

RESEARCH ARTICLE

Relationship between hydrological restoration and the recovery of vegetation communities in boreal forestry-drained peatlands

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Handling Editor: Francesca Pilotto**Abstract**

1. Ecosystem restoration benefits biodiversity but restoration outcomes can vary widely. In forestry-drained boreal peatlands, the limited success in restoration may arise from inadequate restoration of hydrological characteristics, most importantly water-table (WT) level.
2. We study (1) if the restoration effect on vascular plant and moss species communities is explained by WT level of restored sites, and (2) whether species groups predictions can be improved by using information on WT and nitrogen (N) levels. We use data on species communities, WT level and porewater quality before restoration and 2, 5 and 10 years after restoration from 24 restored and 16 pristine boreal peatland sites in Finland.
3. Ten years after hydrological restoration, 70% of the variation in the restoration effect for species communities was explained by the median mid-summer WT level of 2–5 years after restoration, peatland type and their interaction.
4. Species group predictions were not consistently improved by WT or N levels.
5. *Synthesis and applications.* The mid-term (2–5 years after restoration) WT level can be used to assess whether hydrological restoration has been successful. A minimum mid-summer WT level should be at least –25 cm from the peatland surface. A sufficient WT level is more likely to be gained in rich peatland types than in poor peatland types, and even with adequate WT level, poor sites have lower probability of positive restoration effects. Hence, rich site types could be prioritized in restoration planning.

KEYWORDS

joint species distribution models, mire, moss, porewater quality, vascular plant, wetland, WT depth

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1 | INTRODUCTION

Peatlands hold unique biodiversity (Minayeva et al., 2017) and provide important ecosystem services (Bonn et al., 2016), such as water regulation (Meriö et al., 2019) and carbon sequestration (Yu, 2011). Currently, 15% of the global peatland area is degraded (UNEP, 2022). Hence, restoration has become an important tool for improving biodiversity and multiple ecosystem services of peatlands (Andersen et al., 2017). In general, restoration benefits biodiversity, ecosystem functions (Moreno-Mateos et al., 2017; Suding, 2011) and ecosystem services (Benayas et al., 2009). However, species communities rarely fully recover, and the outcomes of restoration vary both between and within ecosystem types (Atkinson et al., 2022; Jones et al., 2018). Yet, monitored time frames are often limited to a few years after restoration actions (Allan et al., 2024). Therefore, long-term monitoring programmes and identifying the factors behind observed variation are crucial for improving restoration success (Brudvig et al., 2017; Paolinelli Reis et al., 2024). This is especially true for slowly recovering ecosystems, such as boreal peatlands (Taylor et al., 2019).

Boreal peatlands have been widely drained due to anthropogenic actions, such as agriculture, peat extraction and forestry (Laine et al., 2009; Tanneberger et al., 2021). In Finland alone, more than 50% of the original peatland area has been drained, mainly for forestry (Turunen, 2008). Forestry-drained peatlands are restored by bringing back the original hydrological conditions, including water-table (WT) level and pathways (e.g. groundwater connection; Kuuluvainen et al., 2002). This hydrological restoration includes damming and filling in the ditches, and it is complemented by removing the trees that have grown after drainage (Similä et al., 2014). Hydrological restoration has been shown to raise WT level even within the following year (Haapalehto et al., 2011; Karimi et al., 2024; Laudon et al., 2023; Menberu et al., 2016) and recover the catchment's hydrological functions (Menberu et al., 2018).

After hydrological restoration, vegetation changes towards, but not completely similar to, pristine reference sites (Haapalehto et al., 2011, 2017; Hedberg et al., 2012; Maanavilja et al., 2014). Yet, the outcomes vary: hydrological restoration has shown to be less successful in so-called 'poor' types than in 'rich' types along a poor-rich vegetation gradient (Elo et al., 2024). This gradient used to classify peatlands in Finland ranges from bogs ('poor') to rich fens, and it is largely based on species occurrences (Lindholm & Heikkilä, 2017). The main determinants of the gradient are pH and base saturation (Tahvanainen, 2004). Higher pH in richer types means higher availability of inorganic nutrients (Sallantausta, 2006), but the linkage to main nutrient concentrations, for example, nitrogen (N) and phosphorus (P) is only partial. Typically, bogs are nutrient-poor, whereas fens range from nutrient-poor to nutrient-rich (Joosten et al., 2017).

The lower probability of successful hydrological restoration in poor peatlands may stem from their slower ecological succession rates. This is supported by the fact that drainage leads to slower changes in relatively poor and dry types, with lower species richness, when compared to rich and wetter types (Laine et al., 1995;

Minkinen et al., 1998). Also, hydrological restoration may be more difficult in poor sites where the peat surface is typically above the surrounding terrain (i.e. they are raised bogs). The increased peat surface compaction and peat density due to drainage (Minkinen & Laine, 1998; Silins & Rothwell, 1999) may prevent the recovery of pristine-like hydrological conditions (Kuuluvainen et al., 2002).

In addition to WT level, chemical properties of the peatland water (porewater quality) determine the abiotic conditions for the moss and vascular plant species (Rydin & Jeglum, 2013). A key characteristic is pH (Sjörs, 1950; Tahvanainen, 2004), but also other chemical properties of porewater, such as N (Gao et al., 2022), impact species occurrence. Drainage strongly affects porewater quality (Laiho & Laine, 1994; Menberu et al., 2017). As WT level lowers, peat is exposed to oxidation, which leads to increased decomposition and nutrient mineralization, resulting in concurrent changes in porewater quality. For instance, N, P and dissolved organic carbon (DOC) have higher concentrations in drained than in pristine peatlands (Laiho & Laine, 1994; Menberu et al., 2017).

Because porewater quality impacts peatland species occurrence, species responses to hydrological restoration may be affected by changes in porewater quality. Indeed, hydrological restoration can partially reverse the drainage-induced changes in porewater quality. Following an initial rise in concentration after restoration (Laudon et al., 2023), levels of N, P and DOC tend to decline (Menberu et al., 2017). However, there is a large between-site variation in porewater quality after restoration, associated with different peatland types, their trophic level, and the level and stability of the WT (Koskinen et al., 2017; Menberu et al., 2017). This calls for studies of how WT level and porewater quality are associated with vegetation community changes in restored peatlands.

We use a long-term before-after control-impact experiment on the restoration of forestry-drained boreal peatlands in Finland. With joint species distribution models, we study how WT level and porewater quality are related to moss and vascular plant species communities during 10 years after restoration. Specifically, we ask whether (1) WT level explains the variation in the restoration effect on species communities, and (2) whether information on WT level and porewater N improves predictions on different species group occurrence.

2 | MATERIALS AND METHODS

2.1 | Field data

The 40 study sites are located in the southern, central and northern boreal climatic-phytogeographical zones in Finland (Figure 1). Forests cover more than 70% of the country's land area. The average annual temperature (1991–2020) varies from 5°C in the southwest to 1°C in the north, whereas average annual precipitation (1991–2020) ranges from 500 to 700 mm (Finnish Meteorological Institute, 2025).

Twenty-four sites have been drained for forestry during the 1960s and 1970s and later restored during the monitoring ('restored'),

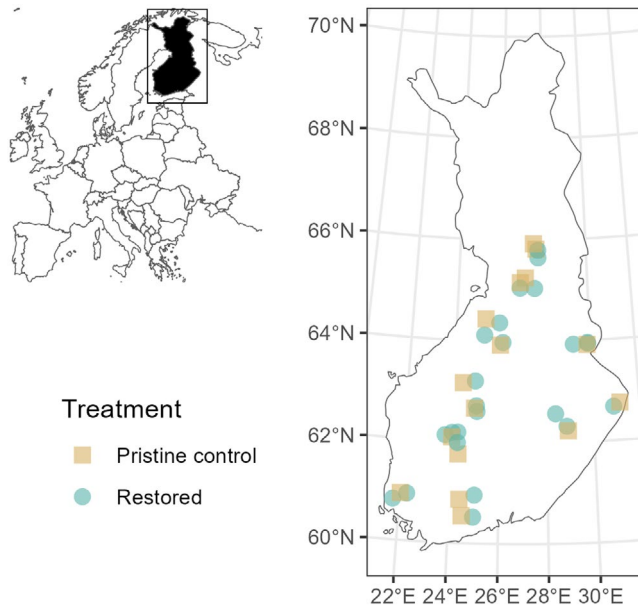


FIGURE 1 A map of the 40 study sites, including 26 restored and 14 pristine peatland sites in Finland.

and 16 sites are relatively pristine with no drainage ('pristine reference') (Figure 1). The sites belong to the Finnish National Peatland Restoration Monitoring program, comprising 151 sites, from which the 40 sites are the only sites with data on both vegetation (previously analysed by Elo et al., 2024) as well as hydrology (previously analysed by Menberu et al., 2016, 2017; Pääkkilä et al., 2025). The sites represent spruce mire forests, pine mire forests and open mires, each with two levels (poor/rich) within the poor-rich vegetation gradient used for mire classification in Finland (Lindholm & Heikkilä, 2017). Spruce mire forests have high, spruce (*Picea abies*)-dominated tree cover and the sites range from oligotrophic to mesoeutrophic (Kaakinen et al., 2018). The peat layer is relatively thin, and the vegetation structure is mosaic-like, including both forest species and boreal peatland species. Pine mire forests and open mires have peat layers dominated by *Sphagnum* species (Kaakinen et al., 2018). The tree cover ranges from relatively high, dominated by pine (*Pinus sylvestris*), to treeless (Kaakinen et al., 2018). Poor sites are (nearly) ombrotrophic, receiving their nutrients mainly from rainwater. Rich types are oligo-mesotrophic, receiving nutrients also from the surrounding mineral land, and have more diverse vegetation. We pooled the sites based on the similarities in their community composition before restoration (Figure S1 in Supporting Information) into (1) poor and rich spruce mire forests ('spruce mires' from now on), (2) poor pine mire forests and open mires ('poor pine and open mires') and (3) rich pine mire forests and open mires ('rich pine and open mires') (Table S1).

Vegetation was monitored during the growing season (June–August) from 2007 to 2022. In restored sites, monitoring was done before restoration (0-year sampling), and 2 (2-year sampling), 5 (5-year sampling) and 10 (10-year sampling) years after restoration. A similar monitoring interval was used in pristine sites. At each site, 10 permanent 1-m² plots were placed systematically in two parallel

lines, 4 m apart from each other. In restored sites, the lines were positioned parallel to the ditches, with a minimum distance of 10 m from the nearest ditch. The location of the lines represented the typical vegetation of each site, and the location of the first plot was randomized, given the criteria above. All vascular plant and moss species in each plot were identified to the species level, and their abundance was visually estimated as a percent cover. The nomenclature follows Finnish Biodiversity Information Facility (2025). For further methodological details, see Elo et al. (2024).

WT level (0 at peatland surface, <0 below peatland surface) in every site was monitored using a single automatic WT logger at 30-min intervals during the frost-free season. The monitoring time frame spanned at least 0–4 years before restoration, and 0–5, 7 and 10 years after restoration. The loggers were placed in 1–1.5-m standpipe wells centrally located between the vegetation plots (described above). The loggers used were Solinstogger Gold (Solinst Ltd., Canada) or, in the later years, Odyssey Xtream (Dataflow Systems Ltd., New Zealand). WT level was also manually measured on average four times per frost-free season to calibrate the WT data relative to the peatland surface. Concurrently with these manual measurements, water samples were collected to analyse six porewater quality parameters: pH, UV absorbance at 254 nm (ABS; cm⁻¹), electrical conductivity (EC; mS m⁻¹), total soluble phosphorus (P; µg l⁻¹) and nitrogen (N; µg l⁻¹) and dissolved organic carbon (mg l⁻¹). The samples were analysed in accredited laboratories using standard methods for each parameter. The hydrological data is fully described in Appendix S1.

Permissions for the field work were not needed: the study sites belong to the Finnish National Peatland Restoration Monitoring program, which is coordinated and the data collection instructed and ordered by Metsähallitus Parks & Wildlife Finland (part of the government-owned enterprise Metsähallitus, which governs all state-owned land in Finland).

2.2 | Data analysis

We calculated the median WT level for two periods: early summer (1 May to 15 June) and mid-summer (1 July to 15 August). In early summer, WT is typically at its highest right after snow melt, and mid-summer represents the climax of thermic summer when WT is typically at its lowest (Isoaho et al., 2024; Sallinen et al., 2023). We calculated mean values for each porewater quality parameter in each site matching the times of vegetation sampling. We combined the data as follows: all data gathered before restoration for 0-year sampling, data from the years 0–2 after restoration for 2-year sampling, data from the years 2–5 for 5-year sampling and data from the years 5 to 10 for 10-year sampling (Tables S1 and S2). To characterize the effect of restoration on species communities, we used 'restoration effect' for each of the 26 restored sites as calculated in Elo et al. (2024). To derive the restoration effect, the whole dataset of 151 sites was used because our 40 sites did not include drained control sites, which are needed to calculate restoration effects.

Restoration effect was derived from a model-based ordination, using generalized linear latent variable models using the R package *gllvm* (Niku et al., 2019). The ordination was based on two latent variables and can be presented graphically: the closer the sites are, the more similar they are in their community composition (Figure S1). The restoration effect for each restored site was the change in the average distance to drained sites minus the change in the average distance to pristine sites from before restoration to 10 years after restoration. Thus, a positive value indicates a larger change towards pristine than drained sites. Conversely, a negative value indicates a larger change towards drained than pristine sites.

We analysed the association between restoration effect and WT level with general linear models using the function 'lm' in the R package 'stats' (R Core Team, 2023). We set the restoration effect as the response variable and formed two options for explanatory variables: (1) peatland type + median WT, and (2) peatland type + median WT + peatland type × median WT. We fitted the two models separately for early summer and mid-summer WT values, and for different years (before restoration/2/5/10 years after restoration), resulting in 12 models. We also ran a null model with peatland type as the only explanatory variable. To compare the alternative models, we used Akaike Information Criteria corrected for small sample size (AICc) (Burnham & Anderson, 2002) within the R package *MuMIn* (Bartoń, 2023).

We classified vascular plant and moss species into three groups ('pristine', 'drainage' and 'none') according to their abundance in different sites before restoration, following Elo et al. (2024). Separately for the three type groups (spruce mires; poor pine and open mires; rich pine and open mires), we classified species as 'pristine' if the species were more abundant in pristine than in drained and restored sites before restoration (in one or both peatland types within the group); 'drainage' if the species were less abundant in pristine than in drained and restored sites before restoration; and 'none' for other species. The information was available for 100 out of 139 species (72%) in spruce mires, 42 out of 51 species (86%) in poor pine and open mires and 82 out of 114 species (72%) in rich pine and open mires.

We also classified species according to their relation to different peatland surfaces (Euroala et al., 1995; Finnish Biodiversity Information Facility, 2025). Separately for *Sphagna* and other mosses, we classified species that occur (i) only on hummock, (ii) on lawn or on hummock and lawn and (iii) on hollow or on lawn and hollow. Some *Sphagnum* species are easily mixed with other *Sphagnum* species in the identification, and their occurrences cannot be reliably separated. We grouped them as 'mixed'.

For analysing species group associations with WT level and porewater quality, we applied Hierarchical Modelling of Species Communities (HMSC; Jantunen et al., 2025; Ovaskainen et al., 2017), a Bayesian joint species distribution modelling framework. We modelled the three peatland types separately. For each site and each species group, we averaged the species group %-cover of the 10 plots. We selected species groups with >5 occurrences and modelled the occupancies (presence/absence) by a probit model. Conditionally

on the presence, we modelled the cover (log-transformed, normalized to zero mean and unit variance within each species group) of the species groups with a normal model. We added hydrological variables (early summer WT, mid-summer WT, pH, ABS, EC, log-transformed N, log-transformed P and log-transformed DOC) as response variables in the same model to infer their associations with species groups. We normalized all eight hydrological variables to zero mean and unit variance. As random effects, we included 'site', modelled as a spatially explicit random effect, 'sampling year' and 'sample' (unique for each observation). The explanatory variables were 'Type' (a factor with two levels [poor/rich in spruce mire model; and pine/open mire in the other two]), 'Treatment' (a factor with two levels [restored/pristine]), 'Time' (a continuous variable [0, 2, 5, 10]) and its second order polynomial 'Time²' to allow for unimodal responses, and the interactions of 'Treatment' and 'Time' as well as of 'Treatment' and 'Time²'.

We ran the HMSC models using the R package *Hmisc* 3.0 (Tikhonov et al., 2019). The package uses the Bayesian framework with Gibbs Markov chain Monte Carlo (MCMC) sampling. We assumed the default prior distributions. We sampled the posterior distribution with four chains, each for 250 samples with thinning of 1000, using a transient phase of 500,000 and adaptation (the number of MCMC steps at which the adaptation of the number of latent factors is conducted) of 400,000. We evaluated the chain mixing by assessing the effective size of the posterior sample and with a potential scale reduction factor (Figures S2 and S3) and the explanatory power of the model by Tjur's R^2 (species occupancy) and R^2 (hydrological variables, species cover given presence) (Figure S8).

Based on the models, we calculated three parameters ('Start', 'Change', 'Difference') describing water table level, porewater quality parameters and species group cover (probability of presence × cover given presence) and their changes. First, we calculated whether WT level, porewater quality parameters or species group cover differed in the beginning of the experiment between the restored and pristine sites:

$$\text{Start} = v_0^R - v_0^P \quad (1)$$

where v_0^R and v_0^P are values on the time 0 (before restoration) in restored sites and pristine sites, respectively. Second, we calculated change in restored sites:

$$\text{Change} = v_{10}^R - v_0^R \quad (2)$$

where v_0^R and v_{10}^R are values in restored sites on the time 0 and 10 (10 years after restoration), respectively. Third, we calculated whether the difference between restored and pristine sites grew smaller or larger during the study period:

$$\text{Difference} = \text{abs}(v_{10}^P - v_{10}^R) - \text{abs}(v_0^P - v_0^R) \quad (3)$$

For all the parameters, we calculated the median as well as posterior probability for the median being larger than zero.

We calculated sample-level residual association matrices between WT level, porewater quality and species group occurrence/cover given presence to describe whether they are positively or negatively associated, after taking into account the explanatory variables in the model (Ovaskainen et al., 2017). We performed site-level leave-one-out cross-validation. To see whether the prediction on species occurrence/cover given presence is improved when including information on WT or porewater quality parameters, we used conditional cross-validation based on median mid-summer WT level and N. We chose mid-summer WT level; mid-summer and early summer WT levels were highly correlated and mid-summer WT level was a more important predictor for restoration effect (Table S3). N had positive residual associations with all porewater quality parameters except pH (Figure 4).

Because the convergence of the omega parameters describing the associations was unsatisfactory, we fitted another, identical model (Appendix S2). Based on the high similarity of the results (Figures S4–S7), we consider our results robust and report the average values from the two individual model fittings.

All analyses were conducted in R version 4.3.0 (R Core Team, 2023).

3 | RESULTS

3.1 | WT level and restoration effect

We explored the relationship between restoration effect and different WT levels. The best model explained 70% of the variance in restoration effect, and it included peatland type, median mid-summer WT level 2–5 years after restoration and their interaction (Table S3). In spruce mires and poor pine and open mires, restoration effect increased with increasing median WT level 2–5 years after restoration (Figure 2). When median WT level was deeper than approximately 25 cm from the peatland surface, the restoration effect was negative or non-existent. In rich pine and open mires, positive restoration effects slightly decreased with increasing median WT level, which was above the 25 cm threshold in all sites (Figure 2).

3.2 | Changes in WT level, porewater quality and species groups

The change in median WT levels during the study period differed between peatland types. In spruce mires, both early summer and mid-summer median WT levels increased ca. 14–16 cm (Figure 3), although the change varied between sites (Figure S9). In poor and rich pine and open mires, median WT levels increased during the first 5 years but then dropped (Figure S9), resulting in a small (<2 cm) or no increase in median WT levels 10 years after restoration (Figure 3).

Almost all porewater quality variables decreased towards pristine levels in poor and rich pine and open mires (Figure 3). In spruce mires, only N and DOC decreased towards pristine levels; the other

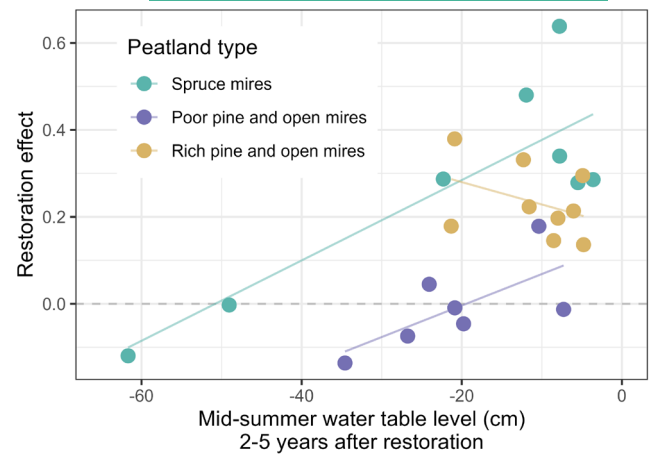


FIGURE 2 The relationship between restoration effect and median mid-summer WT level from 2 to 5 years after restoration for different peatland types (coloured lines). Increasing negative WT levels indicate increasing distances from the peatland surface (WT=0). Positive restoration effect indicates that restored sites change towards pristine sites in their vascular plant and moss community composition (the larger the value, the larger the change), whereas negative values indicate a change towards drained and unrestored sites. Zero denotes no change either towards pristine or drained sites.

variables tended to be similar in pristine and drained sites already before restoration.

As expected, species groups' responses to restoration varied (Figure 3). The most congruent changes among peatland types were the decrease of hummock mosses and the increase of mixed *Sphagnum* mosses as well as species related to the pristine stage (Figure 3). Also, drainage-related species and species with no relation increased, often away from the pristine levels (Figure 3).

3.3 | Associations and predictions for species groups

Sample-level associations between species groups and hydrological variables, after accounting for treatment, time and their interaction, were infrequent and rarely strong in spruce mires and rich pine and open mires (Figure 4). In poor pine and open mires, the associations were more frequent and stronger (Figure 4). We further assessed the relationship between species groups and mid-summer WT level and N with conditional cross-validation. Including information on mid-summer WT level or N yielded mostly no or relatively small improvements in predictive power. In general, cross-validated predictive powers of the models were mostly modest and often negative, although cover of drainage-related species and hummock mosses in poor pine and open mires was predicted exceptionally well (0.78 R^2) (Figure 5). Mid-summer WT level substantially (>0.4) improved predictions for the occurrence of lawn *Sphagna* and cover, given presence, of pristine-related species and mixed *Sphagnum* in spruce mires as well as

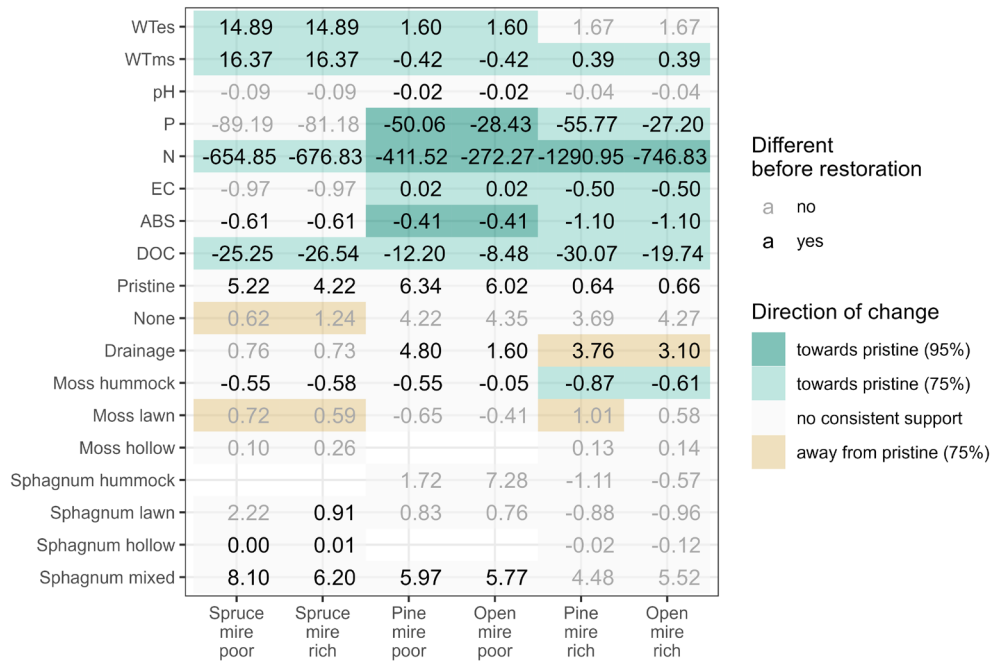


FIGURE 3 Median changes of WT level in early summer (WTes) and mid-summer (WTms), porewater quality (pH, phosphorus [P], nitrogen [N], electrical conductivity [EC], UV absorbance [ABS], dissolved organic carbon [DOC]) and species group cover (probability of occurrence \times cover given presence) from before restoration to ten years after restoration in restored sites. 'Pristine' includes moss and vascular plant species related to pristine stage, 'Drainage' includes drainage-related species, and 'None' all other species. *Sphagnum* mosses ('Sphagnum') and other mosses ('Moss') are grouped according to their affinity to different moisture levels ('hummock', 'lawn' and 'hollow'). The probability of the change towards the values in pristine sites is shown by the colour (green = towards pristine, brown = away from pristine). Whether the variable values differ before restoration is indicated by the font colour (grey = no difference with 95% posterior probability, black = difference).

cover given presence of hummock *Sphagna* in poor pine and open mires (Figure 5). These species groups were positively associated with WT level. In addition, mid-summer WT level improved predictions for pristine-related species for which the counterintuitive negative residual association likely results from the negative association between WT level and N (Figure 4). Including information on N substantially improved predictive power for cover given presence of pristine-related species (even more than mid-summer WT) and cover given presence of hummock mosses in rich pine and open mires.

4 | DISCUSSION

Hydrological restoration of forestry-drained peatlands should increase WT levels to initiate the vegetation community changes towards those on pristine sites. We showed that median mid-summer WT level 2–5 years after restoration largely explained the variation in restoration effect for vascular plant and moss communities. The lack of recovery in vascular plant and moss communities at some sites appeared to be linked to an insufficient rise in the WT. In addition, WT level was positively related to species related to pristine stage as well as mixed *Sphagnum* species, and it was an important factor for predicting their cover in spruce mires with the widest variation in restoration success. Yet, WT level did not explain all the

differences in restoration effect between different peatland types. Some poor pine mire and open mire sites, even the ones with sufficient WT level, showed little or no response to restoration. This suggests that peatland type, rather than hydrology alone, impacts the effectiveness of hydrological restoration—with richer peatland types responding more strongly in terms of species composition.

As WT level is one of the key environmental predictors for the vegetation communities in peatlands (Rydin & Jeglum, 2013), it is not surprising that restoration effect increased with increasing mid-summer WT level in spruce mires and poor pine and open mires. In rich pine and open mires, the restoration effect seems to be the highest at -20 cm mid-summer WT level. Yet, the decreasing trend towards -5 cm WT levels is relatively weak, warranting further research. Our results suggest that mid-summer WT level limit for vegetation recovery is -25 cm in pine and open mires, and likely deeper for spruce mires. This aligns with the previously found minimum WT levels for peat-forming species which range from -30 cm in spruce and pine mires to -20 cm in fens (Menberu et al., 2016). The -25 cm likely indicates a threshold for vegetation water uptake possibility and capillary rise potential in peat and living *Sphagnum* (Price & Whitehead, 2001), which are key target species in boreal peatland restoration (Allan et al., 2024), and it seems to be enough to initiate the recovery towards a pristine-like stage.

We found that WT level 2–5 years after restoration explained the restoration effect best. This suggests that the response of

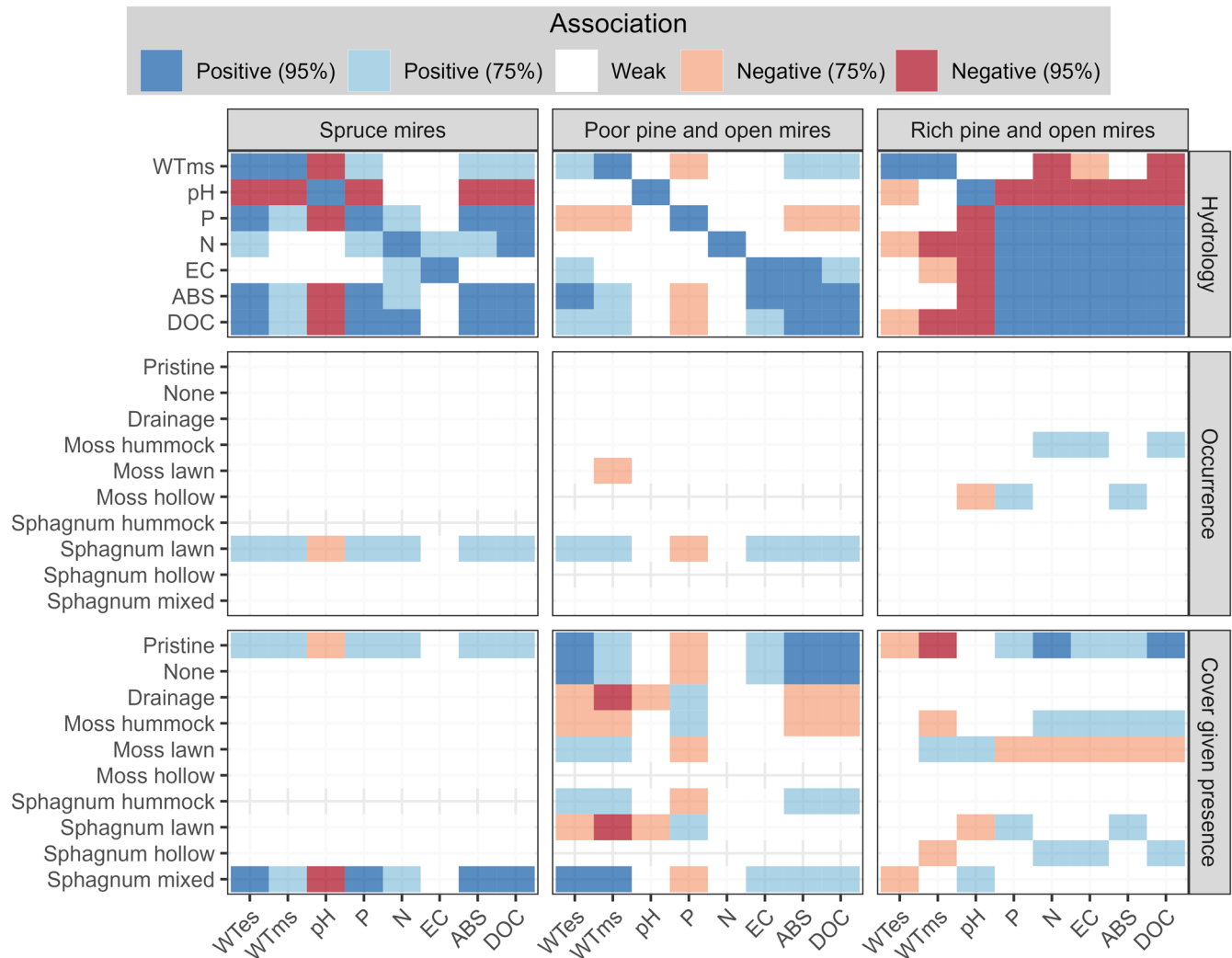


FIGURE 4 Sample-level associations between early summer WT level (WTes) and mid-summer WT level (WTms), porewater quality (pH, phosphorus [P], nitrogen [N], electrical conductivity [EC], UV absorbance [ABS], dissolved organic carbon [DOC]) and species group occurrence and cover given presence in spruce mires, poor pine and open mires, and rich pine and open mires. 'Pristine' includes moss and vascular plant species related to pristine stage, 'Drainage' includes drainage-related species, and 'None' for other species. *Sphagnum* mosses ('Sphagnum') and other mosses ('Moss') are grouped according to their affinity to different moisture levels ('hummock', 'lawn' and 'hollow'). The intensity of the colour indicates the strength of statistical support (dark: >95% posterior probability for positive/negative association; light: >75% posterior probability for positive/negative association). White indicates weak associations ($\leq 75\%$ posterior probability for positive/negative association).

species communities to hydrological restoration is the fastest during the first years after restoration (Jones et al., 2018). An additional reason for the importance of the WT level 2–5 years after restoration may arise from the WT level dynamics (Päkkilä et al., 2025). Our results showed that WT levels increased shortly (0–5 years) after restoration but then decreased again. The lowering of the WT level after a few years' initial rise has been observed also previously and may link to the technical challenges of hydrological restoration (Haapalehto et al., 2011). However, our result may be due to the very dry summer in 2018 (Koebsch et al., 2020; Rinne et al., 2020), which substantially lowered the WT level also in pristine peatlands (Päkkilä et al., 2025). The decrease was notable particularly in restored pine and open mires, which suggests that restored sites may be less resilient to extreme hydrological events (Koebsch et al., 2020; Kreyling

et al., 2021). It is possible that the drought hindered further vegetation recovery in restored sites. Whether increasing drought frequency due to climate change (Ault, 2020; Rantanen et al., 2023) slows down the effect of restoration in peatlands remains an important research topic (Loisel & Gallego-Sala, 2022).

Previous research has shown that nutrient-rich peatlands tend to respond more quickly and positively to hydrological restoration compared to nutrient-poor ones (Komulainen et al., 1999). We found that a sufficient WT level is more likely to be gained in richer sites than in poor sites, and even with an adequate WT level, poor sites have a lower probability of positive restoration effects. In practice, this means that restoration could be targeted to rich types where the probability of successful hydrological restoration is higher and where changes in vegetation are faster. Yet, the potential risk for nutrients

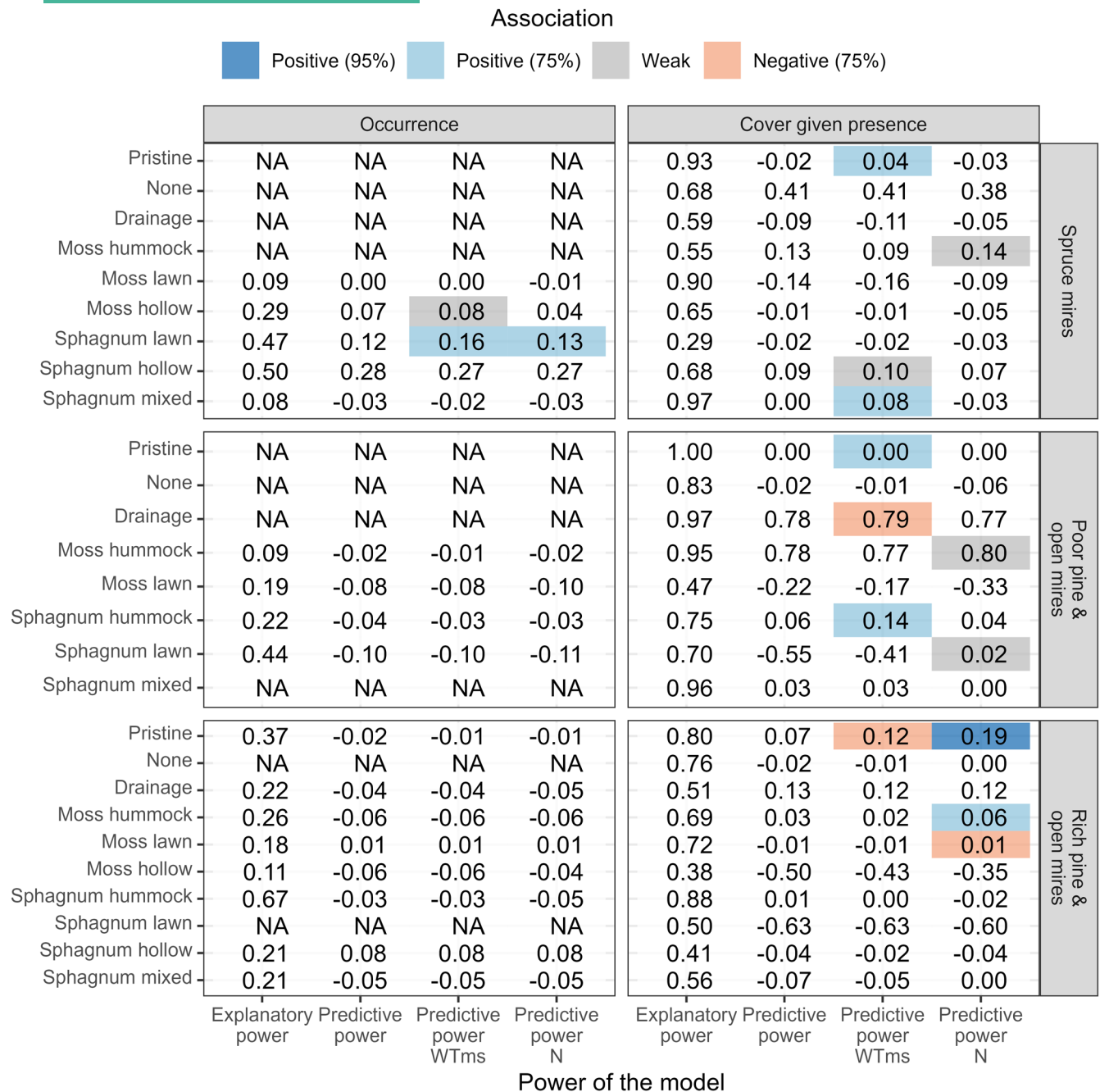


FIGURE 5 Explanatory power, predictive power based on cross-validation, predictive power based on conditional cross-validation using median mid-summer WT level ('predictive power WTms'), and nitrogen concentration ('predictive power N') for each species group in each peatland type (spruce mires; poor pine and open mires; rich pine and open mires), separately for occurrence (T_{jur} 's R^2) and cover given presence (R^2). 'Pristine' includes moss and vascular plant species related to pristine stage, 'Drainage' includes drainage-related species, and 'None' all other species. *Sphagnum* mosses ('Sphagnum') and other mosses ('Moss') are grouped according to their affinity to different moisture levels ('hummock', 'lawn' and 'hollow'). If the predictive power increases when using information of median mid-summer WT level (or N) and it is positive, the sample-level residual association with the median mid-summer WT level (or N) is denoted by the colour. The intensity of the colour indicates the strength of statistical support (dark: The posterior probability that association is positive/negative is >95%; light: The posterior probability that association is positive/negative is >75%). Grey indicates weak associations ($\leq 75\%$ posterior probability for positive/negative association). Species groups with occurrence=NA were always present.

and DOC leaching from nutrient-rich peatlands during the first years after restoration (Koskinen et al., 2017) must be considered.

Hydrological restoration partly reversed the drainage-induced changes in porewater quality, including decreasing N concentration.

Although peatland vegetation has shown to be affected by the increase of N (Gao et al., 2022; Hedwall et al., 2017), we found that N was clearly important to one species group: species related to the pristine stage in rich pine and open mires. This group involved many

vascular plants which may benefit from adequate N levels, even in pristine sites. For other species groups, N was not important, possibly because the groups included species with different tolerances and optimum levels. For instance, *Sphagnum* species may adapt to different N levels (Granath et al., 2009). Moreover, our study sites did not include the peatland types having the most demanding species in terms of porewater quality: In alkaline fens, increasing acidity and N concentration may be truly detrimental (Mälson et al., 2010). Altogether, the impact of porewater quality on individual species responses and how this depends on the site conditions deserves further research. Even when taking into account porewater quality, WT level and peatland type, the large variation in the outcomes of restoration remains. Part of this variation may relate to species responding to decreased shadowing due to tree felling (Hedberg et al., 2012; Maanaviija et al., 2014), and also community composition before restoration (so-called priority effects) likely plays a role in species' responses (Fukami, 2015).

5 | CONCLUSIONS

Our long-term monitoring of forestry-drained peatlands revealed that WT level largely explained the overall restoration effect on vegetation. As WT level 2–5 years after restoration strongly predicted long-term restoration effect, relatively short-term WT level changes can be used to assess whether hydrological restoration has been successful. A mid-summer WT level should be at least –25 cm from the peatland surface in pine and open mires. Moreover, sufficient WT level is more likely to be reached in rich pine and open mire sites than in poor pine and open mire sites, and even the poor sites with adequate WT level have a lower probability of having a positive restoration effect. Hence, the richer sites could be prioritized in restoration planning. Finally, as the vegetation changes during the first 10 years after hydrological restoration are still rather modest, there is a need to conduct large-scale and long-term monitoring to guide restoration planning.

AUTHOR CONTRIBUTIONS

Merja Elo, Aleksii Räsänen, Hannu Marttila, Lassi Pääkkilä, Otso Ovaskainen, Parvez Rana and Aleksii Isoaho conceived the ideas and designed the methodology; Merja Elo, Lassi Pääkkilä and Petra Korhonen gathered and processed the data; Merja Elo and Otso Ovaskainen analysed the data; Merja Elo led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available from the Zenodo Digital Repository <https://doi.org/10.5281/zenodo.17301631> (Elo et al., 2025).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Description of hydrological data.

Figure S1. Deriving restoration effect for each restored site.

Appendix S2. HMSC modelling.

Figure S2. Model convergence for beta parameters.

Figure S3. Model convergence for omega parameters.

Figure S4. Associations from two independent model fits.

Figure S5. Results of two independent model fits for spruce mires.

Figure S6. Results of two independent model fits for poor pine mires and poor open mires.

Figure S7. Results of two independent model fits for rich pine mires and rich open mires.

Figure S8. Variance partition.

Figure S9. Predicted mid-summer water table level in different peatland types.

Table S1. Study site information and combination of vegetation and hydrological data.

Table S2. Hydrological characteristics of pristine and restored sites.

Table S3. Model selection for the linear model explaining the restoration effect.

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