Spring-season flooding is a primary control of vegetation succession trajectories in primary mires

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SUMMARY

Major regime shifts in mires such as the fen–bog transition and the transition from non-forested to forested peatland are driven by ecohydrological changes. However, little is known about how the magnitudes and/or durations of hydrological shifts relate to these regime shifts. Here we analyse long-term water table data in conjunction with plant community data collected from primary mires on the Finnish coast of the Gulf of Bothnia. These ecosystems represent various stages of drainage: undrained, drained sites with developing tree stands, and unsuccessfully drained sites not supporting tree encroachment. The varying success of drainage provides an ideal field laboratory for investigation of thresholds of water table control on the successional trajectories of primary mire. Our data indicate a likely mechanism for the control of vegetation regime shifts in northern peatlands by water table, with time of year being as important a factor as the magnitude of change. Spring flooding rather than summer water table level appeared to be crucial for controlling state shifts in primary mire vegetation. As the effects of climate change on peatlands are most likely to be mediated by changes in hydrology and water table level, our study indicates a need for more thorough investigation of seasonal variability in the controlling factors.

KEY WORDS: forestry drainage, regime shift, water table

INTRODUCTION

Peatlands are limited to areas with humid climate or local water excess (Joosten *et al.* 2017). At various stages during the development of peatlands, their vegetation communities undergo successional changes which are partly controlled by autogenic processes related to environmental changes caused by the increasing thickness of the peat layer. While multiple potential trajectories for succession are recognised (Walker *et al.* 2010), the typical successional trajectory of northern peatlands is from minerotrophic fen towards ombrotrophic bog (Klinger & Short 1996, Hughes & Dumayne-Peaty 2002). Any specific peatland trajectory arises from external forcing factors (e.g. climate), boundary conditions (e.g. drainage basin characteristics) and internal or autogenic processes (Charman 2002). However, successional change seems to be extremely slow or stagnant in some regions; for example, in the aapa mire zone of northern Eurasia (Väliranta *et al.* 2017) which is characterised by high spring-season water excess due to a combination of snowpack melt, catchment size and high effective precipitation minus evapotranspiration (P - ET) in spring/early summer (Ruuhijärvi 1982). Solantie (1986) places the southern limit of aapa mire occurrence at the latitude where June ET exceeds precipitation.

Ecotones are transition zones between ecosystem types and are considered to be highly vulnerable to climate change (Allen & Breshears 1998, Neilson 1993). Within the ecotone between aapa mires and raised bogs the persistence of aapa mires relies on local water excess; in other words, the ratio of catchment to peatland area needs to exceed a certain threshold. Accordingly, when a connection delivering catchment runoff to an aapa mire located within the southern ecotone of the aapa mire zone was disrupted, a vegetation transition towards ombrotrophication occurred in the mire within a few decades (Tahvanainen 2011). Peatland regime shifts or state changes other than fen–bog transitions are also associated with changes in water table; for example, the transition from non-forested to forested peatland (Laine *et al*. 1995). However, little is known about how the nature, magnitude and/or duration of a hydrological shift relates to a regime shift.

In a few parts of the world, peatland initiation via

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primary paludification still occurs, and small altitudinal and hydrological differences on newly exposed land determine whether the succession will proceed towards peatland or forest (Laine *et al*. 2016). Areas that become peatlands (Tuittila *et al.* 2013) are termed *primary mires* (Joosten *et al.* 2017), and their peat layers are not yet thick enough to allow autogenic hydrological regulation (e.g. Leppälä *et al.* 2011). On the Finnish coast of the Gulf of Bothnia, where postglacial rebound provides new land for ecosystem development, newly exposed wet parts of the landscape have been intentionally drained since the 1960s–1980s in order to direct succession towards forest instead of peatland. These areas are naturally poorly drained due to low, flat relief and relict shoreline ridges, but their sandy soils are prone to percolation and may therefore readily dry out, i.e. the amplitude of water table fluctuations may be large (Rehell & Heikkilä 2009, Laine *et al*. 2016). The low (2 m a.s.l.) flat terrain gives a poor prognosis for drainage success although, on the other hand, the poor hydrological self-regulation of the thin organic layers of primary mires means they are responsive even slight forcing of their hydrology, which is completely governed by basin characteristics (including any ditches). Therefore, these sites are particularly sensitive to alterations of drainage. Within this coastal landscape various stages of drainage can be found: undrained mires in early phases of development towards peatlands, drained sites with developing tree stands, and unsuccessfully drained sites not supporting tree encroachment. We have previously studied both the natural successional development of peatlands in this setting along the 10 km spatial continuum from the seashore to a 3000-year-old bog, and the effects of forestry drainage and restoration on vegetation structure and greenhouse gas emissions in the youngest sites. We found that the current vegetation assemblages formed a continuum from minerotrophic to ombrotrophic plant communities, consistent with the past succession revealed by vertical peat sequences at the older sites (Tuittila *et al.* 2013); and that vegetation structure and greenhouse gas emissions were rather resilient to environmental changes, i.e. restoration rather quickly reinstated functions typical of undrained conditions (Laine *et al.* 2016, 2019).

Here we analyse long-term water table data in conjunction with plant community data collected from two undrained and two drained primary mires on the Finnish coast of the Gulf of Bothnia (Figure 1). Because the sites are located within the aapa mire region and in a natural environment it is likely that, if their central parts stay wet, (ombrotrophic) bog vegetation will develop only at their edges as mire succession proceeds, similar to ‘true well-developed’ aapa mires. We aim to study the mechanism of water table change required to divert the successional trajectory from open mire to forested habitats. The specific hydrological regime of the sites makes it possible to quantify the threshold of water-level drawdown, as well as the seasonality of drainage effectiveness, that is most likely to causally connect to drainage succession.

METHODS

The study was carried out on the Finnish land-uplift coast of the Gulf of Bothnia in Tauvo, Siikajoki (64° 48′ N, 24° 38′ E, Figure 1). The 30-year (1979–2009) average precipitation and mean annual temperature are 539 mm and 2.6 °C, respectively, and the length of growing season is 150 days (Revonlahti, Siikajoki, 64° 41′ N, 25° 05′ E, 48 m a.s.l.; Finnish Meteorological Institute). We selected four primary mires, two undrained (*Undrained mire*, tree stand volume < 1 m^3 ha^{-1}) and two that have been drained for forestry purposes since the 1960s. At one site, drainage has led to tree stand formation (*Drained forest*, tree stand volume 106 m^3 ha^{-1}); at the other drained site, drainage has been much less successful in terms of forestry (*Poorly forested drained mire*, tree stand volume 37 m^3 ha^{-1}). Before drainage, the sites were all coastal primary mires in small (~0.5–3 ha) depressions between sand dunes, formed on nutrient-poor sandy soil 100–200 years ago via primary paludification of newly exposed uplifted land. The sites are now 1.5–2 m a.s.l. and have a 5–10 cm thick peat layer. The field layer vegetation of the *Undrained mires* is composed of graminoids (*Carex nigra, C. canescens*) and forbs (*Comarum palustre, Equisetum fluviatile, Peucedanum palustre*), while the moss layer is composed mainly of *Warnstorfia exannulata* and *Calliergon* species, with scattered patches of *Sphagnum* mosses (e.g. *S. squarrosum, S. fimbriatum*). At the drained sites, the field layer vegetation is dominated by shrubs (*Vaccinium uliginosum, V. vitis-idaea, Salix repens*) and the moss layer by feather mosses (*Pleurozium shreberii, Polytrichum commune*), although at the *Poorly forested drained mire* sedges (*Carex nigra, C. canescens*) are also abundant. More detailed site descriptions are given in Laine *et al.* (2016, 2019).

In the drained sites, the vegetation composition of field and ground layers (not including trees) was surveyed at 13–14 points using 1 × 1 m plots along transects covering the sites during the years 2006, 2009 and 2013. In undrained sites vegetation was surveyed in 2007, 2010 and 2013 at six 60 × 60 cm plots. Projection cover (%) of vascular plants and moss species was quantified visually. Water table depth (*WT*) was measured in May, August, and October, as the distance between water table and moss carpet surface or soil surface where mosses did not occur. At each site *WT* was measured in 6–14 dipwells (perforated plastic tubes ~ 3 cm i.d.) located next to vegetation sample plots. *WT* measurements were made from 2005 to 2014 in the drained sites and in 2007 and 2010–2014 in the undrained sites. Occasionally, the water table was below the bases of some of the dipwells; in those cases, the greatest

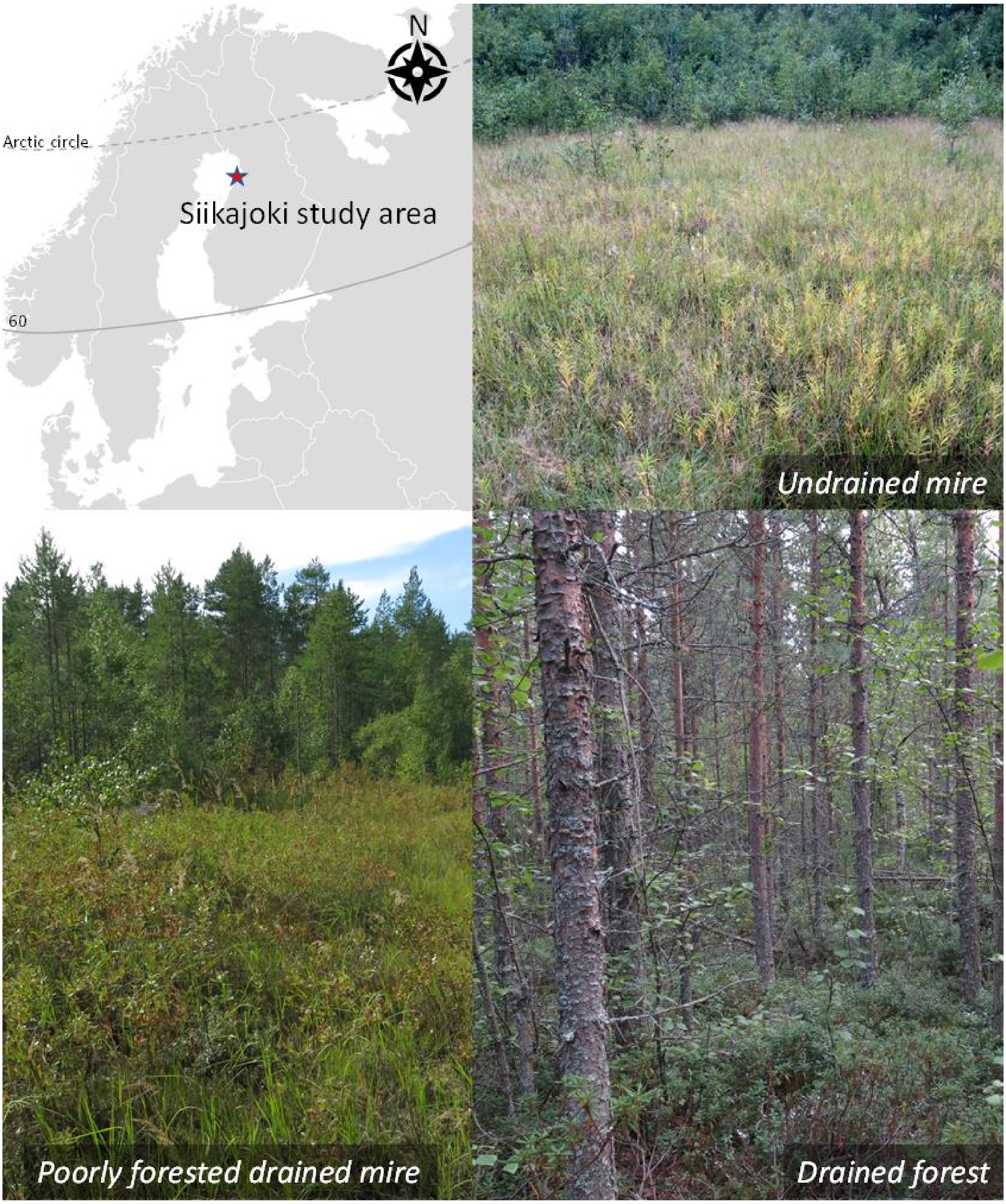

Figure 1. Map showing the study area, Siikajoki, Finland and photographs of the *Undrained mire*, *Poorly forested drained mire* and *Drained forest* sites.

value of *WT* recorded at the site during that measurement round (>60 cm below surface) was adopted in place of any missing values. Multivariate analyses, carried out with Canoco 5.02, were used to analyse the vegetation composition data; analysis details are reported in the Figure legends.

RESULTS

The sample plots from the *Poorly forested drained mire* scattered widely over the ordination space but could be divided into three groups along CCA Axis 1 that separated *Undrained* and *Drained forest* sites as constrained by canonical function of drainage state (0/1) (Figure 2). The vegetation composition of Group A of the *Poorly forested drained mire* grouped closely with the *Undrained mire* plots, indicating that vegetation had not gone through a significant successional change despite the long-term ditching. Therefore, this group is regarded as a *"Failed drainage"* group. The vegetation composition of Group C was closely related to the *Drained forest* plots and had experienced the intended regime shift towards a forest ecosystem. It is therefore classified as a *"Successful drainage"* group. The plots of Group B did not align within either the *Drained forest* or *Undrained* plots and we refer to these as *Transitional* plots.

During the study period *WT* varied from 68 cm below to 31 cm above the moss/soil surface (Figure 3). The deepest *WT* values were measured during August and at the *Drained forest* site, while May and the *Undrained* sites were generally wettest. The vegetation differences of the *Failed drainage* and *Successful drainage* groups within the *Poorly forested drainage* site prompted us to further investigate the differences in their *WT* patterns. The largest differences in *WT* between the failed and successful drainage groups were observed during May, when the *Failed drainage* plots were always inundated (Figure 3a). During August and October, the differences were less distinct (Figures 3b, 3c). During the study period, the relative seasonal *WT* differences between *Successful drainage* and *Failed drainage* were on average 12, 6 and 11 cm in May (Figure 3a), August (Figure 3b) and October, respectively (Figure 2c) and these differences did not change markedly over the years.

When we further compared average May *WT* with the vegetation composition of the sample plots (Figure 4), we observed a clear division; in *Failed*

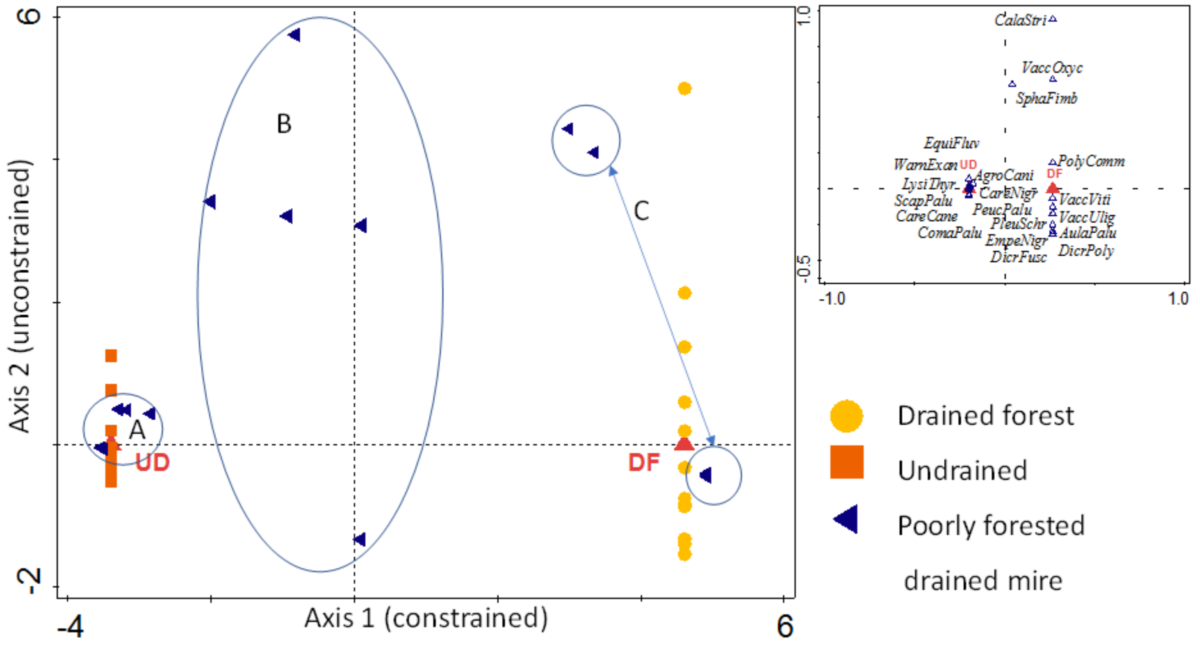

Figure 2. Vegetation ordination based on CCA analysis of *Undrained* and *Drained forestry* sites using their drainage status (0/1) as canonical explanatory variable. The sample plots from the *Poorly forested drained mire* are included as supplementary samples so that their positions are freely determined. Based on their sample scores along Ordination Axis 1 the *Poorly forested drained mire* site plots are divided into three categories A, B and C. Eigenvalues of Axis 1 and Axis 2 are 0.936 and 0.315, respectively. The small panel shows the 20 best fitting plant species.

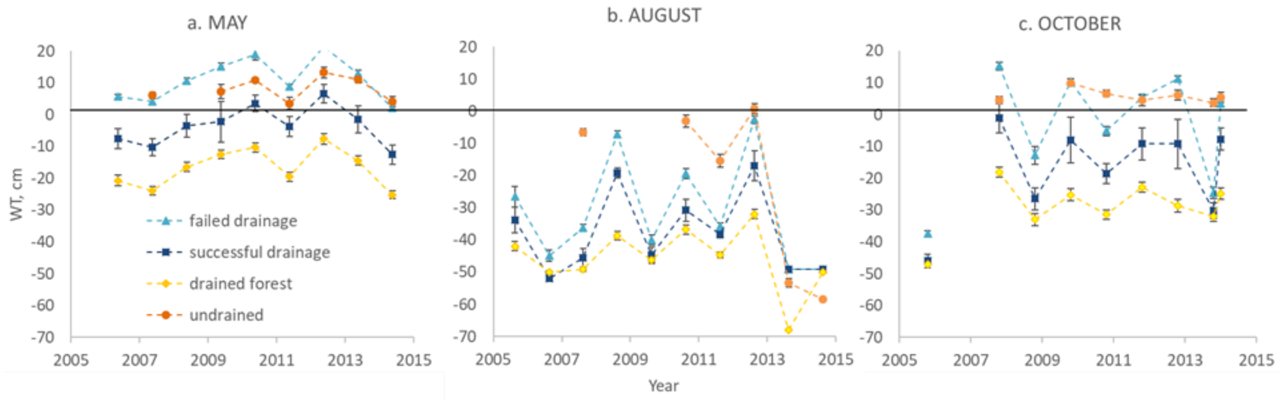

Figure 3. Time series of (a) May, (b) August, and (c) October water table depths with standard error during 2005–2014 for *Undrained* (orange), *Drained forest* (yellow), and two subsets of *Poorly forested drainage* sites: *Failed drainage* (turquoise) and *Successful drainage* (dark blue).

drainage plots the May water table was above the soil surface (*WT* = 8 to 13 cm), giving similar readings to the *Undrained* plots (*WT* = 0 to 20 cm), whereas in *Successful drainage* plots it was mostly below the soil surface (*WT* = 3 to -13 cm) as in *Drained Forest* plots (*WT* = 1 to -27 cm) (Figure 4). During August and October the water table in *Failed drainage* plots was lower than in *Undrained* plots but remained shallower than in *Successful drainage* plots (results not shown).

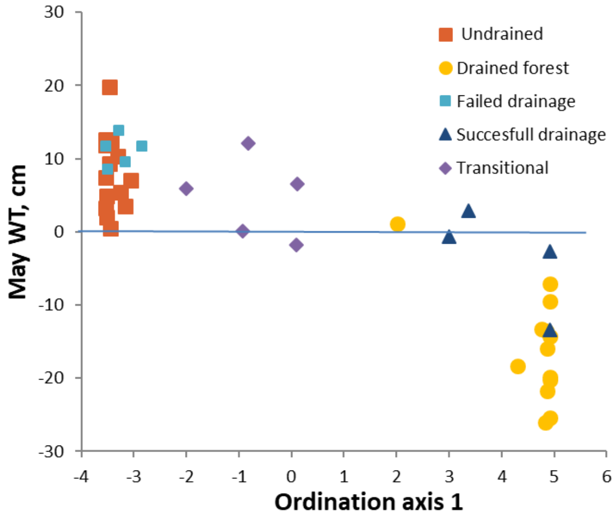

Figure 4. Relationship between average May *WT* and sample plot scores along the CCA Ordination Axis 1 (see Figure 2 for the ordination). Residual variation is added to the *Undrained* and *Drained forest* plot scores shown in Figure 2.

DISCUSSION

The data collected over the course of ten years, although limited to four sites, appear to support the idea that small seasonal changes in water table depth may initiate a regime shift in peatland vegetation. Spring flooding rather than summer water table drawdown appeared to be crucial for controlling vegetation state shifts in primary mire.

It is well established the peatland drainage leads to a transition to forest vegetation (Laine *et al*. 1995, Minkkinen *et al*. 1999, Talbot *et al*. 2010). At our study sites, drainage ditches were installed ~ 50 years before we started our monitoring. The vegetation of *Drained forest* and *Successful drainage* sites clearly differed from that of *Undrained* sites, and the vegetation states at all sites remained stable during our ten-year monitoring period. The tree cover of the drained sites was established during the first decades following ditching, probably due to lowered water table, as has been observed in peatlands with thicker peat layers (Laiho & Laine 1997). At the *Failed drainage* plots, where vegetation remained similar to that of *Undrained* sites after 60 years of drainage, there were no signs that they had been forested at any time prior to or since drainage ditches were installed.

In our study, the water table in the *Failed drainage* plots consistently drops well below the soil surface in summer (August), as it does in all other plots except *Undrained* ones. Yet the *Failed drainage* plots are not transitioning to forest. Interannual variability in *WT* is most pronounced in August, particularly for the *Failed drainage* and *Successful drainage* plots, which show similar patterns (Figure 3). Since *Failed drainage* and *Successful drainage* plots had different drainage outcomes, we conclude that interannual variability did not play a major role in the effects of *WT* on the system. It appears that low summer *WT* alone is not a sufficient driving force for secondary forest succession if spring flooding continues. This is consistent with a palaeological study in a northern aapa mire by Väliranta *et al.* (2017), who concluded that the reason why the dry mid-Holocene climate did not trigger bog development in a northern Finnish fen, but instead produced a dramatic slowing of peat accumulation (Mathijssen *et al.* 2014), was that the spring flood patterns did not change in this region. Spring season flooding seems to play a stabilising role.

We propose that the difference in *WT* observed in May, from 5 cm (inundated) to -5 cm (shallow), has a greater effect on vegetation, particularly for tree stand establishment, than the equal difference from -45 cm to -55 cm observed in August, as most of the local tree species (e.g. *Picea abies* and *Pinus sylvestris*) have low tolerance to flooding, particularly in late spring, when their seasonal growth has just started (Glenz *et al*. 2006, Repo *et al*. 2016, Wang *et al*. 2016). For trees such as *Pinus sylvestris* that have deep rooting systems, extended flooding is likely to be more disruptive than extended periods of deep water table during summer. In our sites *WT* was seldom lower than -60 cm (our measurement limit due to the lengths of the dipwells), and in the humid climate of Finland forestry drainage that commonly leads to deeper water table has never been shown to be too powerful for forest growth (Paavilainen & Päivänen 1995). October (Autumn), typically outside the growing season in this region, is eco-physiologically less important to vegetation stability and state transitions than May (Spring) or August (Summer). Overall, we propose that spring flooding is a crucial modifier of vegetation transition for these ecosystems or, to be more precise, a factor that prevents regime shift.

Climate change scenarios predict changes in the hydrological cycle driven by increased temperature and evapotranspiration and changes in atmospheric circulation (IPCC 2014). In many northern areas like Finland, winter precipitation is expected to increase, while summer conditions are likely to be dryer in the future (Pal *et al.* 2004, Lehtonen *et al.* 2014). Earlier predictions suggested an 8–22 cm drop in water tables for northern peatlands (Gorham 1991, Roulet *et al.* 1992) but these estimates did not consider changes in the seasonality of precipitation. The timing of increased precipitation is important as it affects the intensity and duration of spring flooding. Thus, a focus on growing season conditions (only) may be misplaced.

Our data introduce a likely mechanism for the control of vegetation regime shifts in northern peatlands by water table, with time of year being as important a factor as the magnitude of change. Because climate change effects on peatlands are most likely to be mediated via changes in hydrology and water table level (e.g. Munir *et al*. 2015, Buttler *et al*. 2015, Mäkiranta *et al*. 2018), our study highlights the need for a more thorough investigation of seasonal variability in controlling factors. Northern boreal and subarctic fens are widespread ecosystems covering large areas in Canada, Fennoscandia and Russia (Joosten *et al.* 2017), where hydrological changes have the capacity to alter the ecosystem regime.

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