Received: 18 June 2025 | Accepted: 17 September 2025

DOI: 10.1111/1365-2664.70182

BRITISH ECOLOGICAL SOCIETY Journal of Applied Ecology

RESEARCH ARTICLE

# Restoration induced long-term vegetation change in oligotrophic peatlands

Nina Kumpulainen[1] | Eeva-Stiina Tuittila[1] | Anne Tolvanen[2] | Oili Tarvainen[2] | Henni Ylänne[1] | Anna M. Laine[1]

[1]School of Forest Sciences, University of Eastern Finland, Joensuu, Finland

[2]Natural Resources Institute Finland, Oulu, Finland

**Correspondence**
Nina Kumpulainen
Email: nina.kumpulainen@uef.fi

**Funding information**
Finnish Ministry of Agriculture and Forestry, Grant/Award Number: VN/32577/2021-MMM-2 and VN/32577/2021-MMM-4; Research Council of Finland, Grant/Award Number: 337550; EU LIFE Nature Fund, Grant/Award Number: LIFE04 NAT/FI/000078; Finnish Cultural Foundation's Regional Fund of North Karelia, Grant/Award Number: 55241419

**Handling Editor:** Kevin Wood

## Abstract

1. Ecological restoration of forestry-drained peatlands is an increasingly acknowledged mean to halt the biodiversity loss, yet little is known on the long-term responses of vegetation—a key factor in judging the success of various restoration measures.
2. In this study, we follow long-term succession in vegetation composition from a year before through 11 years after peatland rewetting by ditch filling. Tree harvesting as a part of restoration was conducted by removing the whole trees or stems only.
3. For both restoration approaches, the restoration trajectory of vegetation was non-linear, and the recovery time differed between plant functional groups. We first observed an initial loss of species, followed by increases in species indicative of undrained peatlands and an increase in trait heterogeneity. Additionally, we observed that sedges responded to restoration faster than *Sphagnum* mosses.
4. *Synthesis and applications*: Here we show that restoration increases the resemblance to undrained peatlands, with little differences between the tree harvesting methods. We suggest that *Sphagnum* moss cover could be used in monitoring the success of restoration of nutrient poor peatlands. Our results highlight the necessity of long-term monitoring. The difference between strip and near former ditch lines showed spatial variability long after the restoration, which should be accounted for in monitoring.

KEYWORDS
forestry drainage, functional diversity, plant functional traits, rewetting, tree stand removal

## 1 | INTRODUCTION

Peatlands, defined as peat accumulating wetlands, are facing growing pressure from both land use and climate change (United Nations Environment Programme, 2022). In Europe, this is seen as increased exploitation and drainage since the 1800s (Swindles et al., 2019), where about 60% of peatlands have been subjected to agricultural use, forestry and peat extraction (United Nations Environment Programme, 2022). Especially in Northern Europe, forestry has had the major role in peatland degradation; in Finland, around 4.8 million hectares of the 9.1 million hectares' total peatland area have been drained to promote timber growth (Natural Resources Institute Finland [Luke], 2017) at the expense of biodiversity and nature conservation values (Elo et al., 2024; Laine et al., 1995). Altogether, forestry drainage contributes to the ongoing global biodiversity crisis (e.g. Carroll et al., 2011; Dohong et al., 2017; Fraixedas et al., 2017). Hence, ecological restoration of drained peatlands, aiming to return communities and functions characteristic of undisturbed peatlands, is urgently needed to enhance biodiversity and safeguard peatland functions and services (Aapala et al., 2013; Gann et al., 2019). This is acknowledged in the Kunming-Montreal Global Biodiversity Framework, European Union's (EU) Biodiversity Strategy for 2030 (CBD, 2022), and the newly adopted EU's Nature Restoration Law, which obligates restoration of 30% of the EU's directive habitats by the year 2030 (EU Regulation 2024; EU 2022/869).

In Finland, the restoration of forestry-drained peatlands, which began in the early 1990s, typically includes the removal of trees and blocking or filling in the drainage ditches (Aapala et al., 2013). The approach often results in an elevated water table (WT) and re-establishment of peatland species soon after restoration (Jauhiainen et al., 2002; Komulainen et al., 1999; Laine, Leppälä, et al., 2011). Yet, to confirm the direction of ecosystem changes and the suitability of the technical approach (i.e. are the dams holding, is the WT still high), the initial surveys need to be followed by long-term studies. The few existing long-term studies covering the first 10 years or more (e.g. Haapalehto et al., 2011, 2017; Hancock et al., 2018; Maanavilja et al., 2014; Strobl et al., 2020) encouragingly report continued improvement of peatland conditions, although the biological communities still differ from the natural reference sites that represent the target state.

Restoration success is commonly defined by the abundance of indicator plant species, for example *Sphagnum* and *Eriophorum* species (e.g. Hancock et al., 2018), or by comparing the species composition to a target state (e.g. Laine, Leppälä, et al., 2011). However, these approaches focus on the return of communities, while the return of ecosystem functions could be better assessed via changes in functional composition (Gann et al., 2019; Lavorel & Garnier, 2002). Incorporating trait-based ecology (Moor et al., 2017) into restoration monitoring could offer a means for a more mechanistic understanding of whether the communities established shortly after restoration fill the same functional niche as the communities of the long-term target state, even if the species composition is not exactly the same. Trait databases that provide species-specific data provide a means for this (e.g. the TRY database, Kattge et al., 2020) and are commonly used in trait-based studies (Hedberg et al., 2013; Piqueray et al., 2015). In plant ecology, commonly used traits include specific leaf area (SLA, the ratio of leaf area to leaf dry mass) and leaf dry matter content (LDMC, the ratio of leaf dry mass to leaf fresh mass) that are associated with plant resource acquisition strategies and provide information on plants' capacity to respond to changed environmental conditions that alter nutrient, water and/or light availability (Laine, Korrensalo, et al., 2021; Lavorel & Grigulis, 2012).

Plant functional traits have rarely been used in the restoration monitoring of forestry-drained peatlands. However, those few existing studies have reported a decrease in SLA during the first decades following restoration (Hedberg et al., 2013; Konings et al., 2018) in line with the difference between drained and undrained areas. Yet, we still know very little about functional trait responses to peatland restoration.

The aim of this study was to assess the long-term succession in plant species and trait composition following the restoration of forestry-drained peatlands. We followed >12 years of vegetation changes in oligotrophic pine fens in response to rewetting by ditch filling with (a) standard tree harvesting, where only stems were removed from the sites and (b) whole-tree removal, where both stems and branches were removed from the sites, comparing these to undrained control sites. The tree harvesting methods have been shown to lead to differences in mineralization and decomposition rates after restoration (Tarvainen et al., 2013), which may be reflected in vegetation composition. As noted above, earlier findings have shown that a decade after restoration the vegetation composition still differs from the target state. We thus hypothesized that (i) vegetation community composition and community-weighted mean traits have continued to shift towards plant species, functional types and traits that benefit from the newly restored open and high-WT level conditions, like sedges and *Sphagnum* mosses. Additionally, we hypothesized there would be (ii) an initial increase in species richness, functional richness and functional dispersion driven by the presence of both forest and peatland species and (iii) a subsequent decrease in species richness, functional richness and functional dispersion when peatland species outcompete forest species. For the functional traits, we hypothesized that (iv) SLA will first increase as restoration measures release nutrients (forest residue, mechanical disturbance to peat) and then decrease later as nutrient availability decreases. An opposite pattern is expected for LDMC and leaf thickness. In addition, we expect plant height to decrease in response to tree removal and decreased light competition. For *Sphagnum* mosses, the restoration causes two opposing pressures affecting their trait composition: While tree removal alters microclimate by removing the humid conditions that favour loose moss stands, ditch blocking increases the availability of water that is likely to favour loose moss stand characteristics in lawns and hollows. Therefore, it is possible that *Sphagnum* moss traits are not strongly impacted by restoration.

## 2 | METHODS

### 2.1 | Research areas and restoration arrangements

The study was carried out in 21 undrained and originally forestry-drained oligotrophic pine fen sites located in three protected Natura 2000 areas: Elimyssalo (64°10′ N 30°20′ E), Iso-Palonen (64°20′ N 30°10′ E) and Teerisuo-Lososuo (63°50′ N 29°20′ E) in Kainuu, Eastern Finland (Table S1.1). The mean annual temperature of the region is 2.2°C and the mean annual precipitation is 674 mm (period 2006–2018, Finnish Meteorological Institute [FMI], 2024).

The eight undrained fen sites are characterized by sparse cover of Scots pine (*Pinus sylvestris*) with an understory vegetation dominated by *Sphagnum* mosses, mire dwarf shrubs such as *Ledum palustre* and *Andromeda polifolia* and sedges (mainly *Eriophorum vaginatum*; Laine, Leppälä, et al., 2011).

The 13 restored sites were drained for forestry in the 1970s and 1980s, and mean tree volume had increased to 26.0 ± 4.3 $m^3$ ha compared to 8.5 ± 2.9 $m^3$ ha in the undrained sites (Laine, Leppälä, et al., 2011). Restoration of the sites began with felling and removing the trees in winter 2007. Trees were harvested with two different treatments. In the stem-only treatment, stems of trees (diameter >10 cm at breast height) were harvested, and the slash was left at the site. In the whole-tree harvest, stems and slash were removed from the site, but root systems were left intact. In both treatments, ditches were filled with peat in autumn 2007 (Laine, Leppälä, et al., 2011; Tarvainen et al., 2013).

Within each of the three protected areas, the sites next to each other were clustered into subareas typically including one undrained and one restored stem only harvested site. However, two subareas included one restored whole tree harvested site and one restored stem only harvested site, while one subarea included both tree harvest methods next to the control (undrained) area.

Before restoration in 2006, WT was on average 13, 20 and 24 cm below the surface at undrained sites and 25, 34 and 32 cm below the surface at drained sites of Elimyssalo, Iso-Palonen and Teeri-Lososuo, respectively. Soon after the ditch filling, the WT at the drained sites rose to a similar level and resembled the WT of the undrained sites (Figure S1.1).

## 2.2 | Vegetation inventories

For vegetation inventories, 8–18 permanent sample plots (size 1 $m^2$) were established at even distances 20–30 m apart along transects in each study site (Table S1.1). At the restored sites, half of the transects and sample plots were located at a 5 m distance from the ditches (referred to as 'near ditch'), whereas the other half were in the middle of the 40 m wide strip between ditches (referred to as 'strip') (see also Laine, Leppälä, et al., 2011). Vegetation surveys were carried out in the middle of the growing season in the years 2006 (before restoration), 2009, 2012 and 2018, by visually estimating the percentage cover (0–100) of each plant species. This field work did not require permission.

## 2.3 | Grouping of plants, and calculation of community-weighted functional traits

Based on their growth form and ecology, plant species were grouped into the following plant functional types (PFTs): forest dwarf shrubs, mire dwarf shrubs, forbs, sedges, tree seedlings and bushes, forest mosses, lichens, liverworts as well as hummock, lawn and hollow-associated *Sphagnum* mosses (Table S1.2).

Community-weighted mean (CWM) functional traits for each sample plot were obtained by combining the species cover data with species traits using the *R package BAT* (Cardoso et al., 2022). Vascular plant traits included SLA ($cm^2$/g), LDMC (mg/g), plant height (cm) and leaf thickness (mm), whereas *Sphagnum* traits included capitulum diameter (mm), fascicle density (number per cm), capitulum dry weight (g), capitulum water content (g) and stand density (number of shoots per $cm^2$). Trait values were taken from published sources, mostly measured from Fennoscandian peatlands (Laine, Korrensalo, et al., 2021; Laine, Lindholm, et al., 2021) and complemented from the TRY database (Kattge et al., 2020) or by estimating trait values based on close relative species (Table S1.2).

## 2.4 | Vegetation data analysis

Variation in plant species cover across the undrained and restored peatlands was visualized with non-metric multidimensional scaling (NMDS) of Hellinger-transformed cover data using package *vegan* (v. 2.6-4, Oksanen et al., 2022). The impact of the year and restoration on the community composition was tested with a permutational multivariate ANOVA (*adonis*) using Bray–Curtis distance and 999 permutations.

To limit the evaluation of plant species and groups to the most responsive and indicative ones, we (1) assessed the changes of species and PFTs indicative of the undrained and drained peatlands (Table S1.3) using multivariate analyses to detect the species/PFTs responsive to restoration (Tables S1.4 and S1.5). Using the package *indicspecies* (De Cáceres & Legendre, 2009), we identified indicator species and PFTs in the undrained or drained peatlands using only the cover data during the first survey, that is prior to restoration. The identified groups were used to count the cumulative cover of undrained and drained peatland indicator species and PFTs for each plot on each studied time point. We used the package *mvabund* (v. 4.2.1, Wang et al., 2022) to assess the influences of restoration on the cover of each species/PFT with a generalized linear model (*glm*) using negative binomial distributions. For the analysis, species present in less than three plots were omitted, and prevailing cover data were assessed as integers, re-coding cover values between 0 and 1 to 1. The models were constructed to assess the individual and interacting effects of Year (as a factor) and Restoration (undrained vs. restored), taking into account the repeated and nested study design by setting the sample plot, nested within the site, subarea and area as a random factor.

To gain a quantitative measure of the changes in species cover over time, we followed Legendre (2019), where a temporal beta-diversity index (TBI, $D_{\%diff}$) and its components—species losses and species gains—were calculated for each plot using the package *adespatial* (v. 0.3-21, Dray et al., 2023). We used species cover data and counted the annual change between each measurement

BRITISH ECOLOGICAL SOCIETY Journal of Applied Ecology



occasion, correcting the obtained values for the duration of each interval. As one subarea (stem only harvest, Iso-Palonen) and three plots (one in whole tree harvest site, two in stem only harvest site, Elimyssalo) were not assessed in 2006, they were removed from this analysis.

To assess the impacts of restoration on functional diversity, we used the following functional diversity indices: number of species, functional richness (Fric), functional evenness (Feve), functional divergence (Fdiv), functional dispersion (Fdis) and Rao's quadratic entropy (see definitions in Table S1.6) using the dbFD function of package *FD* (v. 1.0-12.1, Laliberté & Legendre, 2010). Due to *Sphagnum* moss communities being naturally quite homogeneous and species-poor, we obtained estimates for *Sphagnum* functional richness, functional evenness and functional diversity for only 595 data points out of 1014 and therefore assessed the functional diversity indices separately for vascular plants and *Sphagnum* mosses.

To assess the impact of restoration, tree harvest method or the sample plot location (near ditch or strip) on the vegetation trajectories (indicative and responsive species and PFTs), their temporal turnover (TBI), traits (CWMs) and functional diversity, we used model selection based on Akaike's information criteria (AICc, package *AICcmodavg* v. 2.3-4, Mazerolle, 2023). For this approach, nine alternative mixed-effect models (package *nlme*, Pinheiro et al., 2022) were constructed to explain the influence of year only, year and restoration and their potential interaction on each of the three variables. In this approach, the added value of tree harvest method or sample plot location was assessed by dividing restored plots into these categories and comparing the explanatory value of the model to restoration only. The influence of restoration/tree harvest method/location was further assessed in comparison to the null model (impact of Year only), without and with interaction to assess whether the impact persisted throughout the years (no interaction) or changed with time (interaction included). Thus, the models were (1) $x \sim \text{Year}$, (2) $x \sim \text{Year} + \text{Restoration}$, (3) $x \sim \text{Year} \times \text{Restoration}$, (4) $x \sim \text{Year} + \text{Tree harvest method}$, (5) $x \sim \text{Year} \times \text{Tree harvest method}$, (6) $x \sim \text{Year} + \text{Location}$, (7) $x \sim \text{Year} \times \text{Location}$, (8) $x \sim \text{Year} + \text{Location}$ within tree harvest methods and (9) $x \sim \text{Year} \times \text{Location}$ within tree harvest methods (where $x$ = assessed variable). In all alternative models, Year was treated as a factorial variable, and the repeated and nested study design was accounted for by setting the sample plot, nested within the site, subarea and area as a random factor. Before running the model comparisons, each explanatory variable was checked for normality, applying square-root and log-transformations when necessary. Variance of the residuals was visually assessed and collinearity between Year and Restoration was checked with package *performance* (Lüdecke et al., 2021). All variance inflation factors were <6.09, allowing us to keep all nine alternative models. This model comparison approach (Tables S1.7–S1.10) identified the best explanatory models for each variable, which we report in Tables 1–5 and Table S1.11, testing the pairwise differences with Tukey's Post hoc tests (package *emmeans*; Lenth, 2023).

All analyses were performed in RStudio version 2022.07.2 (RStudio Team, 2022) in R version 4.2.2. Package *ggplot2* (Wickham, 2016) was used for data visualization.

## 3 | RESULTS

### 3.1 | Change in species composition and diversity

Prior to restoration, forestry-drained peatlands had a higher abundance of forest and mire shrubs, such as *Betula nana*, *Vaccinium uliginosum* and *Empetrum nigrum*, and forest mosses when compared to the undrained control sites, characterized by *Sphagnum* mosses and sedges such as *Eriophorum vaginatum* (Figure 1).

During the 10-year period, restoration shifted vegetation composition towards that of undrained sites (Figure 1b). Altogether, the cover of species indicating undrained conditions increased rapidly after restoration and was similar to undrained sites after 5 years (Figure 2a; Table 1). The change was faster, and the cover of species indicating undrained conditions was higher near the prior ditches five and 11 years after restoration than that in undrained peatlands (Figure 2a). Despite the general trend, we observed differences between the responses of indicator species (Table S1.3; Table 2): *E. vaginatum* cover first showed exponential increase leading to significantly higher amounts than in undrained sites, but with time it decreased to a similar level as in undrained sites (Figure 3a). The increase of *E. vaginatum* was most pronounced near the former ditches (Figure 3a). For *Sphagnum angustifolium*, the trajectory was more linear, although again steeper closer to former ditches than in strips (Figure 3c). The cover of species indicating drained conditions decreased at a clearly slower pace, and the difference between restored and undrained sites persisted throughout the observation period (Figure 2c).

Restoration did not impact the temporal beta-diversity index (TBI), which remained at a higher level in the restored than in the undrained peatlands (Figure 4a; Table 3) and showed the highest temporal turnover during the first years after restoration (2006–2009), after which it steadily declined across all treatments (Figure 4a). During the early years after restoration (2006–2009), changes in TBI were driven by species losses, whereas the species gains were highest later, between 2009 and 2012 (Figure 4b,c). In general, the pattern in TBI was similar within the restored sites, yet the differences were more prominent near ditches (Figure 4; Table 3).

The tree stand harvesting method had no additional impact on the species composition.

### 3.2 | Change in plant functional types

The cover of PFTs indicative of undrained peatlands increased to a level similar to undrained sites within 5 years after restoration

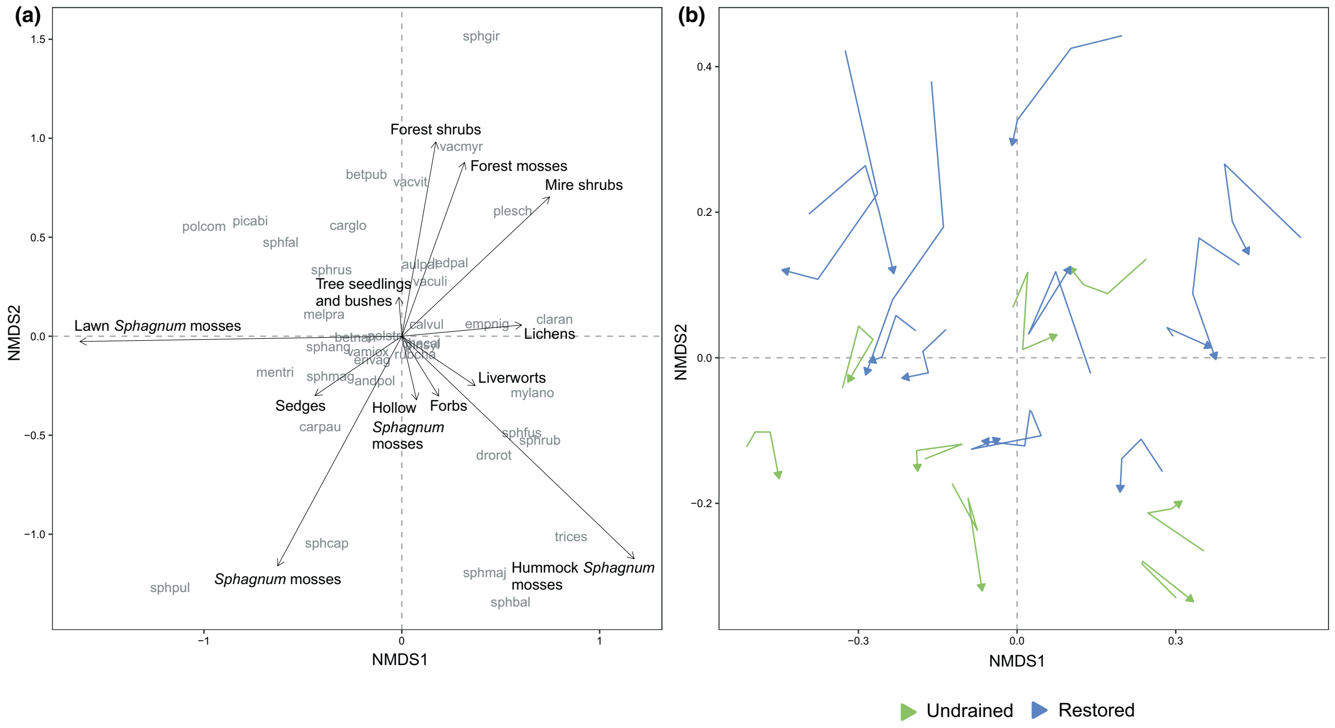


FIGURE 1 Plant species composition (a) and temporal trends within sites (b) as indicated by non-metric multidimensional scaling (NMDS) of plant cover data across the studied years (2006, 2009, 2012, 2018; stress of the NMDS plot: 0.233). In (a), the cover of plant functional groups are indicated by arrows lain over the most abundant species (for species full names, see Table S1.2). (b) Displays study site and treatment centroids and their shifts over time, with the arrow indicating the direction of change from 2006 to 2018. Blue arrows represent restored sites, whereas undrained control sites are represented with green arrows. Vegetation communities differed among the years (*adonis*, $p = 0.001$), and depending on the initial drainage ($p = 0.001$), yet the impact of restoration did not vary with years (Year:Restoration: $p = 0.132$).

(Figure 2b; Table S1.3). Accordingly, sedges and *Sphagnum* mosses displayed a significant response to restoration (Table S1.5; Figure 3b,d; Table 2). Following the development of *E. vaginatum* cover, the sedge cover in restored sites peaked near the former ditches 5 years after restoration, when it was significantly higher than in the undrained sites (Figure 3b). The *Sphagnum* cover, which originally was higher at strips than near ditches, took more time to increase to a level similar to the undrained site (Figure 3d). The changes in the cover of PFTs indicative of drained peatlands were marginal; restored sites with stem-only harvest treatment had higher cover of PFTs indicative of drained peatlands throughout, whereas restored sites with whole-tree harvest treatment did not differ from undrained sites (Figure 2d).

## 3.3 | Change in functional plant traits and functional diversity indices

There was no clear indication that the vascular plant traits in restored sites increased resemblance to undrained sites with time since restoration (except for leaf thickness at whole tree harvested sites) (Figure 5b; Table 4). Conversely, vascular plant height increased as time passed from restoration, especially near the former ditches (Figure 5a). Additionally, SLA in whole-tree harvested sites decreased after restoration to a level similar to undrained sites, although the difference between restored and undrained sites was not significant in the beginning (Figure S1.2a).

None of the CWM trait values of *Sphagnum* mosses differed significantly between undrained and restored sites (Table 4). However, in restored sites capitulum dry weight significantly increased after restoration both near former ditches and on strips, with constantly higher values near the former ditches (Figure S1.2b). A similar pattern was observed for fascicle density; *Sphagnum* mosses growing on strips had denser fascicle growth than mosses growing near to former ditches and after restoration fascicles were growing significantly less densely in both locations (Figure S1.2c).

The vascular plant functional diversity (measured as functional divergence and functional dispersion) at the restored sites increased during the first 5 years to a higher level than in undrained sites and then slowly decreased over the next 5 years (Figure 6a; Figure S1.3; Table 5). The response of *Sphagnum* moss functional diversity to restoration was more subtle (Figure 6b; Table 5). At strips, the functional divergence decreased to a similar level as in undrained peatlands, while near the former ditches it decreased to a significantly lower level over time (Figure 6b). The other aspects of *Sphagnum* moss functional diversity showed only modest temporal trends over the study period (Table S1.10).

BRITISH ECOLOGICAL SOCIETY Journal of Applied Ecology



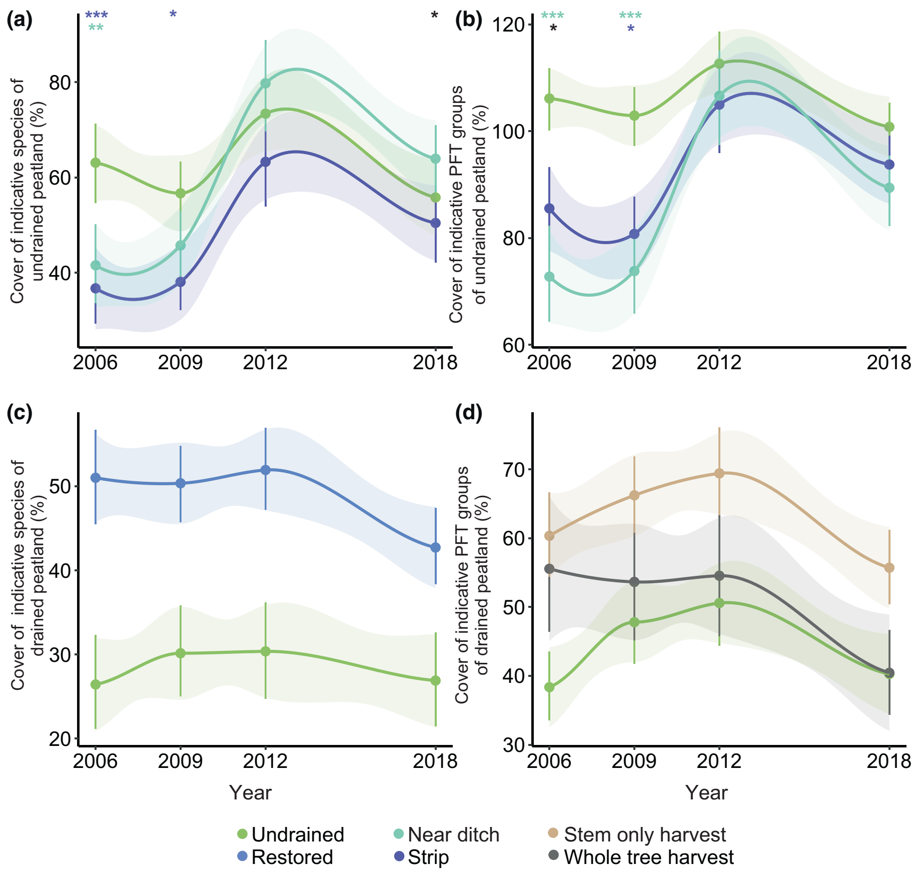


**FIGURE 2** Trends in species cover and plant functional type (PFT) groups indicative of undrained (a, b) and drained peatlands (c, d) in the restored and undrained peatlands. In (a, b) the restoration trajectory is presented separately based on plot location (near ditch vs. strips). In (d) the restoration trajectory separates the two tree harvest methods. Figure presents mean ± 95% confidence interval of cover (counted as the sum of cover percentages of indicator species/PFTs on each sample plot, Table S.1.3) for each observation year; lines between years have been smoothed using locally estimated scatterplot smoothing (loess). When the impact of restoration differed among years (interaction in Table 1) here (a, b), the pairwise differences indicated by Tukeys' post hoc test (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$) are shown, comparing the plot location within drained to the undrained peatlands separately in each year. Black stars indicate a significant difference between the plots near ditches and the plots on strips (a, b).

**TABLE 1** Summary of the best explanatory model results for indicator species and PFTs, where the impact of year, restoration and their potential interaction was assessed with a mixed repeated measures model.

| | Year | | Location | | Year × location | | Tree harvest | | Year × tree harvest | | Restoration | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *F* | *p* | *F* | *p* | *F* | *p* | *F* | *p* | *F* | *p* | *F* | *p* |
| log(Indic species cover) | 54.94 | <0.001 | 4.09 | 0.018 | 11.03 | <0.001 | | | | | | |
| log(Indic PFTs cover) | 31.13 | <0.001 | 3.02 | 0.051 | 8.40 | <0.001 | | | | | | |
| log(Drained species cover) | 14.56 | <0.001 | | | | | | | | | 22.61 | 0.001 |
| log(Drained PFTs cover) | 22.21 | <0.001 | | | | | 11.87 | 0.003 | 3.85 | 0.001 | | |

*Note*: Location refers to the sample plot's location in undrained sites in general or within restored sites near ditches or the middle of the strips. Abbreviation: PFT, plant functional type.

## 4 | DISCUSSION

Our results support our first hypothesis as well as the earlier findings (e.g. Elo et al., 2024; Haapalehto et al., 2011, 2017; Hancock et al., 2018; Maanavilja et al., 2014; Strobl et al., 2020), demonstrating that during the 10 years after restoration, the species community is still undergoing a change towards the composition of undrained peatlands. The restoration trajectory was, however, non-linear; at the beginning, high species turnover was characterized by a net loss of species, while peatland species increased in abundance later. This

TABLE 2 Summary of the best explanatory models for species and plant functional type groups responsive to restoration.

| | Year | | Location | | Year × location | |
|---|---|---|---|---|---|---|
| | *F* | *p* | *F* | *p* | *F* | *p* |
| log(Sedges) | 105.83 | <0.001 | 2.04 | 0.133 | 10.14 | <0.001 |
| log(Erio vag) | 140.06 | <0.001 | 4.26 | 0.015 | 10.67 | <0.001 |
| log(*Sphagnum* mosses) | 40.15 | <0.001 | 7.27 | 0.001 | 8.01 | <0.001 |
| log(Spha ang) | 33.46 | <0.001 | 3.03 | 0.05 | 9.08 | <0.001 |

*Note*: Location refers to the sample plot's location in undrained sites in general or within restored sites near ditches or the middle of the strips.

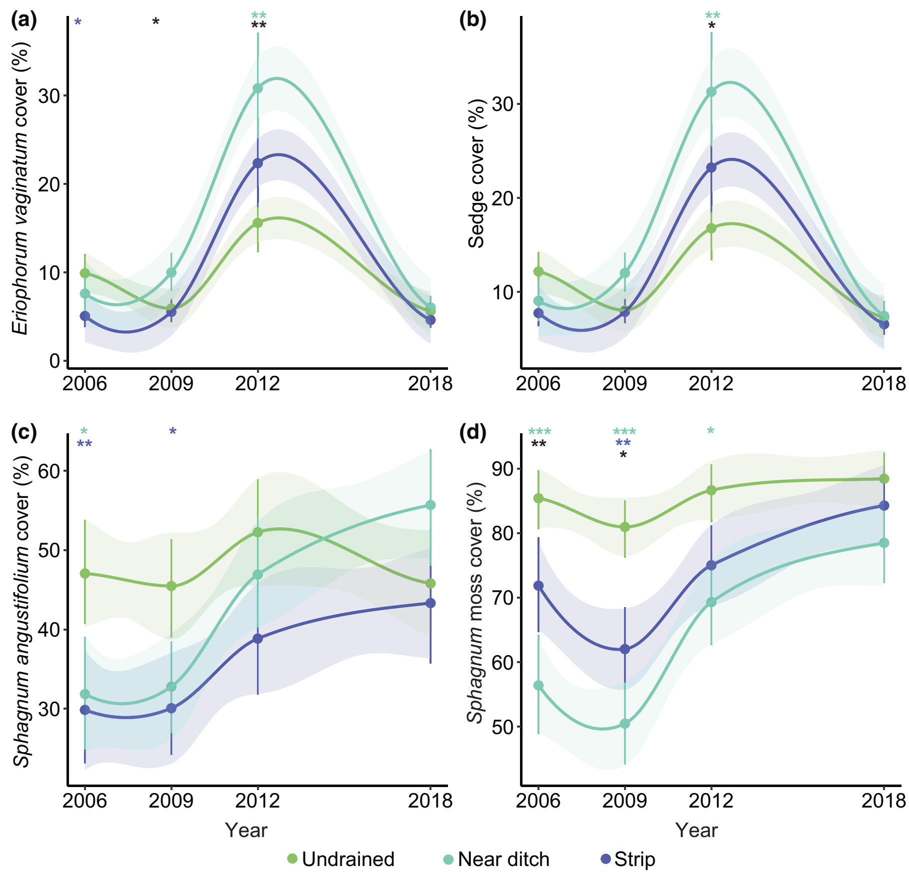


FIGURE 3 Temporal changes in the cover of (a) *Eriophorum vaginatum*, (b) PFT sedges, (c) *Sphagnum angustifolium* and (d) PFT *Sphagnum* mosses in the restored and undrained peatlands, presenting the restoration trajectory separately based on sample plot location (near ditches vs. in the middle of the strips in the drained sites). Figure presents mean ± 95% confidence interval for each observation year and smoothed (using loess) trendlines between years. When the impact of restoration differed among years (interaction in Table 2), the pairwise differences indicated by Tukeys' post hoc test (*$p<0.05$, **$p<0.01$, ***$p<0.001$) have been added to the upper panel of each frame, comparing the plot location within drained to the undrained peatlands in each year. Black stars indicate a significant difference between the plots near ditches and the plots on strips. Note the different scale in *y*-axis in subplots.

indicates that reduced competition from the previously dominating species is needed for peatland species to take advantage of the more favourable, wetter conditions.

## 4.1 | Change in species composition

We observed only a moderate decrease in the cover of species typical of drained conditions, reflecting the rather small change following drainage typical of nutrient-poor peatlands (Laine et al., 1995). Most of the species indicating drainage stage in this study (like *B. nana*, *V. uliginosum*, *E. nigrum*) commonly occur also on the hummock surfaces of undrained peatlands (Eurola et al., 2015; Laine et al., 2018). Particularly, considering such nutrient-poor systems, it seems evident that both drainage and restoration succession generally alter the proportions of the species instead of leading to high species turnover (Laine, Leppälä, et al., 2011). Although we expected to see a decrease in the cover

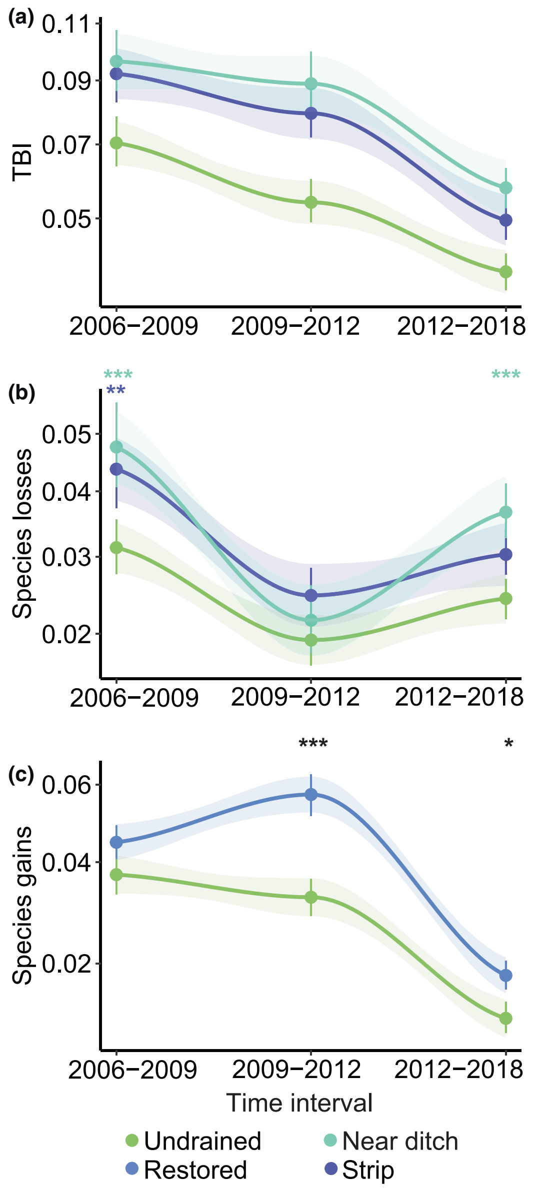


FIGURE 4 Change in annualized temporal beta-diversity (a) and its components, species losses (b) and gains (c), over the course of the study in the restored and undrained peatlands. In (a, b), the restoration trajectory is presented separately based on plot location (near ditch vs. strips). Figure presents mean ± 95% confidence interval on each occasion; lines between years have been smoothed (using loess). The *y*-axis in the plots has been square-root-transformed. When the impact of restoration differed among years (interaction in Table 3), the pairwise differences indicated by Tukey's post hoc test (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$) have been added to the upper panel of each frame, where plots near ditches and in the middle of strips are compared to the undrained peatlands (b) and restored plots to undrained plots (c) separately in each year. In (a), both plots near ditches and in the middle of strips differ from the undrained control plots throughout the studied time.

of plant functional type groups indicating drainage such as forest dwarf shrubs and forest mosses after restoration, the decrease in their cover was small. Most of the species' losses that occurred during the first years after restoration (2006–2009) can be explained by the rapid change in moisture and light conditions (Laine, Leppälä, et al., 2011).

More species' gains occurred only after the peak in the loss of species. The difference in the cover of species indicative of undrained conditions between restored and undrained sites had vanished within 5 years. However, when looking in more detail into species-level changes, some species indicating undrained conditions, like *Scheuchzeria palustris* and *Trichophorum cespitosum*, did not re-establish after restoration. Similar patterns of missing vascular species with narrow ecological niches and limited dispersal abilities have been reported long after restoration (e.g. Haapalehto et al., 2011; Hedberg et al., 2013). Unlike vascular species, some of the *Sphagnum* mosses typical of the lawn or hollow surfaces of undrained peatlands, but missing in our survey plots, like *Sphagnum pulchrum*, *Sphagnum squarrosum* and *Sphagnum balticum*, were actually found in the former ditches of restored peatlands studied here (Table S1.12). These wetter depressions with disturbed surfaces provide habitat heterogeneity for *Sphagnum* diversity, as also found by Haapalehto et al. (2017). The different return success between vascular plants and mosses with a narrow niche might relate to different dispersal potential, but solving the mechanism behind this observation calls for experimental studies. Successful immigration requires many successfully performed steps one after another: dispersal of propagules, establishment of individuals, survival until reproductive state and continued reproduction (Jackson & Sax, 2010).

### 4.2 | Two winners in early restoration succession

One of the species indicating undrained conditions and quickly increasing in cover after restoration was the sedge *E. vaginatum*, aligning with findings from earlier studies (e.g. Komulainen et al., 1999, Tuittila, Vasander, & Laine, 2000, Jauhiainen et al., 2002, Haapalehto et al., 2011, Laine, Leppälä, et al., 2011, Laine et al., 2016). The rapid increases of *E. vaginatum* may be explained by its opportunistic nature and efficient use of open space, and increased nutrient and light levels created by restoration activities (Komulainen et al., 1999; Laiho, 2006; Tuittila, Vasander, et al., 2000). In rewetted cutaway peatlands, *E. vaginatum* has been shown to facilitate initiation of peatland vegetation, such as *Sphagnum* mosses (Tuittila, Rita, et al., 2000; Tuittila, Vasander, et al., 2000). Our decade long monitoring was able to show that the high abundance of the *E. vaginatum* cover was not permanent but started to decrease after peaking 5 years after restoration, which may be an indication that also in restored forestry-drained peatlands *E. vaginatum* facilitates the recovery of other peatland species.

We hypothesized that *Sphagnum* moss cover, in general, will keep increasing a decade after restoration. Based on our study, a large share of this increase was due to *S. angustifolium*, a species clearly benefiting from restoration and indicating undrained conditions. Whereas the cover of *E. vaginatum* increased rapidly and in quite a non-linear manner, *S. angustifolium* cover increased

**TABLE 3** Summary of the best explanatory models for temporal beta-diversity and its components; species losses and species gains.

| | Year | | Location | | Year × location | | Restoration | | Year × restoration | |
|---|---|---|---|---|---|---|---|---|---|---|
| | *F* | *p* | *F* | *p* | *F* | *p* | *F* | *p* | *F* | *p* |
| sqrt(Species losses) | 54.84 | <0.001 | 10.95 | <0.001 | 2.58 | 0.037 | | | | |
| sqrt(Species gains) | 172.11 | <0.001 | | | | | 27.37 | <0.001 | 8.22 | <0.001 |
| sqrt(TBI) | 137.51 | <0.001 | 14.88 | <0.001 | | | | | | |

*Note*: Location refers to the sample plot's location in undrained sites in general or within restored sites near ditches or the middle of the strips.

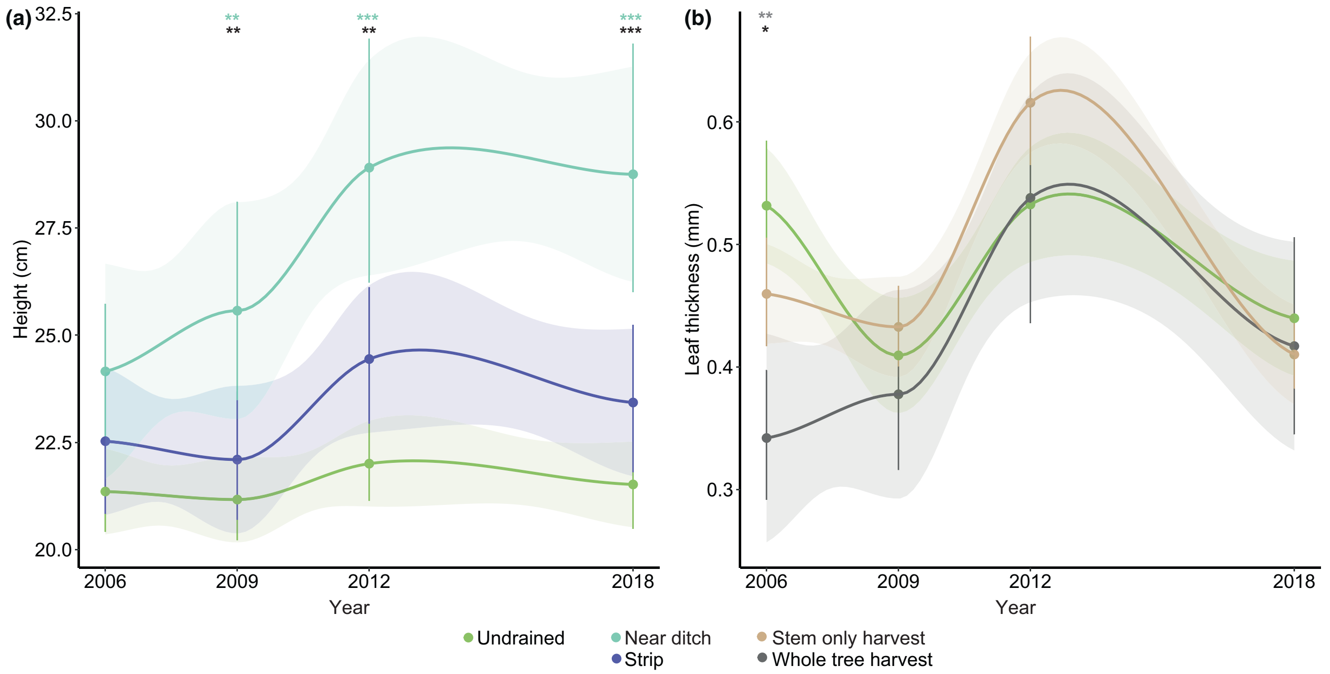


**FIGURE 5** Changes in community-weighted mean of vascular plants' height (a) and leaf thickness (b). Figure presents mean ± 95% confidence interval for each observation year; trendlines between years have been smoothed (using loess). In (a), the restoration trajectory is presented separately based on plot location, whereas in (b), the restoration trajectory separates the two tree harvest methods. When the impact of restoration differed among years (interaction in Table 4), the pairwise differences indicated by Tukeys' post hoc test (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$) have been added, comparing the influence of plot location within drained (a) or tree harvest method (b) to undrained control plots with the colour coding of location/tree harvest method. Black stars indicate significant differences between the two sample locations or tree harvest methods.

**TABLE 4** Summary of the best explanatory models for community-weighted mean traits (CWM).

| | Year | | Location | | Year × location | | Tree harvest | | Year × tree harvest | |
|---|---|---|---|---|---|---|---|---|---|---|
| | *F* | *p* | *F* | *p* | *F* | *p* | *F* | *p* | *F* | *p* |
| log(Height) | 19.03 | <0.001 | 11.18 | <0.001 | 3.97 | 0.001 | | | | |
| log(Leaf thickness) | 23.94 | <0.001 | | | | | 4.20 | 0.057 | 4.07 | 0.001 |
| LDMC | 8.14 | <0.001 | | | | | | | | |
| SLA | 7.07 | <0.001 | | | | | 0.62 | 0.564 | 2.32 | 0.032 |
| Capitulum dry weight | 16.36 | <0.001 | 7.28 | 0.001 | 3.02 | 0.006 | | | | |
| Stand density | 3.71 | 0.011 | 7.78 | 0.001 | 2.10 | 0.051 | | | | |
| Fascicle density | 16.72 | <0.001 | 6.48 | 0.002 | 2.73 | 0.013 | | | | |
| Capitulum diameter | 8.03 | <0.001 | 6.53 | 0.002 | | | | | | |
| Capitulum water content | 22.31 | <0.001 | 3.35 | 0.037 | | | | | | |

*Note*: Location refers to sample plot's location in undrained sites in general or within restored sites near ditches or the middle of the strips.
Abbreviations: LDMC, leaf dry matter content; SLA, specific leaf area.

Journal of Applied Ecology


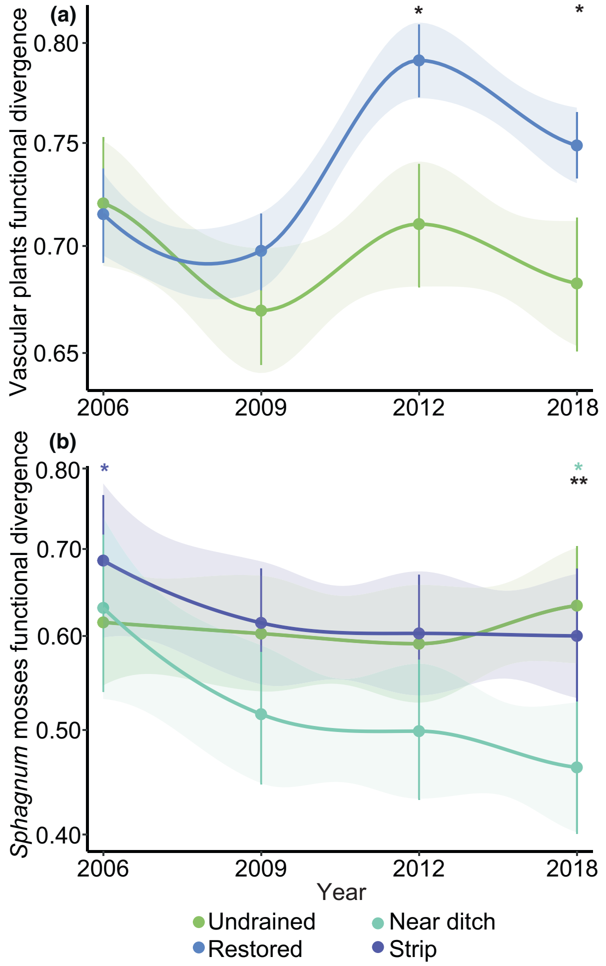


**FIGURE 6** Development of functional divergence of vascular plant (a) and *Sphagnum* mosses traits (b). Figure presents mean ± 95% confidence interval under each observation year; lines between years have been smoothed (using loess). In (b), the restoration trajectory is presented separately based on plot location. When the impact of restoration differed among years (interaction in Table 5), the pairwise differences indicated by Tukeys' post hoc test (* $p < 0.05$, ** $p < 0.01$) have been added to the upper panel of each frame, comparing the influence of restoration (a) or plot location within drained (b) to undrained control plots using the colour coding of location. The black stars in (b) indicate a significant difference between the two sample locations in 2018.

more steadily. *S. angustifolium* has a wide niche (Bengtsson et al., 2016), making it tolerant of different conditions and capable of persisting after drainage. When conditions improved (WT rise, mechanical disturbance to peat layer), the moss was able to start spreading. This capability of *S. angustifolium* to rapidly spread from remnant populations is important for peatland recovery and has been noted in earlier studies (Haapalehto et al., 2017; Maanavilja et al., 2014).

### 4.3 | Change in plant functional traits and functional diversity

We observed changes in vascular plant traits after restoration, yet the direction of change did not always follow our hypotheses. In contrast to our hypothesis, SLA decreased in whole-tree harvested sites after restoration, and an initial increase, following expected increased nutrient availability, was not observed. Experimental work with light-level manipulations (Eskelinen et al., 2022) demonstrated that species with low SLA are more likely to benefit from additional light, and increased light availability might also explain the trend in our study. Additionally, vascular plant height increased instead of our hypothesized decrease, likely resulting from the ability of taller plants to capture light more efficiently (Westoby et al., 2002) after tree removal. Observed change in vascular plant leaf thickness was connected to changes in *E. vaginatum* cover, first strongly increasing and later decreasing.

*Sphagnum* moss traits did not significantly differ from undrained sites before or after restoration. However, there was a slight increase in capitulum dry weight and a decrease in fascicle density following restoration, which may indicate a shift towards a higher resource acquisition growth strategy (Bengtsson et al., 2016; Laine, Juurola, et al., 2011; Mazziotta et al., 2019; Rice et al., 2008). Loose stands allow light to penetrate to deeper levels, enabling a higher rate of photosynthesis, which in turn means faster growth. The observed trend was stronger near the former ditches than on strips. As *Sphagnum* cover also significantly increased during the study period, it seems that restoration activities initiated the *Sphagnum* spreading.

**TABLE 5** Summary of the best explanatory models for functional diversity indices.

| | Year | | Location | | Year × location | | Restoration | | Year × restoration | |
|---|---|---|---|---|---|---|---|---|---|---|
| | *F* | *p* | *F* | *p* | *F* | *p* | *F* | *p* | *F* | *p* |
| Vascular plants | | | | | | | | | | |
| Functional divergence | 34.21 | <9.001 | | | | | 2.27 | 0.163 | 11.96 | <0.001 |
| Functional dispersion | 30.74 | <0.001 | 3.14 | 0.045 | 7.65 | <0.001 | | | | |
| *Sphagnum* mosses | | | | | | | | | | |
| Functional divergence | 3.37 | 0.019 | 4.38 | 0.014 | 4.89 | <0.001 | | | | |

*Note*: Location refers to sample plot's location in undrained sites in general or within restored sites near ditches or the middle of the strips.

Functional divergence (i.e. trait heterogeneity) showed a steep increase soon after the initiation of restoration. This resulted from an increase in species cover from the opposing ends of the functional trait range, reflecting different trait values in forest and peatland species. The increased trait heterogeneity may also have resulted from ongoing differentiation between wetter and drier parts of the peatland, as observed in an earlier study by Hancock et al. (2018). These two explanations may be related to each other: drier parts, such as strips between former ditches, can provide suitable habitat for forest species, while ditches and their surroundings provide wetter habitats.

One reason behind the moderate response in functional traits and functional diversity could be that traits were not measured from the plants present at the site, but, as is common in trait studies (Moor et al., 2017), database averages were used. Accordingly, trait values come from various soil and climatic conditions, and potential for intraspecific trait variation is not accounted for. In future studies, the response of traits and trait diversity could be better captured by measuring site-specific traits directly.

## 5 | CONCLUSIONS

Here we show that the restoration of drained peatlands (oligotrophic pine fens) by rewetting with ditch filling and using either the harvesting of whole trees or tree stems only increased resemblance to undrained peatlands over a period of 11 years. The restoration trajectory was, however, non-linear and characterized by an asynchronous pattern in species losses and species gains. We observed that indicator species covers behaved differently after restoration; the peatland sedge *Eriophorum vaginatum* had first a rapid increase and later a decrease of cover, whereas the cover of a common peatland moss, *Sphagnum angustifolium*, increased more linearly.

The significant difference before restoration and rather straightforward development of *Sphagnum* moss cover towards that of undrained peatlands after restoration suggests that *Sphagnum* cover is an effective indicator of restoration success of nutrient-poor peatlands. *Sphagnum* cover monitoring does not necessarily have to include species-level identification and could potentially be evaluated with remote sensing methods, making it an efficient tool for restoration monitoring (Lees et al., 2020; Salko et al., 2023; Wolff et al., 2024).

Additionally, the non-linear trends in many of the monitored variables indicate the need for long-term (more than 10 years) monitoring. Furthermore, the observed spatial variability within the restored peatlands suggests that monitoring should cover the habitats developing on (i) former strips, (ii) next to former ditches and (iii) in the former ditches.

### AUTHOR CONTRIBUTIONS

Anna M. Laine, Oili Tarvainen and Eeva-Stiina Tuittila conceived the ideas and designed the methodology; Anne Tolvanen, Oili Tarvainen and Anna M. Laine collected the data; Nina Kumpulainen and Henni Ylänne analysed the data; Nina Kumpulainen led the writing of the manuscript under the supervision of Eeva-Stiina Tuittila and Anna M. Laine. All authors contributed critically to the drafts and gave final approval for publication. Our study was carried out in Finland, which is the home country of all authors in this paper.

### ACKNOWLEDGEMENTS

The restoration experiment was established by the Finnish Forest Research Institute (Metla), presently Natural Resources Institute Finland (Luke) as part of the GreenBelt Life project (LIFE04 NAT/FI/000078). Vegetation monitoring was carried out by several projects in Metla and Luke. This research was funded by the Catch the Carbon research and innovation programme by the Ministry of Agriculture and Forestry, Finland (Project Turvahiili) as part of the European Union NextGenerationEU Recovery and Resilience Facility (VN/32577/2021-MMM-2, VN/32577/2021-MMM-4) and supported by the Academy of Finland Flagship funding for ACCC (Grant No. 337550) as well a by Finnish cultural foundation's regional fund of North Karelia (55241419). Open access publishing facilitated by Ita-Suomen yliopisto, as part of the Wiley - FinELib agreement.

### CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

### DATA AVAILABILITY STATEMENT

Trait data available from PANGAEA, https://doi.org/10.1594/PANGAEA.926827 (Laine, Lindholm, et al., 2021), PANGAEA, https://doi.org/10.1594/PANGAEA.932829 (Laine, Korrensalo, et al., 2021), TRY plant trait database—enhanced coverage and open access, https://doi.org/10.1111/gcb.14904 (Kattge et al., 2020). Vegetation cover data available from Etsin-service (https://doi.org/10.23729/fd-5e2a4ffc-3aa4-30cd-b059-165f62ec3e3c) (Tolvanen & Tarvainen, 2025).

### ORCID

*Nina Kumpulainen* https://orcid.org/0009-0007-6382-4276

### REFERENCES

Aapala, K., Similä, M., & Penttinen, J. (Eds.). (2013). *Ojitettujen soiden ennallistamisopas* (*Handbook for the restoration of drained peatlands*). Metsähallituksen julkaisuja.

Bengtsson, F., Granath, G., & Rydin, H. (2016). Photosynthesis, growth, and decay traits in *Sphagnum* – A multispecies comparison. *Ecology and Evolution*, *6*(10), 3325–3341. https://doi.org/10.1002/ece3.2119

Cardoso, P., Mammola, S., Rigal, F., & Carvalho, J. (2022). *BAT: Biodiversity assessment tools*. R package version 2.9.2. https://CRAN.R-project.org/package=BAT

Carroll, M. J., Dennis, P., Pearce-Higgins, J. W., & Thomas, C. D. (2011). Maintaining northern peatland ecosystems in a changing climate: Effects of soil moisture, drainage and drain blocking on craneflies. *Global Change Biology*, *17*(9), 2991–3001. https://doi.org/10.1111/j.1365-2486.2011.02416.x

CBD. (2022). *The Kunming-Montreal global biodiversity framework*. https://www.cbd.int/doc/c/e6d3/cd1d/daf663719a03902a9b116c34/cop-15-l-25-en.pdf

De Cáceres, M., & Legendre, P. (2009). Associations between species and groups of sites: Indices and statistical inference. *Ecology*, *90*, 3566–3574. https://doi.org/10.1890/08-1823.1

Dohong, A., Aziz, A. A., & Dargusch, P. (2017). A review of the drivers of tropical peatland degradation in South-East Asia. *Land Use Policy*, *69*, 349–360.

Dray, S., Bauman, D., Blanchet, G., Borcard, D., Clappe, S., Guénard, G., Jombart, T., Larocque, G., Legendre, P., Madi, N., & Wagner, H. H. (2023). *adespatial: Multivariate multiscale spatial analysis*. R package version 0.3-21. https://CRAN.R-project.org/package=adespatial

Elo, M., Kareksela, S., Ovaskainen, O., Abrego, N., Niku, J., Taskinen, S., & Kotiaho, J. S. (2024). Restoration of forestry-drained boreal peatland ecosystems can effectively stop and reverse ecosystem degradation. *Communications Earth & Environment*, *5*(1), 680.

Eskelinen, A., Harpole, W. S., Jessen, M. T., Virtanen, R., & Hautier, Y. (2022). Light competition drives herbivore and nutrient effects on plant diversity. *Nature*, *611*(7935), 301–305. https://doi.org/10.1038/s41586-022-05383-9

EU Regulation. (2024). 2024/1991 of the European Parliament and of the Council of 24 June 2024 on nature restoration and amending regulation (EU) 2022/869 2024. *Official Journal L*, 29.7.2024.

Eurola, S., Huttunen, A., Kaakinen, E., Kukko-oja, K., Saari, V., & Salonen, V. (2015). *Sata suotyyppiä: Opas Suomen suokasvillisuuden tuntemiseen*. Thule-instituutti.

Finnish Meteorological Institute. (2024). *Tilastot / Havaintojen lataus*. https://www.ilmatieteenlaitos.fi/havaintojen-lataus

Fraixedas, S., Lindén, A., Meller, K., Lindström, Å., Keišs, O., Kålås, J. A., Husby, M., Leivits, A., Leivits, M., & Lehikoinen, A. (2017). Substantial decline of Northern European peatland bird populations: Consequences of drainage. *Biological Conservation*, *214*, 223–232. https://doi.org/10.1016/j.biocon.2017.08.025

Gann, G. D., McDonald, T., Walder, B., Aronson, J., Nelson, C. R., Jonson, J., Hallett, J. G., Eisenberg, C., Guariguata, M. R., Liu, J., Hua, F., Echeverría, C., Gonzales, E., Shaw, N., Decleer, K., & Dixon, K. W. (2019). International principles and standards for the practice of ecological restoration. Second edition. *Restoration Ecology*, *27*(S1), S1–S46. https://doi.org/10.1111/rec.13035

Haapalehto, T., Juutinen, R., Kareksela, S., Kuitunen, M., Tahvanainen, T., Vuori, H., & Kotiaho, J. S. (2017). Recovery of plant communities after ecological restoration of forestry-drained peatlands. *Ecology and Evolution*, *7*(19), 7848–7858. https://doi.org/10.1002/ece3.3243

Haapalehto, T. O., Vasander, H., Jauhiainen, S., Tahvanainen, T., & Kotiaho, J. S. (2011). The effects of peatland restoration on water-table depth, elemental concentrations, and vegetation: 10 years of changes. *Restoration Ecology*, *19*(5), 587–598. https://doi.org/10.1111/j.1526-100X.2010.00704.x

Hancock, M. H., Klein, D., Andersen, R., & Cowie, N. R. (2018). Vegetation response to restoration management of a blanket bog damaged by drainage and afforestation. *Applied Vegetation Science*, *21*(2), 167–178. https://doi.org/10.1111/avsc.12367

Hedberg, P., Saetre, P., Sundberg, S., Rydin, H., & Kotowski, W. (2013). A functional trait approach to fen restoration analysis. *Applied Vegetation Science*, *16*(4), 658–666. https://doi.org/10.1111/avsc.12042

Jackson, S. T., & Sax, D. F. (2010). Balancing biodiversity in a changing environment: Extinction debt, immigration credit and species turnover. *Trends in Ecology & Evolution*, *25*(3), 153–160. https://doi.org/10.1016/j.tree.2009.10.001

Jauhiainen, S., Laiho, R., & Vasander, H. (2002). Ecohydrological and vegetational changes in a restored bog and fen. *Annales Botanici Fennici*, *39*(3), 185–199.

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Tautenhahn, S., Werner, G., Werner, G. D. A., Aakala, T., Abedi, M., Acosta, A. T. R., Adamidis, G. C., Adamson, K., Aiba, M., Albert, C. H., Alcántara, J. M., Alcázar C, C., Aleixo, I., … Wirth, C. (2020). TRY plant trait database – Enhanced coverage and open access. *Global Change Biology*, *26*(1), 119–188. https://doi.org/10.1111/gcb.14904

Komulainen, V.-M., Tuittila, E.-S., Vasander, H., & Laine, J. (1999). Restoration of drained peatlands in southern Finland: Initial effects on vegetation change and $CO_2$ balance. *Journal of Applied Ecology*, *36*, 634–648.

Konings, W., Boyd, K. G., & Andersen, R. (2018). Comparison of plant traits of sedges, shrubs and *Sphagnum* mosses between sites undergoing forest-to-bog restoration and near-natural open blanket bog: A pilot study. *Mires and Peat*, *23*, 1–10. https://doi.org/10.19189/MaP.2017.OMB.307

Laiho, R. (2006). Decomposition in peatlands: Reconciling seemingly contrasting results on the impacts of lowered water levels. *Soil Biology and Biochemistry*, *38*(8), 2011–2024. https://doi.org/10.1016/j.soilbio.2006.02.017

Laine, A. M., Juurola, E., Hájek, T., & Tuittila, E. S. (2011). *Sphagnum* growth and ecophysiology during mire succession. *Oecologia*, *167*(4), 1115–1125. https://doi.org/10.1007/s00442-011-2039-4

Laine, A. M., Korrensalo, A., Kokkonen, N. A. K., & Tuittila, E. S. (2021). Impact of long-term water level drawdown on functional plant trait composition of northern peatlands. *Functional Ecology*, *35*(10), 2342–2357. https://doi.org/10.1111/1365-2435.13883

Laine, A. M., Leppälä, M., Tarvainen, O., Päätalo, M. L., Seppänen, R., & Tolvanen, A. (2011). Restoration of managed pine fens: Effect on hydrology and vegetation. *Applied Vegetation Science*, *14*(3), 340–349. https://doi.org/10.1111/j.1654-109X.2011.01123.x

Laine, A. M., Lindholm, T., Nilsson, M., Kutznetsov, O., Jassey, V. E. J., & Tuittila, E. S. (2021). Functional diversity and trait composition of vascular plant and *Sphagnum* moss communities during peatland succession across land uplift regions. *Journal of Ecology*, *109*(4), 1774–1789. https://doi.org/10.1111/1365-2745.13601

Laine, A. M., Tolvanen, A., Mehtätalo, L., & Tuittila, E. (2016). Vegetation structure and photosynthesis respond rapidly to restoration in young coastal fens. *Ecology and Evolution*, *6*(19), 6880–6891. https://doi.org/10.1002/ece3.2348

Laine, J., Vasander, H., Hotanen, J.-P., Nousiainen, H., Saarinen, M., & Penttilä, T. (2018). *Suotyypit ja turvekankaat – kasvupaikkaopas* (2nd ed.). Tapio Palvelut Oy.

Laine, J., Vasander, H., & Sallantaus, T. (1995). Ecological effects of peatland drainage for forestry. *Environmental Reviews*, *3*(3–4), 286–303. https://doi.org/10.1139/a95-015

Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, *91*, 299–305.

Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Functional Ecology*, *16*(5), 545–556. https://doi.org/10.1046/j.1365-2435.2002.00664.x

Lavorel, S., & Grigulis, K. (2012). How fundamental plant functional trait relationships scale-up to trade-offs and synergies in ecosystem services. *Journal of Ecology*, *100*(1), 128–140. https://doi.org/10.1111/j.1365-2745.2011.01914.x

Lees, K. J., Artz, R. R. E., Khomik, M., Clark, J. M., Ritson, J., Hancock, M. H., Cowie, N. R., & Quaife, T. (2020). Using spectral indices to estimate water content and GPP in *Sphagnum* moss and other peatland vegetation. *IEEE Transactions on Geoscience and Remote Sensing*, *58*(7), 4547–4557. https://doi.org/10.1109/TGRS.2019.2961479

Legendre, P. (2019). A temporal beta-diversity index to identify sites that have changed in exceptional ways in space–time surveys. *Ecology and Evolution*, *9*(6), 3500–3514. https://doi.org/10.1002/ece3.4984

Lenth, R. (2023). *emmeans: Estimated marginal means, aka least-squares means*. R package version 1.8.9. https://CRAN.R-project.org/package=emmeans

Lüdecke, D., Ben-Shachar, M., Patil, I., Waggoner, P., & Makowski, D. (2021). performance: An R package for assessment, comparison and testing of statistical models. *Journal of Open Source Software*, *6*(60), 3139. https://doi.org/10.21105/joss.03139

Maanavilja, L., Aapala, K., Haapalehto, T., Kotiaho, J. S., & Tuittila, E. S. (2014). Impact of drainage and hydrological restoration on vegetation structure in boreal spruce swamp forests. *Forest Ecology and Management*, *330*, 115–125. https://doi.org/10.1016/j.foreco.2014.07.004

Mazerolle, M. J. (2023). *AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c)*. R package version 2.3.3. https://cran.r-project.org/package=AICcmodavg

Mazziotta, A., Granath, G., Rydin, H., Bengtsson, F., & Norberg, J. (2019). Scaling functional traits to ecosystem processes: Towards a mechanistic understanding in peat mosses. *Journal of Ecology*, *107*(2), 843–859. https://doi.org/10.1111/1365-2745.13110

Moor, H., Rydin, H., Hylander, K., Nilsson, M. B., Lindborg, R., & Norberg, J. (2017). Towards a trait-based ecology of wetland vegetation. *Journal of Ecology*, *105*(6), 1623–1635. https://doi.org/10.1111/1365-2745.12734

Natural Resources Institute Finland (Luke). (2017). *Forest resources*. Web document, Natural Resources Institute Finland, Helsinki. http://statdb.luke.fi/PXWeb/pxweb/fi/LUKE/LUKE__04%20Metsa__06%20Metsavarat/

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., … Weedon, J. (2022). *vegan: Community ecology package*. R package version 2.6-4. https://CRAN.R-project.org/package=vegan

Pinheiro, J., Bates, D., & R Core Team. (2022). *nlme: Linear and nonlinear mixed effects models*. R package version 3.1-160. https://CRAN.R-project.org/package=nlme

Piqueray, J., Ferroni, L., Delescaille, L. M., Speranza, M., Mahy, G., & Poschlod, P. (2015). Response of plant functional traits during the restoration of calcareous grasslands from forest stands. *Ecological Indicators*, *48*, 408–416.

Rice, S. K., Aclander, L., & Hanson, D. T. (2008). Do bryophyte shoot systems function like vascular plant leaves or canopies? Functional trait relationships in *Sphagnum* mosses (Sphagnaceae). *American Journal of Botany*, *95*(11), 1366–1374. https://doi.org/10.3732/ajb.0800019

RStudio Team. (2022). *RStudio: Integrated development environment for R*. RStudio, PBC. http://www.rstudio.com/

Salko, S.-S., Juola, J., Burdun, I., Vasander, H., & Rautiainen, M. (2023). Intra- and interspecific variation in spectral properties of dominant *Sphagnum* moss species in boreal peatlands. *Ecology and Evolution*, *13*, e10197. https://doi.org/10.1002/ece3.10197

Schleuter, D., Daufresne, M., Massol, F., & Argillier, C. (2010). A user's guide to functional diversity indices. *Ecological Monographs*, *80*(3), 469–484. https://doi.org/10.1890/08-2225.1

Strobl, K., Moning, C., & Kollmann, J. (2020). Positive trends in plant, dragonfly, and butterfly diversity of rewetted montane peatlands. *Restoration Ecology*, *28*(4), 796–806. https://doi.org/10.1111/rec.12957

Swindles, G. T., Morris, P. J., Mullan, D. J., Payne, R. J., Roland, T. P., Amesbury, M. J., Lamentowicz, M., Turner, T. E., Gallego-Sala, A., Sim, T., Barr, I. D., Blaauw, M., Blundell, A., Chambers, F. M., Charman, D. J., Feurdean, A., Galloway, J. M., Gałka, M., Green, S. M., … Warner, B. (2019). Widespread drying of European peatlands in recent centuries. *Nature Geoscience*, *12*(11), 922–928. https://doi.org/10.1038/s41561-019-0462-z

Tarvainen, O., Laine, A. M., Peltonen, M., & Tolvanen, A. (2013). Mineralization and decomposition rates in restored pine fens. *Restoration Ecology*, *21*(5), 592–599. https://doi.org/10.1111/j.1526-100X.2012.00930.x

Tolvanen, A., & Tarvainen, O. (2025). *Restoration of mires in Northern Finland (version 1)*. Natural Resources Institute Finland. https://doi.org/10.23729/fd-5e2a4ffc-3aa4-30cd-b059-165f62ec3e3c

Tuittila, E., Vasander, H., & Laine, J. (2000). Impact of rewetting on the vegetation of a cut-away peatland. *Applied Vegetation Science*, *3*(2), 205–212. https://doi.org/10.2307/1478999

Tuittila, E.-S., Rita, H., Vasander, H., & Laine, J. (2000). Vegetation patterns around *Eriophorum vaginatum* L. tussocks in a cut-away peatland in southern Finland. *Canadian Journal of Botany*, *78*(1), 47–58. https://doi.org/10.1139/b99-159

United Nations Environment Programme. (2022). *Global peatlands assessment: The state of the world's peatlands – Evidence for action toward the conservation, restoration, and sustainable management of peatlands*. https://wedocs.unep.org/20.500.11822/41222

Wang, Y., Naumann, U., Eddelbuettel, D., Wilshire, J., & Warton, D. (2022). *mvabund: Statistical methods for analysing multivariate abundance data*. R package version 4.2.1. https://CRAN.R-project.org/package=mvabund

Westoby, M., Falster, D. S., Moles, A. T., Vesk, P. A., & Wright, I. J. (2002). Plant ecological strategies: Some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, *33*, 125–159.

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer-Verlag.

Wolff, F., Lorenz, S., Korpelainen, P., Eltner, A., & Kumpula, T. (2024). UAV and field hyperspectral imaging for *Sphagnum* discrimination and vegetation modelling in Finnish aapa mires. *International Journal of Applied Earth Observation and Geoinformation*, *134*, 104201. https://doi.org/10.1016/j.jag.2024.104201

## SUPPORTING INFORMATION

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

**Figure S1.1.** The average difference ± 95% confidence interval in growing season (May–October) water table level between undrained and restored peatlands of each study area.

**Figure S1.2.** Trends in those community-weighted mean (CWM) traits that showed significant interaction between year and location or tree harvest method (a–c) and in those traits that show retained difference between the two locations within the restoration area but not interaction between location and year (d–f).

**Figure S1.3.** Trend in vascular plants functional dispersion.

**Table S1.1.** Number of study sites and permanent sample plots (in brackets) per management type in the three study areas.

**Table S1.2.** List of species observed in the study area, their grouping to functional types and references for the used trait information.

**Table S1.3.** Indicative species and plant functional types of undrained and drained peatlands, prior to restoration in 2006, as indicated by the *indicspecies* analysis.

**Table S1.4.** Effects of restoration (undrained, restored) and year (2006, 2009, 2012, 2018), and their interaction on the cover of plant species as indicated by the multivariate generalized linear mixed model.

**Table S1.5.** Effects of restoration (undrained, restored) and year (2006, 2009, 2012, 2018), and their interaction on the cover of different plant functional types in multivariate generalized linear mixed model.

**Table S1.6.** Functional diversity indices' definitions based on Schleuter et al. (2010) and Laliberté and Legendre (2010).

**Table S1.7.** Model comparison results, based on Akaikes' Information Criterion (AICc) values, for the cumulative weighted means of vascular and moss traits.

**Table S1.8.** Temporal beta-diversity AIC. Model comparison results, based on Akaike Information Criterion (AICc) values, for the temporal diversity index (TBI), and its' components species losses and species gains.

**Table S1.9.** Model comparison results, based on Akaike Information Criterion (AICc) values, for functional diversity indices (FD indices).

**Table S1.10.** Model comparison results, based on Akaike Information Criterion (AICc) values, for species and PFT groups that had Year × Treatment interaction when running multivariate generalized linear mixed model (Tables S1.4 and S1.5) and for species and PFT groups indicative on undrained and drained peatlands (see also Table S1.3).

**Table S1.11.** Summary of the best explanatory models for functional diversity indices (FD indices).

**Table S1.12.** Species list from vegetation survey carried out in 2018 (10 years since restoration).

**How to cite this article:** Kumpulainen, N., Tuittila, E.-S., Tolvanen, A., Tarvainen, O., Ylänne, H., & Laine, A. M. (2025). Restoration induced long-term vegetation change in oligotrophic peatlands. *Journal of Applied Ecology*, *62*, 3142–3155. https://doi.org/10.1111/1365-2664.70182