8.16	3.43	-2.38	0.027	-0.37	0.16
O_2 content of peat water	2.78	0.87	3.19	0.005	0.79	0.25
Conductivity of peat water	0.18	0.06	3.00	0.007	0.72	0.24
pH of peat water	-7.68	2.43	-3.17	0.005	-0.87	0.28
Percentage of bog-specific species						
Intercept	127.80	26.20	4.88	<0.001		
Log-distance from cutoff ditch	16.09	3.92	4.10	<0.001	0.48	0.12
Depth of cutoff ditch	-11.76	2.79	-4.22	<0.001	-0.49	0.12
pH of peat water	-22.03	4.92	-4.48	<0.001	-0.52	0.12
Percentage of fen-specific species						
Intercept	141.93	22.46	6.32	<0.001		
Thickness of transitional mire peat	18.29	6.32	2.90	0.008	0.60	0.21
Absolute height of mire surface	-2.29	0.44	-5.19	<0.001	-2.44	0.47
Depth of cutoff ditch	-20.05	3.82	-5.25	<0.001	-2.00	0.38
Slope of cutoff ditch	-63.72	12.11	-5.26	<0.001	-2.07	0.39
O_2 content of peat water	-4.15	1.88	-2.20	0.038	-0.58	0.26