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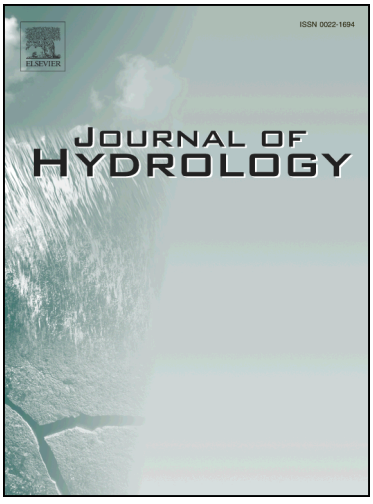

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POST-FIRE ECOHYDROLOGICAL CONDITIONS AT PEATLAND MARGINS IN DIFFERENT HYDROGEOLOGICAL SETTINGS OF THE BOREAL PLAIN

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ABSTRACT

In the Boreal Plain of Canada, the margins of peatland ecosystems that regulate solute and nutrient fluxes between peatlands and adjacent mineral uplands are prone to deep peat burning. Whether post-fire carbon accumulation is able to offset large carbon losses associated with the deep burning at peatland margins is unknown. For this reason, we examined how post-fire hydrological conditions (*i.e.* water table depth and periodicity, soil tension, and surface moisture content) and depth of burn were associated with moss recolonization at the peatland margins of three sites. We then interpreted these findings using a hydrogeological systems approach, given the importance of groundwater in determining conditions in the soil-plant-atmosphere continuum in peatlands. Peatland margins dominated by local groundwater flow from adjacent peatland middles were characterized by dynamic hydrological conditions that, when coupled with lowered peatland margin surface elevations due to deep burning, produced two common hydrological states: 1) flooding during wet periods and 2) rapid water table declines during dry periods. These dynamic hydrological states were unfavorable to peatland moss recolonization and bryophytes typical of post-fire recovery in mineral uplands became established. In contrast, at a peatland margin where post-fire hydrological conditions were moderated by larger-scale groundwater flow, flooding and rapid water table declines were infrequent and, subsequently, greater peatland-dwelling moss recolonization was observed. We argue that peatland margins poorly connected to larger-scale groundwater flow are not only prone to deep burning but also lags in post-fire moss recovery. Consequently, an associated reduction in post-fire peat accumulation may occur

and negatively affect the net carbon sink status and ecohydrological and biogeochemical function of these peatlands.

1. INTRODUCTION

Peatland ecosystems are wetlands characterized by thick organic deposits (NWWG, 1997) and have the highest carbon density per unit area of any ecosystem in the boreal biome (Bradshaw and Warkentin, 2015). Wildfire is the largest disturbance in spatial extent affecting peatlands ecosystems and, in sub-humid regions of the boreal forest, occurs as frequently in peatlands as in mineral uplands at 100 to 120 year intervals (Turetsky et al., 2004). Peatlands are generally resilient to typical (low) burn severity wildfires (depth of burn (DOB) = 0.05 to 0.10 m) (Benscoter and Wieder, 2003; Shetler et al., 2008) and return to a net carbon sink status ~20 years after wildfire (Wieder et al., 2009). However, deep burning (>0.20 m) has recently been observed at peatland margins in some hydrogeological settings of Alberta's Boreal Plain (Hokanson et al., 2016; Lukenbach et al., 2015b). Given that upland-peatland margins are important zones for biogeochemical transformations in this landscape (Dimitrov et al., 2014a; Hartshorn et al., 2003), potential shifts in ecohydrological and biogeochemical function due to deep burning are a concern (Lukenbach et al., 2015b; Kettridge et al., 2015).

The short and long-term effects of wildfire will, in part, be controlled by whether the rate of post-fire carbon accumulation is able to offset large carbon losses associated with deep burning. In peatland ecosystems, the rate and pattern characterizing the recolonization of peat-forming vegetation (e.g. *Sphagnum*, *Carex*) is critical for post-fire carbon (re-)

accumulation and, by extension, the maintenance of ecosystem structure and function (*e.g.* Rydin et al., 2013). As such, the aim of this paper was to examine how both hydrogeological setting and deep burning affect post-fire hydrological conditions at peatland margins and how these hydrological conditions relate to patterns of post-fire moss recolonization.

A peatland's interaction with different scales of groundwater flow has a large control on peatland water table (WT) positions and ecohydrological conditions (Aldous et al., 2015; Godwin et al., 2002; Winter, 1999). To minimize terminological confusion, we refer to this influence of groundwater based on the degree of connection between a peatland margin and larger-scale groundwater flow (*c.f.* Winter 2003). We provide a hypothetical conceptualization illustrating how connection to larger-scale groundwater flow influences WT positions along upland-peatland interfaces (Figure 1). Peatland margins poorly connected to larger-scale groundwater flow systems exhibit dynamic WT positions because water fluxes are dominated by atmospheric exchanges or localized groundwater flow to and from adjacent peatland middles (Ferone and Devito, 2004; Thompson et al., 2015). Rapid responses to near-term climatic conditions, in conjunction with the sub-humid climate of the Boreal Plain, result in rapid and deep (>1 m) WT drawdowns at peatland margins during drought (Ferone and Devito, 2004; Thompson et al., 2015). Such WT drawdowns subject the dense peat within margins to low moisture contents that, when coinciding with wildfire, results in the frequent occurrence of deep burning (Figure 1) (Lukenbach et al., 2015b). Although these margins are a relatively small proportion

(<10%) of the total area of a peatland, deep burning can account for as much as 50 to 90% of the total carbon loss, even in larger (>50 ha) peatlands (Hokanson et al., 2016).

The groundwater-soil-plant-atmosphere continuum (*c.f.* Gou and Miller, 2014) in peatlands is characterized by strong linkages between groundwater and the atmosphere through vadose zone processes (Dettmann and Bechtold, 2016; Thompson et al., 2013a). Our conceptual model demonstrates how shallow and deep WTs influence volumetric moisture content (θ) and soil tension (Ψ) in peat depth profiles (Figure 1) (Thompson and Waddington, 2008). When WTs are shallow, depth to WT-Ψ relationships often exhibit linear, close to 1:1 relationships (Lukenbach et al., 2015a; Lukenbach et al., 2016), indicating that water losses due to evaporation are rapidly replenished by upflux from the WT (Lukenbach et al., 2015a). Alternatively, during large WT drawdowns (>0.70m), this relationship becomes non-linear and near-surface Ψ rises appreciably (Lukenbach et al., 2015a; Lindholm and Markkula, 1984), resulting in water stress on peatland vegetation (Thompson and Waddington, 2008). These interactions helped explain slow post-fire moss recolonization in the middles of peatlands poorly connected to larger-scale groundwater flow systems, as these sites had more frequent and greater WT drawdowns (Lukenbach et al., 2015a). Given the role of hydrogeological setting in determining where peatland margins underwent deep burning (*i.e.* Figure 1a), it is likely that these same locations are also prone to low post-fire WT positions during dry periods and, accordingly, should exhibit a time-lag and/or different trajectory of recovery in post-fire vegetation recolonization.

Deep burning at peatland margins may also interact with the scale and/or type of groundwater flow influencing a peatland. Large organic soil losses at peatland margins may alter water and solute transfer between peatlands and adjacent mineral upland ecosystems. Moreover, deep burning potentially increases flooding frequency by lowering the elevation of the peat surface (Thompson and Waddington, 2013a) and increasing the duration of inundation. While dry conditions are known to limit peatland moss recolonization (Thompson et al., 2008), flooding may limit the ability of peatland vegetation to recolonize margin areas (Granath et al., 2010). This poor peat-forming moss recolonization could initiate a positive feedback, whereby the lack of peat accumulation further alters water and solute transfers at the upland-peatland interface and enables species endemic to uplands to colonize severely burned peatland margins (Johnstone and Chapin, 2006). This is particularly important because the encroachment of upland species onto legacy peat soils has the potential to further decrease soil carbon storage (Alexander and Mack, 2015).

To further understand the controls on the patterns and rates of peatland moss recolonization following wildfire in the Boreal Plain, we characterized post-fire ecohydrological conditions at peatland margins with linkages to different scales and types of groundwater flow (*i.e.* hydrogeological setting) at the Utikuma Region Study Area (URSA) in central Alberta. We hypothesized that peatland margins predominantly fed by local groundwater flow from adjacent peatland middles and poorly connected to larger-scale groundwater flow systems would have lower post-fire moss water availability during dry periods, as indicated by post-fire WTs, Ψ, and surface θ. We also anticipated

that deeply burned peatland margins would undergo more frequent flooding, especially during wet periods, potentially limiting peatland moss recolonization. Furthermore, three years post-fire we expected that flooded and/or dry (low WT, high Ψ, and low surface θ) conditions would be associated with lower surface vegetation (bryophytes) establishment.

2. METHODOLOGY

2.1 Study sites

Located in Alberta's Boreal Plain, URSA (56.107°N 115.561°W) is the location of a hydrogeological research program (Figure 2), which has studied the local and regional hydrology of numerous boreal ecosystems (*i.e.* pond-peatland-upland complexes) since 1999 (Devito et al., 2012; Devito et al., 2016). In this region, peatlands exist in a variety of landscape positions due to deep, heterogeneous glacial deposits overlying marine shale (Vogwill, 1978) and low topographic relief. The climate of the region is sub-humid and in some years potential evapotranspiration is greater than annual precipitation (Devito et al., 2012). In May 2011, a ~90,000 ha fire burned an extensive area of URSA (Devito et al., 2016).

Our study was carried out in lake catchments 16, 208, and 171 (Figures 2 and 3) and focused on the margins of three, small (<5 ha) peatlands. In the Lake 16 catchment, a ~0.5 ha ephemerally perched peatland (EP) is located on a coarse-textured glaciofluvial outwash between Lake 16 and Lake 5, both of which are part of a larger-scale groundwater flow system (Smerdon et al., 2005; Smerdon et al., 2007), in close proximity to a regional topographic high. In the Lake 208 catchment, a ~0.5 ha burned bog is

positioned in a coarse-textured glaciofluvial outwash on a regional topographic low. This flow-through (FT) bog is situated in a large-scale groundwater flow system that connects several large lakes (~450 – 900 ha) (Hokanson et al., 2016). In the Lake 171 catchment, a ~4 ha burned bog is positioned on a lacustrine clay plain (CP) and is part of a large peatland complex (Ferone and Devito, 2004). All three of the study sites are classified as bogs (based on pH and vegetation) and for additional details on the vegetation characteristics of the study peatlands see Lukenbach et al., (2015a).

The peatland margins of EP, FT and CP sites, also referred to as the lagg in humid climates (*cf.* Paradis et al., 2015), were defined as transitional riparian swamp zones bordering the forested upland (~ 8 to 10 m wide). Prior to fire, this zone was typified by a lack of LFH (organic horizon of litter + fibric + hemic) or soil A layer (*i.e.*, minimal or no transition between the LFH and underlying humus), but shallower peat depths than the middle of the peatland and an absence of the *Sphagnum* hummock microtopography. For additional details on the characterization of this zone see Dimitrov et al. (2014b).

To limit disturbance and effectively utilize instrumentation resources, we collected detailed hydrological measurements along one representative upland-peatland transect. These upland-peatland transects were representative of the sites' hydrogeological setting based on measurements at other upland-peatland transects at these same sites (Ferone and Devito, 2004; Hokanson et al., 2016; Lukenbach, unpublished data; Redding, 2009). Furthermore, the DOB at the peatland margins on these transects (Table 1) compared

well with or was lower than site-level averages (0.51 ± 0.02 m, 0.07 ± 0.01 m, and 0.19 ± 0.01 m at the EP, FT, and CP sites, respectively) (Hokanson et al., 2016).

2.2 Groundwater measurements and surveying

To characterize interactions between peatland margins and the groundwater flow systems at each site, a long-term monitoring network of wells and piezometers was augmented and sampled (*c.f.* Ferone and Devito, 2004; Smerdon et al., 2005; Redding 2009). In select locations at each site, we installed additional 0.05 m diameter PolyVinyl Chloride (PVC) wells and 0.025 m PVC piezometers following the method of Smerdon et al. (2005) to better define the groundwater flow systems. Areas that were underrepresented with instrumentation southwest of the EP site were interpreted based on numerical modelling by Smerdon et al. (2007). Wells and piezometers were also installed along upland-peatland transects. Except for the FT site, which did not have a mineral upland installation on the study transect, these installations were positioned at 1) the peatland middle, 2) the peatland margin, 3) the mineral margin, and 4) the mineral upland (Figure 4). The peatland groundwater well was positioned at the closest *Sphagnum* hummock-hollow microform to the peatland margin, while the peatland margin well was located where residual peat depths were >0.10 m and DOB was >0.05 m. The mineral margin well was located just beyond the edge of the peatland and was characterized by <0.03 m residual organic matter, while the mineral upland well was upslope from the mineral margin and characterized by these same substrate conditions.

Water levels and electrical conductivities in wells were measured weekly to monthly from May to September in 2013 and 2014 using a temperature-level-conductivity meter (Solinst, Georgetown, Ontario, Canada). Saturated hydraulic conductivities were measured in piezometers on the upland-peatland transect following the Hvorslev (1951) method. In select wells and piezometers, capacitance water level recorders (Odyssey Data Recording, Christchurch, New Zealand) or pressure transducers (Solinst, Georgetown, Canada) continuously recorded water levels at one-hour intervals. Water levels in wells and hydraulic heads in piezometers were determined by pairing water level data with survey data of the tops of the well and piezometer casings from a real-time kinematic GNSS differential GPS (Trimble R8; accuracy +/- 0.015 m) or theodolite. These survey data were also used to define surface elevations at one meter intervals between the peatland middle well and mineral margin well to calculate the percent of the upland-peatland transects that were flooded. Depth of burn (DOB) measurements were also approximated along these same transects every 0.25 m by measuring the difference in surface elevation between burned areas and surrounding unconsumed areas following the approach of previous studies (Kasischke et al., 2008; Lukenbach et al., 2015b; Mack et al., 2011). These data were used to reconstruct the elevation of the pre-fire peat surface by assuming that the elevation of the peatland surface prior to wildfire was a vertical offset of the DOB at each point on the transect.

2.3 Post-fire moss water availability measurements

At each site, measurements of soil tension (Ψ) were taken at a depth of 0.05 m in three peatland margin (*i.e.*, residual peat depths >0.10 m) locations one to three times each

week from May to September in 2013 and 2014 using tensiometers (Soil Measurement Systems, Tucson, Arizona, USA) and a UMS Infield tensimeter (Munich, Germany). In 2014 only, supplemental measurements of surface moisture content (θ) (top 0.03 m) were concurrently measured with Ψ using a Thetaprobe (Delta-T Devices, Burwell, Cambridge, UK) directly above each tensiometer cup. Measurements were calibrated following the technique of Kasischke et al. (2009). To determine depth to WT, Ψ data were paired with measurements of adjacent wells. Of note, tensiometers were representative of drier margin areas, as areas that were flooded at the start of the study were not instrumented.

2.4 Intensive field survey

2.4.1 Spatial measurements of post-fire moss water availability

Temporal hydrological measurements were supplemented by a one-time intensive field survey to further assess the spatial variability of post-fire moss water availability and examine conditions following an extended dry period. Water stress was expected to be highest in early September due to late summer drying that typically occurs in the sub-humid and continental climate of Alberta's Boreal Plain (Environment Canada, 2010). The intensive field survey consisted of the installation of eight tensiometers in peatland margins at each site at a depth of 0.05 m. The same locations where tensiometers were temporally measured during 2013 and 2014 were included in this sampling. Five days after installation on September 1st, 2014, the tensiometers were measured at all of the sites and all data were collected within a 4-hour period. Surface θ (top 0.03 m) was paired with Ψ measurements and 32 supplemental measurements of surface θ were taken in

peatland margins for a total of 40 surface θ measurements per site. This sampling was paired with DOB measurements using the same approach listed above (see section 2.2). Notably, DOB was >0.05 m at >95% of the margin at both EP and CP, while ~26% of FT's margin was covered by lightly burned feather mosses (DOB <0.03 m). Because a number of previous studies have shown that lightly burned feather mosses have low water availability and undergo delays in post-fire moss recolonization (*c.f.* Lukenbach et al., 2016; Lukenbach et al., 2015a) attributable to their water repellent condition (Kettridge et al., 2014), they were not sampled in this study.

2.4.2 Moss and bryophyte recolonization measurements

During the intensive field survey, measurements of % bryophyte species cover and % *Sphagnum* species cover were estimated in 0.10 x 0.10 m plots above each tensiometer cup and surface θ sampling location (n=8 per site) to examine the association with bryophyte recolonization. Additionally, 17 supplemental vegetation plots (Figure 4) were randomly sampled at each site's peatland margin (residual peat depths >0.10 m) and were paired with DOB measurements. Because the fire resulted in the complete combustion of ground layer vegetation, observations of % bryophyte species and *Sphagnum* cover are a direct measure of the recolonization three years after fire.

2.5 Statistical analyses

Due to limited instrumentation resources and the need to utilize sites that were part of the long-term hydrological research program at URSA, we only carried out measurements in one peatland in each hydrogeological setting. For this reason, the results of our statistical

analyses were carefully interpreted because the research design was pseudoreplicated (*c.f.* Hurlbert, 1984). Specifically, statistical differences between sites were assessed, rather than grouping them based on hydrogeological setting. We then evaluated site differences with respect to their hydrogeological setting (*c.f.* Davies and Gray, 2015 *for a discussion regarding pseudoreplication in landscape-scale natural experiments*). Ψ was natural logarithm transformed and surface θ was converted to a percent and square root transformed prior to statistical analyses to achieve equal variances and normally distributed residuals (normality evaluated using Lilliefors test). For the temporal measurements, repeated measures ANOVA was employed to account for repeated measurements of Ψ/surface θ in each plot (*n* ranged from 10 to 15 per year in each plot). This tested the effect of site (3 levels) and year (2 levels, nested within site) on Ψ and surface θ. For the intensive field survey, a one-way ANOVA of site and Tukey's HSD post-hoc test was used to examine differences between sites. Means and standard errors are reported unless noted otherwise.

To examine the effect of WTs on Ψ, robust (assumed error in both dependent and independent variables) ordinary least squares regression (OLS) was used. Additionally, the amount of time the hydraulic head difference between the near-surface peat (0.05 m depth) and the WT position did not exceed 10 cm was calculated (*c.f.* Thompson and Waddington, 2013b). Effectively, this indicates that moss water stress is low because water losses via surface evaporation are quickly replaced by upflux from the WT due to the high unsaturated hydraulic conductivity of peat under low Ψ (Price et al., 2008).

To associate DOB and hydrological variables measured at each plot with bryophyte recovery, and specifically the recovery of peatland-dwelling mosses (*i.e.* only *Polytricum strictum, Aulocomnium palustre,* and *Sphagnum* mosses; *c.f.* Benscoter and Vitt, 2008; Wieder et al., 2009), we performed two analyses. First, we examined the relationship between maximum WT height and peatland-dwelling moss percent cover to investigate the influence of flooding on the establishment of these typical peatland mosses. Second, we tested if there was a correlation between the ground vegetation composition (*i.e.* bryophytes) and DOB, and maximum, median or minimum WT position. To do the second test, we fitted a Nonmetric Multidimensional Scaling (NMDS) ordination, using Bray-Curtis dissimilarities in the R package vegan (version 2.4-1, Oksanen et al, 2016). An NMDS collapses information from multiple dimensions, here a species abundances matrix converted to a Bray-Curtis dissimilarity matrix, into a two-dimensional configuration (*i.e.* two axes) of the surveyed plots. We ran the NMDS with two or three dimensions and used stress as goodness of fit (a low value means better fit). A stress value <0.20 was considered acceptable for subsequent interpretation and analyses (McCune and Grace 2002). Explanatory variables can then be fit onto a two-dimensional surface through a multiple regression to associate the variables with change in plant community composition. This correlation between the variable and the ordination can be non-linear or linear, and we first tested if a non-linear fit was warranted by comparing quadratic and linear regression models (function *ordisurf* in *vegan*). As we did not find support for more complex non-linear models, we only present linear relationships. Permutation tests were employed to test the significance of the explanatory variable. This

test assumes independence of the data and we also performed permutations tests where we accounted for the within-site dependence by restricting permutations within sites.

3. RESULTS

3.1 Climatic context

For the majority of the study, wetter than average climatic conditions occurred due to the study period being preceded by above average precipitation in 2011 and 2012 and one of the largest snow accumulations in the past 15 years in spring 2013 (Environment Canada, 2010). Rainfall during May to September 2013 (Table 1) was near historical averages, as was rainfall during the fall of 2013 (Environment Canada, 2010). Snow accumulation in spring of 2014 was higher than average, while a dry period occurred during the 2014 study period. This was characterized by 50% less summer precipitation than the historical average (Table 1), and the rainfall deficit was most pronounced during July and August.

3.2 Peatland hydrogeological setting

Dominant interactions between localized groundwater flow at upland-peatland transects and larger-scale groundwater flow systems are shown in Figure 3. At all the sites, local groundwater mounds were consistently present in the peatlands and vertical hydraulic gradients indicated recharge (Figures 3, 4, and 5). However, water levels fluctuations along the upland-peatland transects at the EP and CP sites were much more dynamic than those observed at the FT site (Figure 5). Low hydraulic conductivities characterized underlying mineral substrates and adjacent mineral uplands at the EP and CP sites (Table 1), which minimized groundwater fluxes into and out of these peatlands. In contrast, the

mineral substrate and mineral uplands at the FT site had an approximately two orders of magnitude higher hydraulic conductivity than the site's middle and margin peat (Table 1), resulting in the site's stronger connection to larger-scale groundwater flow.

3.3 Post-fire upland-peatland hydrology

Flow reversals were commonly observed along upland-peatland transects at the EP and CP sites (Figure 5). Following large rainfall events (*i.e.* EP) or during wet periods (*i.e.* CP), water levels at either the mineral margin (*i.e.* EP) or mineral upland (*i.e.* CP) were highest. At the CP site, these wet periods resulted in focused flow to the peatland margin from the peatland middle and mineral upland (Figures 4 and 5). In contrast, the effect of rainfall rapidly dissipated at the mineral margin of the EP site and the peatland margin generally exhibited the highest water level during wet periods. Dry periods at the EP and CP sites were characterized by unidirectional flow moving from the peatland to the mineral upland (Figure 5). At the FT site, flow reversals were rare and the peatland middle water level was consistently highest, while the difference in water levels between the mineral margin and peatland margin was minimal throughout the study (Figure 5).

Large proportions of the peatland margins at the EP and CP sites were persistently flooded due to deep burning coupled with the dominance wet conditions (Figure 6). The onset of a dry period in 2014 reduced flooding at these peatland margins and WTs rapidly receded once they fell below the peat surface, resulting in large WT declines (>1.0 m) (Figures 4 and 5). In contrast, the absence of deep burning and dampened WT responses led to only small proportions of the FT site's peatland margin being flooded. During dry

periods at the FT site, WTs receded slowly and resulted in consistently shallower WTs than the other sites. At all the sites, electrical conductivities were low in peatland middles; however, substantial differences existed between the sites' peatland margins, mineral margins, and mineral uplands (Table 1).

3.4 Temporal post-fire moss water availability

Ψ did not vary across sites ($F_{2, 240}$ = 0.16, p = 0.86, Table 1) or between years ($F_{3, 240}$ = 0.91, p = 0.47), although plot had a significant effect on Ψ ($F_{12, 240}$ = 13.13, p <0.001). In 2014, surface θ was significantly different between plots ($F_{6, 87}$ = 5.74, p <0.001), but not across sites ($F_{2, 87}$ = 3.19, p = 0.11, Table 1). In tensiometer plots, depth to WT averaged 0.19 ± 0.12 m, 0.14 ± 0.06 m, and 0.17 ± 0.13 m at EP, FT, and CP, respectively, while depth to WT ranges were -0.11 to 0.93 m, -0.03 to 0.46 m, and 0.02 to 0.86 m at EP, FT, and CP, respectively, with negative values indicating that WT positions were above the peat surface. WT was a significant predictor of Ψ at all the sites (p <0.001, r^2 = 0.94, 0.86, 0.42 at the EP, FT, and CP sites, respectively) and hydraulic head differences less than 10 cm between near-surface margin peat and the WT position were present 97%, 94%, and 96% of the time at the peatland margins of the EP, FT, and CP sites, respectively. Based on these relationships, implied linear tension profiles in the unsaturated zone at each site are shown as accompanying side panels in Figure 4.

3.4 Intensive field survey

3.4.1 Spatial post-fire moss water availability

DOB averaged 0.26 ± 0.02 m, 0.07 ± 0.01 m, and 0.16 ± 0.01 m at the peatland margins of EP, FT, and CP, respectively (Table 1). Ψ values were generally higher and surface θ values were generally lower during the intensive field survey than the rest of the study because sampling occurred during a dry period (Table 1). In contrast to the temporal sampling, site had a significant effect on Ψ ($F_{2, 21}$ = 25.1, p <0.001) and surface θ ($F_{2, 120}$ = 4.38, p = 0.02). Table 1 shows post-hoc test results for Ψ and surface θ.

Where tensiometers were installed, depth to WT averaged 0.42 ± 0.02 m, 0.72 ± 0.08 m, and 0.94 ± 0.05 m at the FT, EP, and CP sites, respectively, while depth to WT ranges were 0.46 to 1.05 m, 0.39 to 0.51 m, and 0.62 to 1.08 m at the EP, FT, and CP sites, respectively. Robust OLS indicated that the WT was a significant predictor of Ψ at the EP and CP sites (p <0.001, r^2 = 0.79 and 0.48 at the EP and CP sites, respectively). Hydraulic head differences not greater than 10 cm between the WT position and near-surface peat were observed 100% of the time for both the FT and EP sites, and 50% of the time for the CP site.

3.4.2 Bryophyte recolonization

We observed large variation in ground layer vegetation recovery at peatland margins (Table 2). Recolonization of peatland-dwelling mosses were strongly controlled by flooding, as almost no recolonization of these mosses was recorded in plots where the WT had exceeded the peat surface at some point during the measurement period (Figure 7a). The effect of flooding was also evident in the bryophyte community analysis, but DOB also played a major role (NMDS, 2 dimensions, stress 0.18, Figure 7b). Maximum

WT largely explained the variation in bryophyte composition along the two first axes (r^2 = 0.51, p = 0.003), and it was mainly correlated with the first axis. *Marchantia polymorpha* was abundant in flooded plots, while *Polytrichum strictum* and *Sphagnum* are found on the other side of this gradient, except for one plot dominated by *S.magellanicum*. Similarly, DOB was strong predictor for the two first axes (r^2 = 0.42, p = 0.003) and Maximum WT and DOB were moderately correlated (r^2 = 0.42, p = 0.04). Median WT was a weaker, non-significant predictor (r^2 = 0.21, p = 0.08), and not shown in Figure 7b. The correlation between Maximum WT and Median WT was strong (r = 0.85). If permutation tests accounted for the within-site dependence, p-values increased to 0.09 and 0.15 for Maximum WT and DOB, respectively. An NMDS with three dimensions gave a lower stress value (0.11), but yielded similar results as the two dimensional NMDS.

4. DISCUSSION

4.1 Landscape-scale controls on post-fire peatland margin hydrology

Peatland margins at the EP and CP sites were poorly connected to larger-scale groundwater flow, resulting in dynamic hydrological conditions. In contrast, moderated water level fluctuations were observed at the FT site because it was well connected to a larger-scale groundwater flow system. Given that the EP and CP sites are located in substantially different hydrogeological settings, poor connections to larger-scale groundwater flow are attributable to different mechanisms. While coarse-textured geologic substrates in the region where the EP site is located generally means that groundwater fluxes to wetlands are significant in magnitude (Smerdon et al., 2005;

Smerdon et al., 2007), the presence of a fine-textured lens with low hydraulic conductivity resulted in a poor connection to the larger-scale groundwater flow system at the site and fostered the dominance of a localized within-peatland groundwater flow system (Winter, 1999). Although this was the observed interaction of the EP site with the larger-scale groundwater flow system, fluxes from the larger-scale groundwater flow system into the peatland or, potentially more likely, into peatland margins could occur during certain climate periods. This could happen because of the asynchronous response of different scales of groundwater flow to climate. Comparatively, the CP site's location on an expansive fine-textured clay till plain resulted in larger-scale groundwater flow exerting a small influence on the hydrology of the site (Ferone and Devito, 2004; Winter 1999). Moreover, the isolated location of the CP site within the larger peatland complex, attributable to the confining effect of surrounding low hydraulic conductivity mineral uplands, minimized groundwater fluxes from other parts of the peatland complex (Figure 3). In contrast to the EP and CP sites, a larger-scale groundwater flow system had a strong influence on the FT site's hydrology and water level fluctuations at the site were similar to those observed in the larger-scale groundwater flow system. Although a local groundwater flow system was superimposed on the larger-scale groundwater flow system, the magnitude of groundwater fluxes was dependent on the water level in the larger-scale groundwater flow rather than a fine-textured mineral substrate (Ferlatte et al., 2015).

While a hydrogeological systems approach is an effective approach to evaluate the impact of disturbances on wetlands (*e.g.* Winter, 2000), it has been infrequently

employed to assess wildfire impacts. These results demonstrate that post-fire recovery in peatlands should be evaluated in the context of hydrogeological setting and mineral substrate (Winter, 1999). Specifically, landscape-scale hydrological controls that influenced burn severity at peatland margins at the time of fire are also important in determining interactions in the post-fire groundwater-soil-plant-atmosphere continuum (Figure 1).

4.2 Controls on post-fire water availability

The low DOB that occurred at the FT site's peatland margin was similar to burn depths observed at peatland middles in other studies (*e.g.* Benscoter and Wieder, 2003), while deeper burns occurred at peatlands margins of the EP and CP sites (Table 1). Deep burning at the peatland margins of the EP and CP sites reduced the elevation of the peat surface, decreased depth to WT, and increased the frequency of flooding. Strong, linear relationships existed between depth to WT and Ψ at all sites, indicating a strong control of the WT on moss water availability. Notably, the weaker relationship between the WT and Ψ at the CP site was attributable to three measurements of low Ψ (wet) under deeper WT positions. If these data are removed, the r^2 rises to 0.81; however, they were retained in the analyses to avoid bias. Such relationships indicate that evaporative demand rarely exceeded the ability of water to be rapidly replenished by upflux from the WT at all the sites. This departs from our original conceptualization that WT-Ψ relationships are non-linear under low (>0.70 cm) WT positions (Figure 1). Furthermore, this is in contrast to post-fire conditions in the middle of peatlands, where post-fire water availability is more

influenced by pre-fire species cover and water repellency (Lukenbach et al., 2015a; Kettridge et al., 2014).

Small differences in Ψ and θ between the sites during the temporal sampling were likely attributable to the wet climatic period that dominated the majority of the study period. However, differences in moss water availability between the sites were more apparent during the intensive field survey, when dry conditions resulted in appreciably different peatland margin WT positions and, consequently, significant differences in Ψ. The significant difference in θ between the CP and FT sites during the intensive field survey should be interpreted cautiously, as this difference was small on an absolute basis and the power of the statistical test was greater due to larger sample sizes. As was the case during temporal sampling, Ψ was largely controlled by the position of the WT. Notably, although there was a non-significant WT-Ψ relationship at the FT site during the intensive field survey, this was very likely attributable to the narrow range (~0.10 m) in observed depth to WTs. These results demonstrate the influence of hydrogeological setting on moss water availability at peatland margins, given its influence on site-level WTs (section 4.1).

4.3 Post-fire bryophyte recovery at peatland margins

Flooding, as indicated by the maximum height of the WT, and DOB explained a large proportion of the variation in species recolonization at the sites (Figure 7). Not surprisingly, these variables were correlated, but DOB did exhibit explanatory power independent of the maximum height of the WT. The negative relationship between DOB

and peatland moss recolonization may indicate that thicker residual peat depths are more beneficial for recolonization (Salonen, 1994). However, this should be interpreted cautiously because lower burn depths were primarily associated with the FT site, which had conditions suitable for peatland moss recolonization. Median WT may have been a poor explanatory variable because of the prevalence of wet climatic conditions (*i.e.* shallow WTs/flooding) during the majority of the study period. It is also possible that the depth of inundation (*i.e.* maximum height of the WT) determines bryophyte survival in areas frequently flooded, but for locations experiencing minimal or no flooding the median/average depth to WT becomes more important.

Flooding may have created conditions that were too wet for peatland moss recolonization (Rochefort et al., 2002). Due to deeper burns and limited drainage through the fine-textured substrates at the EP and CP sites, flooding was more common and the depth of inundation was greater than at the FT site (Figures 6 and 7). Thus, when accounting for within-site dependence, it is more difficult to detect significant predictor effects in the NMDS because of site differences in flooding or, alternatively, non-hydrological site-specific differences accounted for this unexplained variance (Figure 6). Moreover, flooding may have inundated peatland margins with solute rich water, given the higher electrical conductivities at the EP and CP sites, thereby inhibiting the success of peatland mosses (Granath et al., 2010). Because lower solute concentrations were likely present at the FT site, it is possible that more frequent and deeper flooding at the FT site would have had a less negative effect on peatland moss recolonization than it may have had at the margins of the EP and CP sites. Thus, higher solute concentrations at the EP and CP

sites may explain why flooding was not beneficial for peatland moss recolonization compared to previous observations (Churchill et al., 2015).

Although flooding was a relatively stable state at the peatland margins of the EP and CP sites during wet periods, it rapidly transitioned to much drier conditions once the WT fell beneath the peat surface, likely due to the low specific yield of underlying dense peat and mineral soil (Boelter 1968; Sherwood et al., 2013). While wet conditions generally limited our ability to evaluate the impact of drier conditions on post-fire recolonization, previous research in peatlands has demonstrated that peatland moss recolonization is limited when depth to WT is >0.40 m (Price and Whitehead, 2001). Given that that lower water levels are common at the sites studied herein (*c.f.* Ferone and Devito, 2004; Smerdon et al., 2005; Hokanson et al., 2016), drought stress is likely more prevalent under average and dry portions of the climate cycle.

Previous research by Lukenbach et al. (2015a) in the middles of the same sites studied herein demonstrated that post-fire peatland moss recolonization was lower at the EP and CP sites compared to the FT site. However, species trajectories were generally characteristic of post-fire moss recovery in peatlands (Benscoter and Vitt, 2008). In this study, there were not only differences in the total amount of post-fire moss recolonization three years after fire between the sites but also in post-fire species compositions at peatland margins (Table 2, Figure 7). In particular, peatland margins at the EP and CP sites were either bare or primarily recolonized by *Marchantia polymorpha* and *Ceratadon purpureus*. Both of these species are characteristic of post-fire recovery in mineral upland

areas of the boreal forest (Bradbury, 2006). In contrast, the primary species recolonizing peatland margins at the FT site (*i.e. Polytricum strictum* and *Sphagnum* mosses) were species characteristic of post-fire recovery in the middles of peatlands (Benscoter and Vitt, 2008). The similarity in post-fire recolonization between the FT site's peatland middle (Lukenbach et al., 2015a) and its peatland margin (this study) may be due to the nutrient-poor environment along the upland-peatland transect at the FT site, which is associated with sandy boreal landscapes (Linder, 1987). Comparatively, pronounced differences in post-fire recolonization between peatland middles and margins of the EP and CP sites may be explained by the more prominent gradient in nutrient and solute availability along upland-peatland transition zones in fine-textured mineral substrates (Dimitrov et al., 2014a). Given that post-fire recovery of peat-forming vegetation not only lagged in the peatland margins of the EP and CP sites but also in their respective peatland middles, peatlands that are poorly connected to larger-scale groundwater flow systems may exhibit characteristically different trajectories of post-fire recovery and/or be undergoing a shift in vegetation cover.

4.4 Implications for peatland carbon dynamics and successional trajectories

Peat-forming vegetation (both mosses and vascular plants) is adapted to shallow WTs and less dynamic hydrological conditions than those observed at the peatland margins of the EP and CP sites (Rydin et al., 2013; Potvin et al., 2015). Therefore, peat-forming vegetation may have difficulty recolonizing in the long-term. Because thick (>0.20 m) peat deposits were present in areas that underwent deep burning at the EP and CP sites (Hokanson et al., 2016), legacy carbon lost during deep burning may not currently be

balanced by carbon sequestration between fire events (Hokanson et al., 2016; Lukenbach et al., 2015b). Furthermore, upland species, such as aspen (*Populus tremuloides*), can rapidly recolonize severely burned organic and mineral substrates (Johnstone and Chapin, 2006). If upland species successfully establish at peatland margins following wildfire, this may alter the ecohydrological function of such areas by making them drier due to increases in transpiration (Depante, 2016; Holmgren et al., 2015). Alternatively, frequent flooding in deeply burned locations may limit the encroachment of upland species (Bates et al., 1998). Nevertheless, given that climate change may increase total wildfire area burned (Flannigan et al., 2005) and organic layer burn severity (Kettridge et al., 2015; Turetsky et al., 2011) in the boreal forest, the net carbon sink status of peatlands in sub-humid regions may be at risk, especially in peatlands poorly connected to larger-scale groundwater flow systems. Future research should investigate the ubiquity of deep burning events and their associations with climate change to better understand the impacts of wildfire on peatland ecosystems.

5. CONCLUSION

Peatland margins poorly connected to larger-scale groundwater flow systems experienced greater burns depths, dynamic hydrological conditions, frequent flooding, and post-fire trajectories that resembled mineral uplands in the boreal forest. In contrast, a peatland margin well connected to a larger-scale groundwater flow system experienced lower burn depths, moderated hydrological conditions, infrequent flooding, and a post-fire trajectory of recovery similar to the middles of peatlands. Our study highlights that the interplay between flooding and drought stress at peatland margins is particularly important in

determining post-fire recovery and is influenced by hydrogeological setting. Indeed, it is possible that both peatland and upland vegetation are likely to have difficulty establishing at deeply burned peatland margins, given the dual stressors of flooding and WT drawdowns. Thus, if peat is unable to re-accumulate over the long-term following deep burning, areas that were once peatland margins may be best characterized as boreal swamps (*c.f.* Locky et al., 2005) following deep burning.

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TABLE AND FIGURE CAPTIONS

Table 1: Hydrological variables along the upland-peatland transect at each site. Abbreviations for locations are: P (peatland middle), PM (peatland margin), MM (mineral margin), and MU (mineral upland). Abbreviations for variables are: EC (electrical conductivity), K_{sat} (hydraulic conductivity), DOB (depth of burn), surface volumetric water content (VWC), and intensive field survey (IFS). Study area mineral K_{sat} for the FT (flow-through), EP (ephemerally-perched), and CP (clay plain) sites are from Redding (2009), Smerdon et al. (2005), and Ferone and Devito (2004), respectively. Rainfall totals shown are from May 1 to September 30 in peatlands. Significant differences within rows are denoted by lowercase letter superscripts for tension (n=3), VWC (n=3), intensive field survey tension (n=8), and intensive field survey VWC (n=40). Means and standard errors (in parentheses) are reported.

Table 2: Percent bryophyte recolonization of each species from 100 cm^2 plots (n=25) three years after fire on residual peat substrates (>0.10 m deep) at peatland margins, where tensiometers and surface moisture were measured during the intensive field survey (see Table 1). Means are reported and standard errors are shown in parentheses.

Figure 1: Hypothetical conceptual model of the groundwater-soil-plant-atmosphere continuum along upland-peatland transition zones at two disparate locations on a hydrogeological gradient: a) a site poorly connected to larger-scale groundwater flow and b) a site well connected to larger-scale groundwater flow. Dashed red, black, and blue lines indicate water table configurations during wet, mean, and dry conditions, respectively. Faint boxes on the cross sections correspond to the location of peat margin soil profiles shown on the right side of the figure. Soil profiles show pre and post-fire tension profiles (dotted lines), volumetric water content profiles (solid lines), and water tables (dashed lines) under dry (red) and wet (blue) conditions with the likely burn scenarios (high versus low severity) influencing post-fire conditions. Under saturated conditions, tension profiles are not shown. In both the cross sections and profiles, the peat color gradient represents differences in bulk density (darker = denser). Trees are scaled according to their anticipated size under the different water table depths.

Figure 2: Geology and hydrologic response areas (HRA) of the Utikuma Region Study Area (URSA), showing the location of the study sites (FT = flow-though, EP = ephemerally perched, and CP = clay plain) relative to generalized landforms indicating coarse versus fine-textured glacial deposits (modified from Fenton et al., 2013). Red boxes show the extent of the study areas shown in Figure 3.

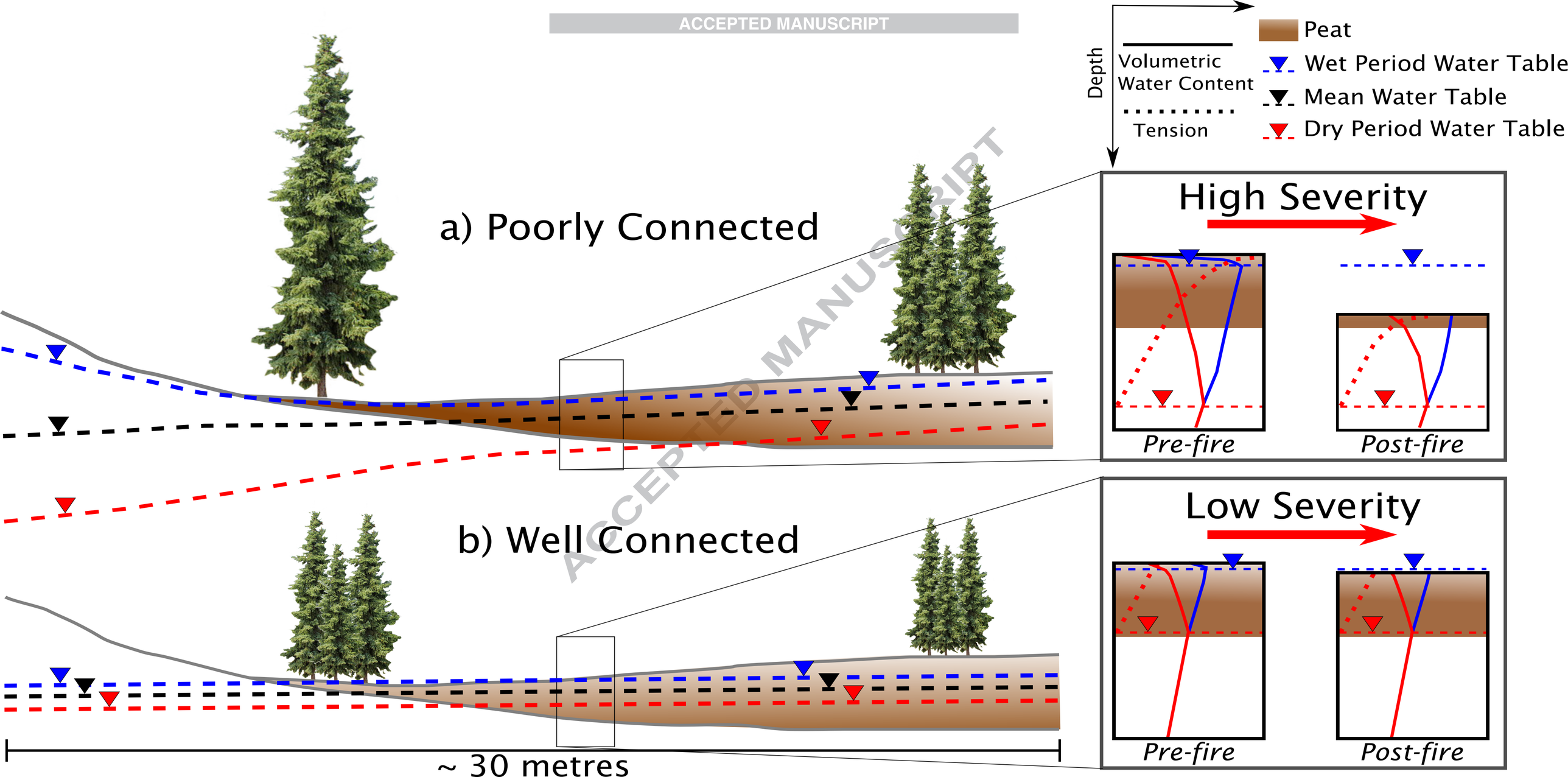
Figure 3: Water table (WT) contours (solid lines) at a) EP, b) FT, and c) CP with black dots denoting the locations of wells and/or piezometers nests and red lines indicating the study transects (letters correspond to upland positions in Figure 4). Red stars mark the location of lakes and groundwater wells with data shown in Figure 5. Peatland areas are hatched and un-hatched areas are comprised of mineral soils. WT contours are based on data from July 1, 2014 at the EP and FT sites and from July 3, 2014 at the CP site. Black arrows are indicative of the larger-scale groundwater flow systems, while magenta arrows highlight the interaction of groundwater flow at the upland-peatland transect with the larger-scale groundwater flow systems. Arrow lengths indicate the relative magnitude of groundwater fluxes within and between sites and reflect the approximately five order of magnitude range in hydraulic conductivity (10^{-3} – 10^{-8} m/s, Table 1). Note the difference in contour intervals: 0.5 m for (a) and 0.2 m for (b) and (c). Shading represents ground surface elevation in masl. In the northwest section of panel a), all open water is Lake 5 and in panel b) open water on the west, south, and east sides are the same lake. The interpreted water tables in the southeast corner of panel a) are based on simulations by Smerdon et al. (2007).

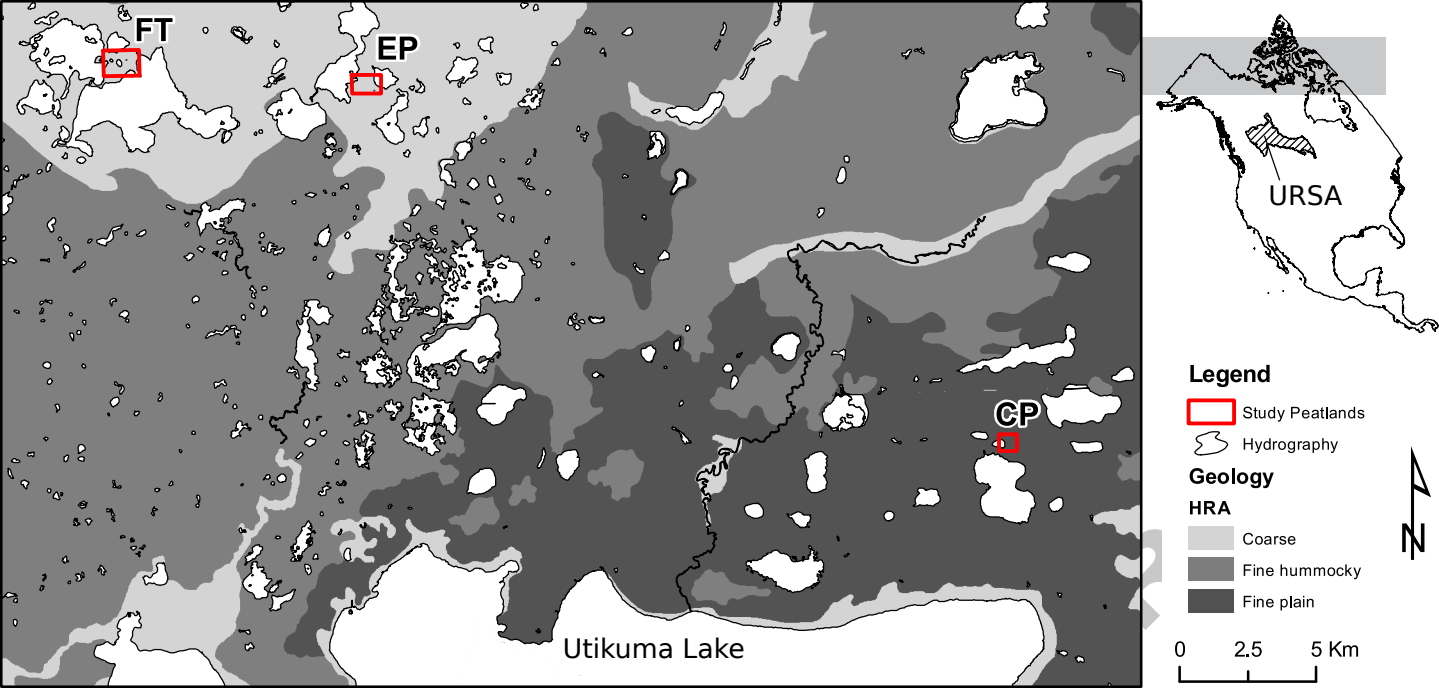
Figure 4: Cross-sections of upland-peatland transects at a) EP, b) FT, and c) CP showing high (blue lines and numbers) and low (red lines and numbers) WT positions as well as high (in parentheses) and low (no parentheses) hydraulic heads in piezometers and wells during the study period. High WT positions are based on data from June 2nd, 2013, June 1st, 2014, and June 15, 2014 at EP, FT, and CP, respectively, while low WT positions are based on data from August 16th, 2014 at all three sites, respectively. Black horizontal bars indicate the zone where tensiometer and vegetation measurements were collected at peatland margins. The estimated pre-fire peat surface is also shown (black dashed line) at EP and CP (see section 2.2 for details). Accompanying plots for each cross section reflect the implied (linear) mean and driest tension profiles in the unsaturated zone from the inset red boxes at each site's peatland margins.

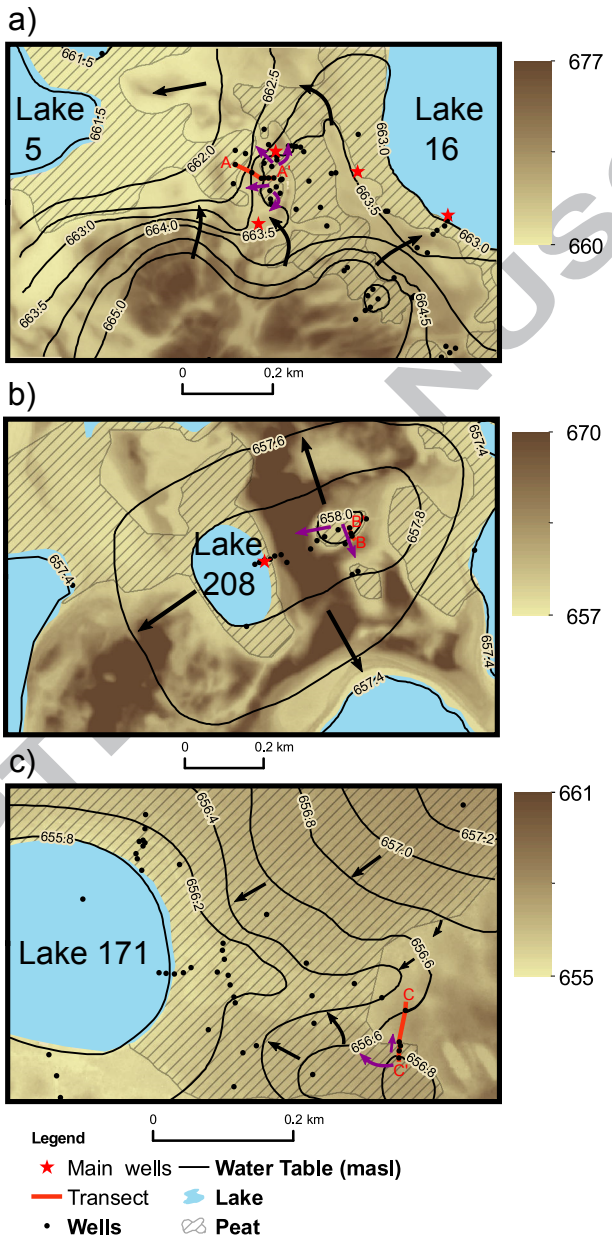
Figure 5: Water levels at EP (a & b), FT (c & d), and CP (e & f) in the peatland middle, peatland margin, mineral margin, and mineral upland in 2013 and 2014. Water levels at nearby lakes (EP and FT) and larger-scale groundwater flow system wells (Int. GW Flow, only EP) highlight the position of these sites relative to their respective groundwater flow systems. Continuous lines are water level recorder or pressure transducer data, while points indicate manual measurements.

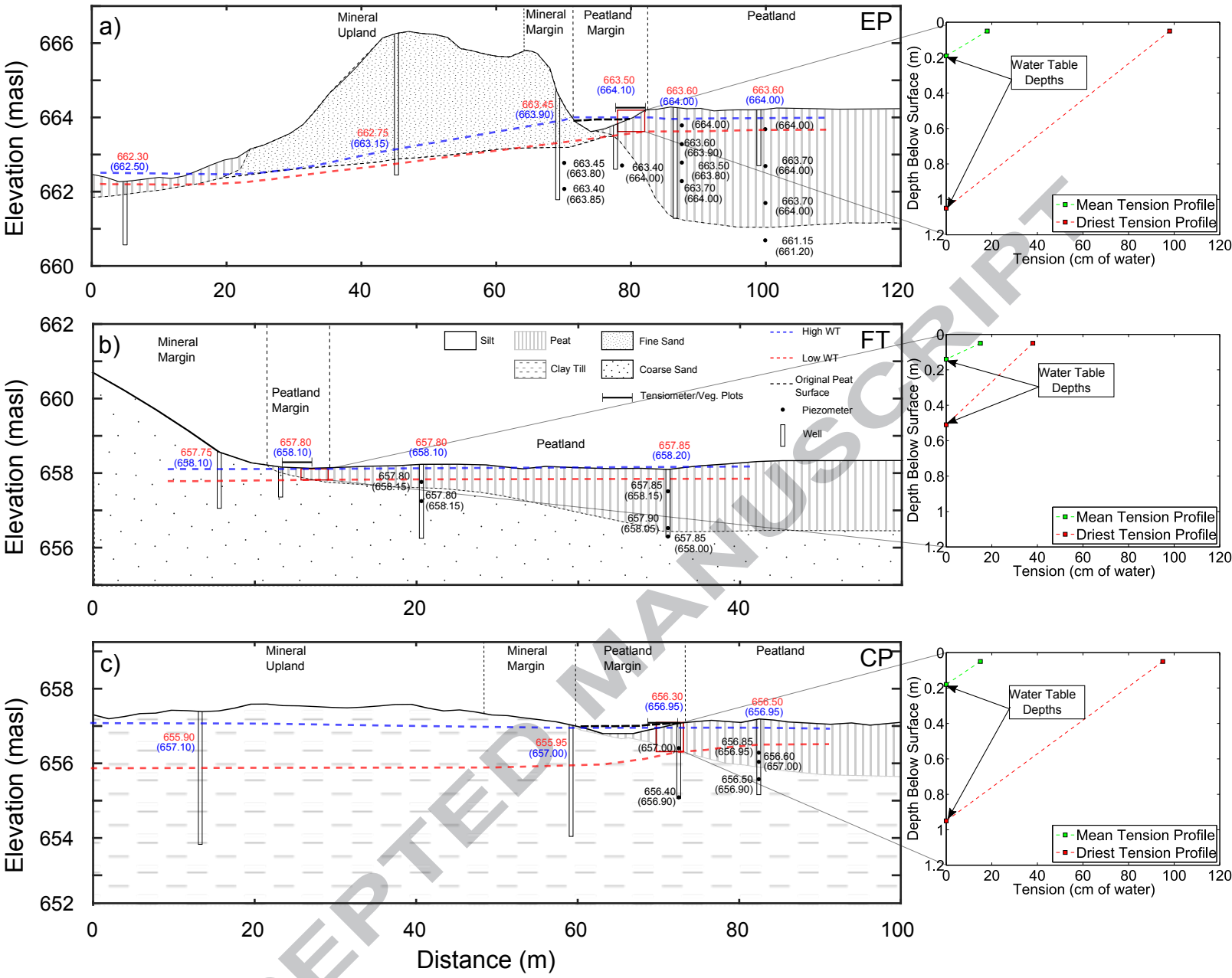
Figure 6: Histograms with 5% bin increments showing the percent of the upland-peatland transect flooded (between the peatland middle well and mineral margin well) versus the proportion of time (%) each flooding condition was present in 2013 and 2014 for EP (a & b), FT (c & d), and CP (e & f). Empty gaps between bins occur due to the resolution of surface elevation survey, sharp changes in surface elevation along each one-dimensional transect, or subtle changes in the WT having a large inundating effect.

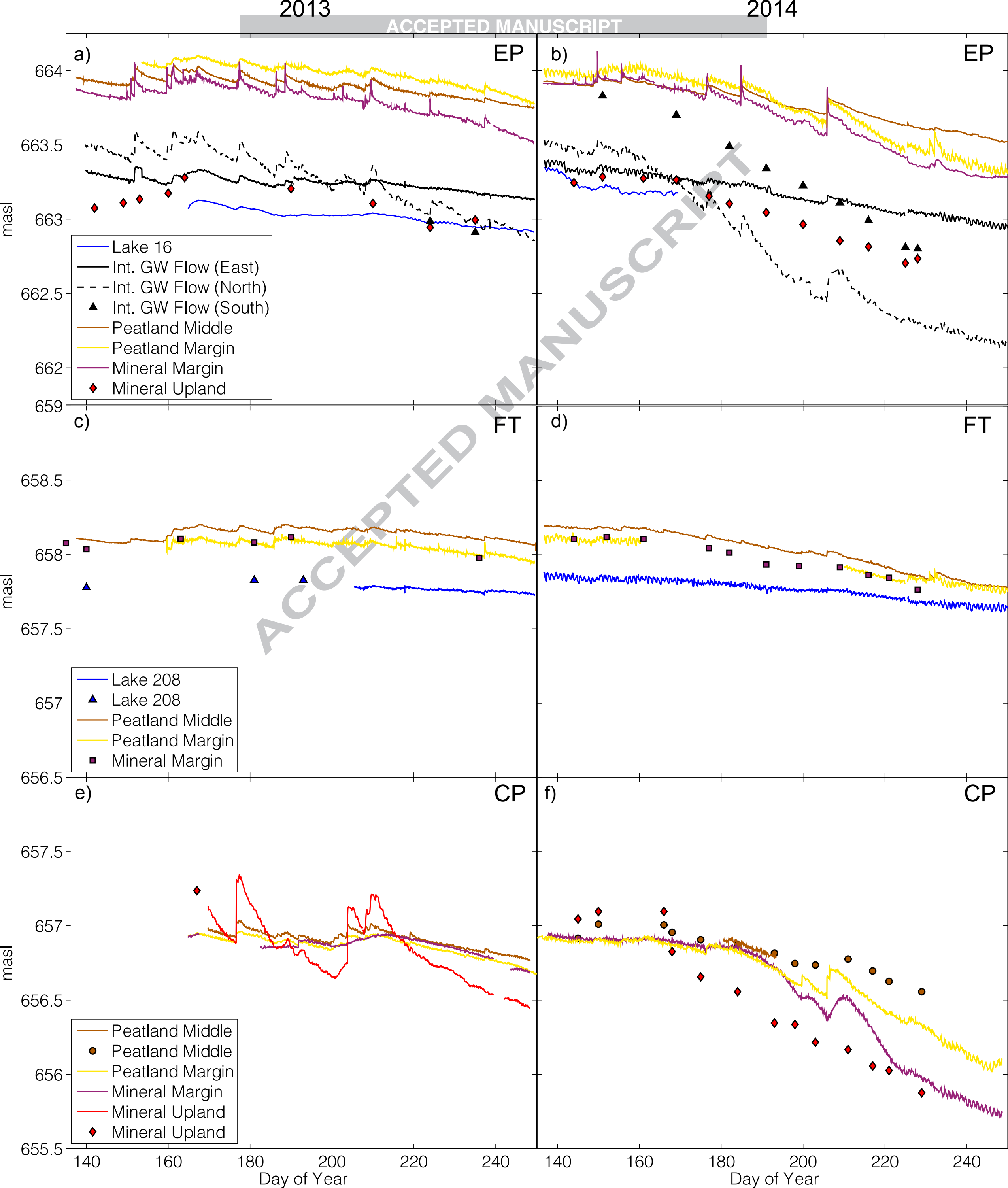
Figure 7: Influence of hydrological variables and DOB on ground vegetation recovery in the peatland margin of three investigated sites. a) the effect of maximum WT recorded during the measuring period (positive values indicate inundation) on the total cover of peatland-dwelling mosses (*i.e.* only *Polytricum strictum*, *Aulocomnium palustre*, and *Sphagnum* mosses). b) an ordination plot (NMDS, 2 dimensions, stress = 0.18) illustrating the bryophyte communities at sample plots (n = 75) along the first two axes. Species location in the NMDS space are weighted averages of the drawn sample plot points. For better visibility, not all species are shown and some species names have been adjusted to avoid overlap. Colors represent the three sites according to their hydrogeological setting abbreviation (*i.e.* EP, FT, and CP) and the cross sign shows plots where hydrological variables (*e.g.* WT) were measured. Arrows are the direction of the gradients (*i.e.* the fitted variables) and arrow lengths indicate the strength of the correlation between the ordination and the variable (n = 24). See text for statistical results. Full species names are given in Table 2.

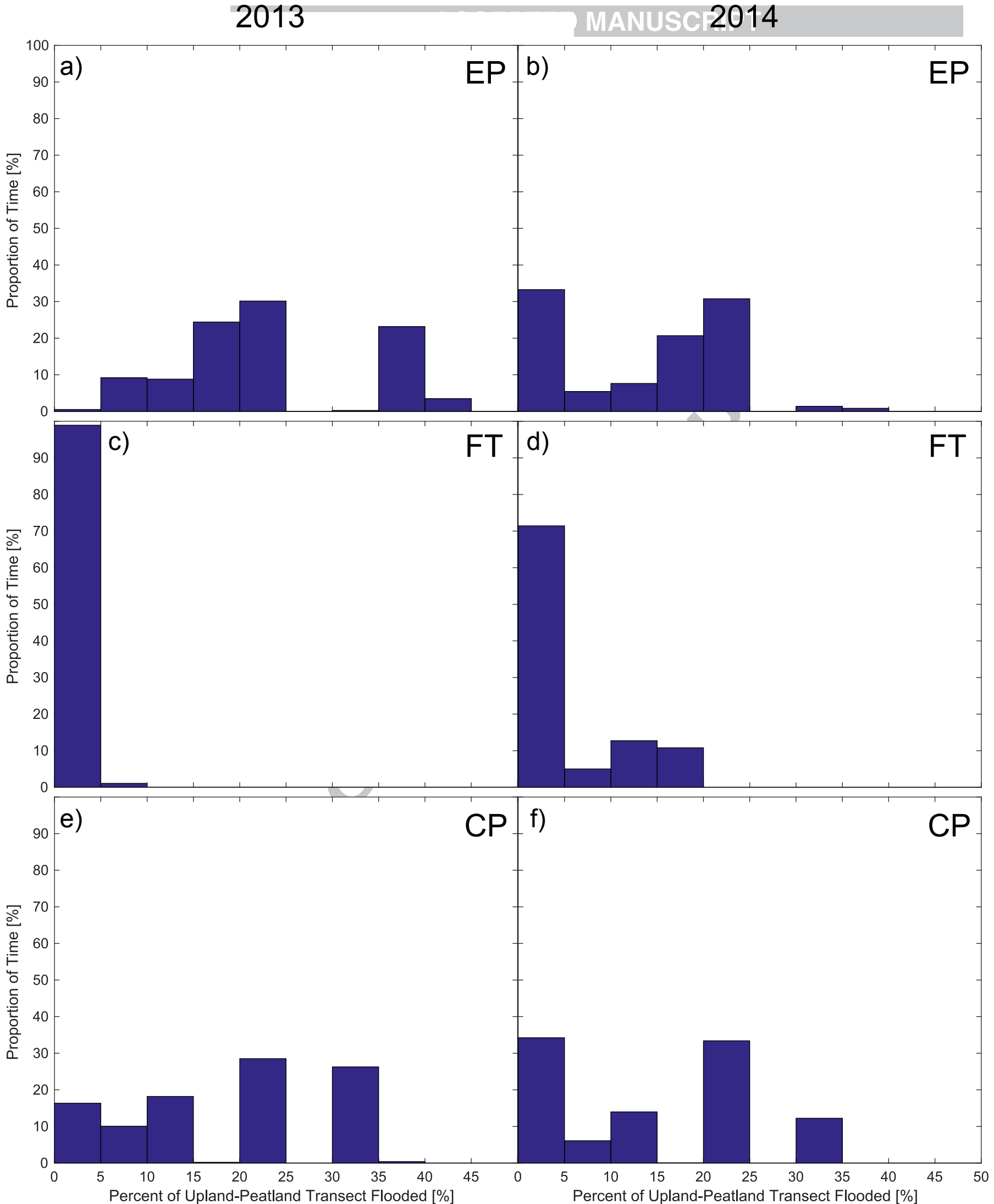


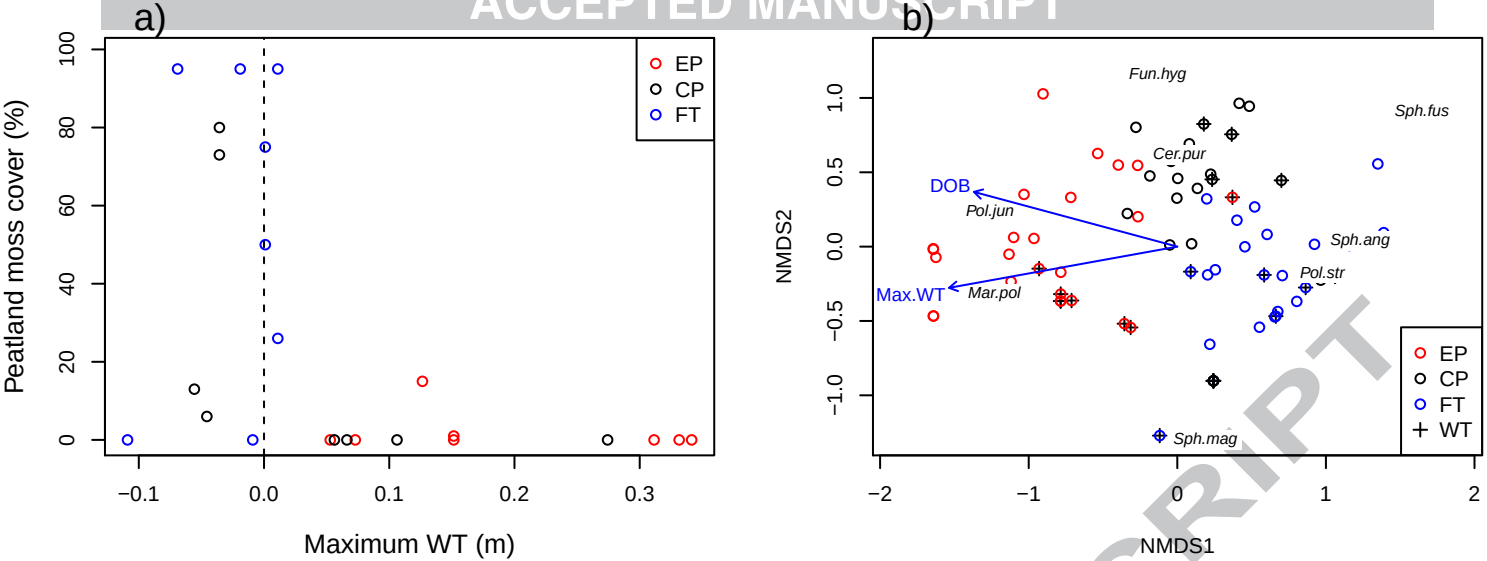

FT
EP
CP
Utikuma Lake
URSA
Legend
Study Peatlands
Hydrography
Geology
HRA
Coarse
Fine hummocky
Fine plain
N
0
2.5
5 Km








2013
2014
a)
EP
b)
EP
c)
FT
d)
FT
e)
CP
f)
CP
Proportion of Time [%]
Percent of Upland-Peatland Transect Flooded [%]
0
10
20
30
40
50
60
70
80
90
100
0
5
10
15
20
25
30
35
40
45
50



	Site											
	EP				FT				CP			
	P	PM	MM	MU	P	PM	MM	MU	P	PM	MM	MU
Rainfall 2013 (mm)	280	-	-	-	229	-	-	-	271	-	-	-
Rainfall 2014 (mm)	166	-	-	-	152	-	-	-	165	-	-	-
Shallow Well EC (μS cm^{-1})	77 (11)	94 (8)	113 (7)	986 (80)	54 (3)	40 (3)	22 (1)	-	91 (5)	104 (9)	959 (56)	3100 (249)
Lake Study Area K_{sat} (m s^{-1})	-	-	-	10^{-3}	-	-	-	10^{-5}	-	-	-	10^{-8}
Shallow Peat K_{sat} (<1.0 m, m s^{-1})	10^{-4}	10^{-4}	-	-	10^{-5}	10^{-6}	-	-	10^{-5}	10^{-7}	-	-
Deep Peat K_{sat} (>1.0 m, m s^{-1})	10^{-6}	-	-	-	10^{-5}	-	-	-	10^{-6}	-	-	-
Mineral K_{sat} (m s^{-1})	10^{-3}	10^{-3}	10^{-3}	-	10^{-8}	10^{-8}	10^{-8}	-	10^{-8}	10^{-8}	10^{-8}	-
DOB (m)	0.06	0.26	-	-	0.04	0.07	-	-	0.04	0.16	-	-
Peat Depth (m)	2.4	0.35	-	-	0.65	0.15	-	-	0.9	0.6	-	-
Tension (cm)	-	18 (9)[a]	-	-	-	15 (7)[a]	-	-	-	15 (9)[a]	-	-
VWC (cm^3 cm^{-3})	-	0.69 (.07)[a]	-	-	-	0.67 (.05)[a]	-	-	-	0.47 (.09)[a]	-	-
IFS Tension (cm)	-	63 (7)[b]	-	-	-	28 (3)[a]	-	-	-	128 (25)[c]	-	-
IFS VWC (cm^3 cm^{-3})	-	0.50 (.02)[a]	-	-	-	0.49 (.02)[ab]	-	-	-	0.43 (.02)[ac]	-	-

	Percent Cover										
Site	*Ceratodon purpureus*	*Polytricum strictum*	*Polytricum juniperium*	*Aulocomnium palustre*	*Funaria hygrometrica*	*Pohlia nutans*	*Marchantia polymorpha*	*Sphagnum angustifolium*	*Sphagnum magellanicum*	*Sphagnum fuscum*	Total
EP	13 (5)	1 (1)	10 (4)	1 (1)	3 (2)	1 (1)	59 (7)	0	0	0	88 (4)
FT	8 (3)	36 (7)	0	0	0	1 (1)	0	7 (3)	5 (4)	1 (1)	62 (6)
CP	34 (7)	15 (6)	2 (2)	12 (5)	3 (3)	1 (1)	2 (1)	0	0	0	70 (7)

l**Highlights**

1. Peatland margins are susceptible to severe burning and large carbon losses
2. Margins isolated from larger-scale groundwater flow are more hydrologically dynamic
3. Flooding at margins limited post-fire peatland-dwelling moss recolonization
4. Bryophytes characteristic of uplands recolonized hydrologically dynamic margins
5. Deep burning may alter peatland carbon stocks and ecohydrological function