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RESEARCH ARTICLE

Changes in satellite-derived spectral variables and their linkages with vegetation changes after peatland restoration

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Remote sensing (RS) can be an efficient monitoring method to assess the ecological impacts of restoration. Yet, it has been used relatively little to monitor post-restoration changes in boreal forestry-drained peatlands, and particularly the linkages between changes in RS and plant species remain vague. To understand this gap, we utilize data from the Finnish peatland restoration monitoring network spanning 150 sites and a 10-year post-restoration monitoring period. We employ Bayesian joint species distribution models (Hierarchical Modeling of Species Communities) to study (1) the changes in optical Sentinel-2 and Landsat satellite spectral signatures, (2) whether the RS variables improve predictions of vascular plant and moss species and functional type occurrence and cover, and (3) what kinds of associations exist between RS variables and plant species or functional types. Our results show that peatland restoration increases the reflectance of red and near-infrared (NIR) bands in sparsely treed pine mire forests and open mires but not in densely treed spruce mire forests. Impacts on other tested RS variables consisting of moisture and greenness indices are less clear. Additionally, RS variables increase species- or functional type-specific predictive power only modestly, and there are few clear links between the changes in RS variables and species or functional-type occurrence and cover. We suggest that red and NIR reflectance can be used as satellite-based indicators for peatland restoration success and further studies are required to develop usable methods for detecting species-specific changes with RS.

Key words: bryophytes, joint species distribution models, plant functional types, remote sensing, satellite imagery, vascular plants

Implications for Practice

- Satellite remote sensing is suitable for monitoring post-restoration changes in ground vegetation, land cover, and wetness in peatlands with few or no trees, as trees hamper visibility to the ground.
- High spatial and temporal resolution remote sensing complements field work, and it can be used to scale field-based knowledge to larger area extents or to other sites.
- It should be further tested whether changes in reflectance can be used in operational peatland restoration monitoring and to which kind of changes the reflectance changes are attributable.
- There is a need for cross-fertilization of researchers' and practitioners' knowledge to develop restoration outcome indicators that are ecologically meaningful, operationally implementable, and detectable with remote sensing.

Introduction

Many of the peatlands in northern latitudes have been drained to facilitate forest growth and timber production for the forestry industry (Vasander et al. 2003). However, this drainage has caused widespread and harmful environmental impacts, including loss of peatland species and habitats, greenhouse gas emissions, and deterioration of water quality in recipient water bodies (Chapman et al. 2003; Urák et al. 2017; Nieminen et al. 2018).

To reverse peatland degradation, ecological restoration has been conducted during the past few decades (Andersen

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et al. 2017). In the future, peatland restoration activities are further projected to increase globally. In the European Union (EU) alone, the restoration law targets to restore 90% of the degraded area of the ecosystems, including peatlands before 2050 (Regulation [EU] 2024/1991).

In forestry-drained peatland sites, restoration includes filling or damming of ditches and removal of trees that have grown after the drainage (Haapalehto et al. 2011). The visible changes after restoration include, e.g. (1) decrease in tree cover, (2) replacement of ditches with flow-blocking structures, (3) increase in wetness and local water table level, and (4) changes in ground vegetation composition (Haapalehto et al. 2011). Of these changes, the first three occur almost immediately after restoration, while the changes in ground vegetation are slower (Haapalehto et al. 2011, 2017; Menberu et al. 2016). The most recent studies have indicated that during the first 10 years after restoration, there are changes in the vegetation: particularly the more common species of pristine mires start to colonize the restored sites, but vegetation in the restored sites does not resemble that of pristine counterparts (Elo et al. 2024).

Typical ecological targets of restoration are related to the return of original peatland community structure and functioning. The success can be measured, e.g. through inventories of different taxa, such as plants (e.g. Haapalehto et al. 2011, 2017). Overall, monitoring restoration success is important for validating restoration methods and outcomes but also for improving our understanding of peatland ecosystem changes and processes. Nevertheless, traditional field-based monitoring methods require a considerable amount of labor and other resources, and they are restricted to a limited number of points that are not necessarily representative of the whole peatland in question. Therefore, cost-effective and spatially extensive monitoring methods are required, particularly because of the increasing amount of restoration activities.

A potential solution for detecting changes over large areas cost-effectively is the utilization of satellite remote sensing (RS), as it can provide high spatial and temporal resolution observations of global land cover. The studies so far have indicated that particularly optical satellite data are usable for tracking changes in peatland wetness (Räsänen et al. 2022; Burdun et al. 2023; Isoaho et al. 2024) and land cover and vegetation such as habitat types and plant community structure (Kolari et al. 2022; Ball et al. 2023). The key strength of optical satellite imagery is its temporal availability: seamless and cross-comparable high-resolution data has been available since the 1980s (Wulder et al. 2022; Radeloff et al. 2024).

In peatlands, post-restoration RS assessments have mainly focused on tracking changes in wetness (Räsänen et al. 2022; Burdun et al. 2023; Isoaho et al. 2024), while changes in spectral signatures and vegetation have gained less attention. The few studies include the work by Ball et al. (2023) analyzing whether the spectral signatures of restored sites start to resemble those of pristine peatland areas assessing the possibility of using RS for detecting changes in ground vegetation floristic gradients related to wetness and productivity.

The lack of focus on vegetation changes has been evident overall in RS studies in peatlands, not just those related to restoration. This is surprising given that changes in vegetation composition and abundances of individual species are considered key indicators of peatland restoration success (Haapalehto et al. 2011; Elo et al. 2024; Kyrkjeeide et al. 2024). Even though broad-scale patterns in habitat type changes have been monitored (Kolari et al. 2022; Steenvoorden et al. 2022), more detailed analyses of temporal vegetation changes have not been conducted.

Despite the lack of assessments about temporal changes in vegetation, there have been multiple studies mapping the spatial patterns of vegetation at a specific time point. Examples of monitored vegetation characteristics include plant communities and floristic gradients (Harris et al. 2015; Räsänen et al. 2020b), plant functional types (PFTs), such as shrubs, forbs, graminoids, and mosses (Räsänen et al. 2020b; Pang et al. 2024), functional traits, such as leaf-area index and plant nutrient content (Kalacska et al. 2015; Räsänen et al. 2020a), and the occurrence and cover of single species (Kalacska et al. 2013; Pang et al. 2024; Simpson et al. 2024). It can be hypothesized that the temporal changes after restoration in these characteristics can be monitored if there are systematically collected long-term monitoring data and if the scale of the changes is detectable. Furthermore, for revealing the post-restoration vegetation succession, the RS approaches should simultaneously account for several changes in land cover, including in tree cover and wetness.

We utilize globally unique 10-year before-after control-impact (c.f. Christie et al. 2020) Finnish peatland restoration monitoring initiative data spanning 150 sites that belong to six different peatland types (Elo et al. 2024). We use Bayesian joint species distribution models (Ovaskainen et al. 2017; Ovaskainen & Abrego 2020) that can be used to assess plant community change and the associations between different plant species, PFTs, and RS variables. Our objective is to study how the post-restoration land cover changes in peatlands are linked with spectral signature changes and what kinds of associations there are between spectral and vegetation changes in different peatland types and treatments (pristine, drained, and restored). Our broader objective is to contribute to the work developing RS-based ecological restoration success indicators (c.f. Skidmore et al. 2021) that can be used for automatic restoration success analysis.

Our specific research questions are as follows:

(1) What is the effect of peatland restoration on spectral signatures in different peatland types?
(2) Do satellite imagery variables improve predictions of plant species and PFT occurrences and covers in restored, drained, and pristine sites?
(3) What kinds of associations exist between RS variables and plant species and PFT occurrence/cover?

Methods

Study Sites and Field Data

We used data from 150 sites belonging to the Finnish Metsähallitus Parks & Wildlife peatland restoration monitoring network (Fig. 1; description in Elo et al. 2024). The sites in the network

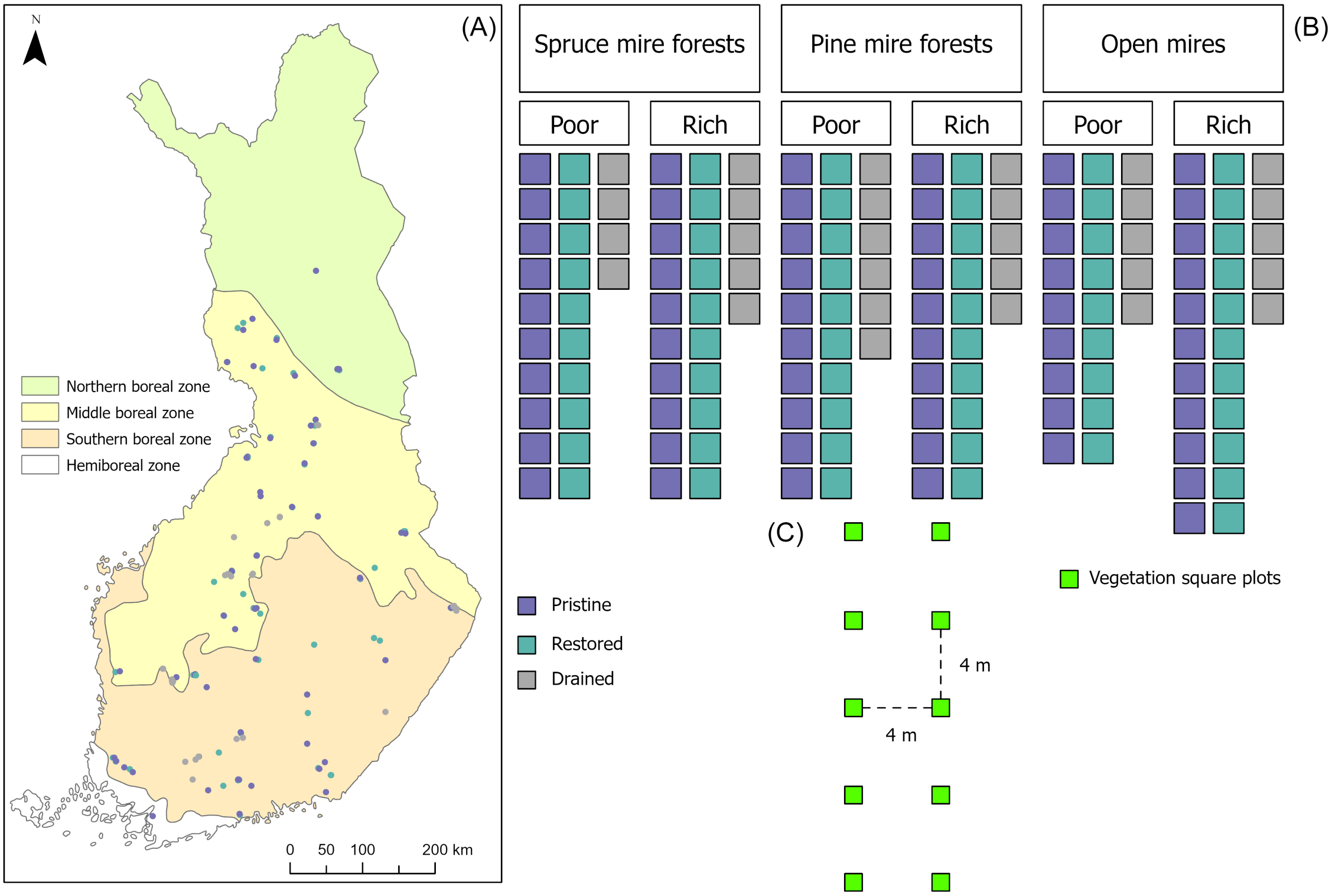

Figure 1. Finnish peatland monitoring network, with locations of the monitoring sites (A), number of monitoring sites for each peatland type and productivity (B), and sampling of vegetation inventory at each site (C).

are located throughout Finland (60–68°N, 21–31°E; Fig. 1; Elo et al. 2024) across elevation and climatic gradients (Fig. S1). They are divided into six different peatland types based on their vegetation: rich and poor spruce mire forests, rich and poor pine mire forests, and rich and poor open mires. For each type, there are data for 10 restored sites and 10 nearby located pristine counterparts, with the exceptions being 9 + 9 sites for poor open mires and 11 + 11 sites for rich open mires. Additionally, there are 30 drained control sites (4–6 sites per type). The restored sites have been drained for forestry between the 1960s and 1970s and subsequently restored between 2007 and 2014, while pristine sites have not been drained, and drained sites have been drained approximately concurrently with the restored sites but have not been restored.

Spruce mire forests are densely treed by *Picea abies* in oligotrophic poor sites, while in meso-eutrophic rich sites, there are also some deciduous trees (esp. *Betula pubescens*). The ground vegetation consists of forbs, graminoids, and *Sphagnum* and feather mosses. Pine mire forests are sparsely treed by low-growth *Pinus sylvestris*, accompanied by *B. pubescens* in rich sites. Pine mire forests are in general more nutrient-poor than spruce mire forests, with poor sites being ombrotrophic and rich sites oligo-mesotrophic. Ground vegetation consists typically of various evergreen and deciduous shrubs (e.g. *Rhododendron tomentosum* and *Vaccinium uliginosum*) and *Sphagnum* mosses. Open mires are mostly treeless sites, with the few trees being *P. sylvestris* in the ombrotrophic poor sites and deciduous trees (e.g. *B. pubescens*) in oligo-mesotrophic rich sites. The ground vegetation in poor sites consists of *Sphagnum* mosses and shrubs, while in the rich sites, the cover of sedges, forbs, and wet brown mosses increases.

Restoration aims to raise the water table and to return the canopy structure as similar as possible to the pre-drained state or an undrained reference site. Typical restoration measures in each type consist of filling in and damming the ditches as well as felling of trees at various extents, depending on the peatland type. In spruce mire forests, a relatively dense tree cover has usually been left after restoration, while in pine mire forests, only some trees have been left, and in open mires, practically all trees have been cut.

In each site, vegetation has been monitored in 10 one-square-meter squared plots. These plots are arranged in two parallel lines, with each line containing five plots spaced four meters apart from each other (see Fig. 1). The lines are located to represent typical vegetation of each site, and the minimum distance to the nearest ditch is 10 m. The exact location of the first plot has been randomized within the criteria defined above. The vegetation sampling has been conducted before restoration (year 0) and 2, 5, and 10 years after restoration. In pristine and drained sites, a similar inventory interval has been utilized. During each inventory, the %-cover of each vascular plant and moss species (Table S1) has been visually estimated. For each site, we have calculated a site-level community by averaging the cover over plots for each site. While the differences between sites are larger in spruce mire forests than in pine mire forests and open mires (Elo et al. 2016), within-site variability is approximately equal between the peatland types (Fig. S1).

For PFT-level analyses, we divided the plant species into the following PFTs that have been widely used in peatland research before (e.g. Räsänen et al. 2020a, 2020b): deciduous shrubs, evergreen shrubs, forbs, graminoids, *Equisetum*, *Pteridophytina*, *Sphagnum*, and other mosses (Table S1). We further divided the shrub, forb, and graminoid PFTs by their primary habitat requirements into mire and other groups, while *Sphagnum* and other mosses were divided into hummock, lawn, and hollow species (Eurola et al. 1995; Finnish Biodiversity Info Facility 2024). This was done because the habitat requirements and potential restoration impact are not uniform within a PFT, but species within a single PFT can react differently to restoration.

Remote Sensing Data

We used five different optical RS variables: red reflectance, near-infrared (NIR) reflectance, shortwave infrared transformed reflectance (STR; Sadeghi et al. 2015), soil-adjusted vegetation index (SAVI; Huete 1988), and normalized difference moisture index (NDMI; Gao 1996). We selected variables that do not strongly correlate with each other and that have been shown to be useful in peatland studies related to land cover, vegetation, and wetness.

Of the visible and NIR wavelength bands, we chose red and NIR due to their capability to track changes in peatland vegetation, habitats (Kolari et al. 2022), and wetness (Isoaho et al. 2023, 2024). STR is a transformation of shortwave infrared (SWIR) reflectance, and it has been shown to function well in wetness prediction (Isoaho et al. 2024; Jussila et al. 2024). Of different vegetation greenness indices, we included SAVI due to its relatively good performance in predicting changes in productivity gradient in open and sparsely treed peatlands. We complemented the list with NIR-SWIR index NDMI that has correlated with peatland soil moisture, water table, and wet area (Meingast et al. 2014; Ludwig et al. 2019). Overall, a versatile set of variables has been recommended due to site-specific differences in the most important variables (Räsänen et al. 2022).

We calculated the variables from the bottom-of-atmosphere reflectance products of 10–20 m spatial resolution European Space Agency Copernicus Sentinel-2 and 30 m spatial resolution National Aeronautics and Space Administration/United States Geological Survey Landsat 5-9 datasets that we harmonized to Landsat 8-9 reflectance (Roy et al. 2016; Zhang et al. 2018). For each variable, we calculated early summer (ES; May 1–June 15) and midsummer (MS; July 1–August 15) annual median imagery, from which we calculated median imagery for each monitoring period (1–5 years before restoration; 1–3 years after restoration, 4–6 years after restoration, and 9–11 years after restoration) for both seasons. We used two seasons as multitemporal analysis has been shown to boost model performance in various studies (Räsänen et al. 2020b; Pang et al. 2022; Wu et al. 2023) and as these seasons have strikingly different hydrological and phenological conditions (Sallinen et al. 2023; Isoaho et al. 2024. We calculated median imagery to filter out noise present in single images and to construct representative datasets for the selected phenological stages. During the ES season, the snow has melt, vegetation starts to emerge, and the water table is at its highest. During the MS season, vegetation peaks and the water table is typically at its lowest. We did not include imagery during late summer or autumn due to persistent cloud coverage during that season. We utilized only images with a maximum of 30% cloud cover and masked out remaining clouds, haze, snow, and shadow with Scene Landcover Classification (Sentinel-2) and Quality Assessment pixel classification (Landsat).

For each variable, we calculated mean values for a 15-m-radius buffer area that contained all vegetation plots in the sites. For dates with multiple Sentinel-2 or Landsat satellite image observations, we calculated the mean values over the observations. We conducted all satellite image processing in Google Earth Engine (Gorelick et al. 2017).

Statistical Analysis

We applied a type of Bayesian joint species distribution modeling: Hierarchical Modeling of Species Communities (HMSC; Ovaskainen & Abrego 2020; Ovaskainen et al. 2017). We conducted two different sets of HMSC analyses: (1) plant species-level and (2) PFT-level analyses. In both analyses, RS variables were included. In Section 3, we mostly report species-level analysis results but complement the information with PFT analysis results.

HMSCs can be used to examine the species-to-species associations (here also RS variable-species and RS variable-PFT associations) when controlling for other covariates, as well as changes in plant communities in different management types. For each peatland type separately, we modeled the occupancy (presence/absence) of the species or PFT having greater than 20 occupancies by a probit model, and conditionally on the occurrence, we modeled the cover (log-transformed, normalized to zero mean and unit variance within each species) of the same species or PFT with a normal model. We included RS variables (normalized to zero mean and unit variance) as response variables in the same model to infer their associations with species. As random effects, we included site, modeled as a spatially explicit random effect and sampling year. As explanatory variables, we included treatment (a factor with three levels: restored/drained/pristine), time (a continuous variable; 0, 2, 5, and 10 since restoration or corresponding period), and its second-order polynomial to allow for unimodal responses, as well as the interaction of treatment and time squared.

We ran the models using R package Hmsc 3.0 (Tikhonov et al. 2020). The package uses the Bayesian framework with Gibbs Markov chain Monte Carlo (MCMC) sampling. We assumed the default prior distributions, with the exception of a1 and a2 parameters for the random effect site, which were set both to 100 to increase the shrinkage and thus avoid modeling noise. We sampled the posterior distribution with four chains, each for 250 samples with thinning of 10,000, 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 with a potential scale reduction factor (Fig. S2) and assessed the explanatory power by Tjur's r^2 (occupancy) and r^2 (cover) (Fig. S3).

Based on the fitted models, we predicted the values of each RS variable in time for different treatments. From these predictions, we calculated the following three measures informing about different aspects of the effects of restoration on the RS variables.

First, we calculated whether restoration affected RS variable as

$$\mathrm{Resp} = \left(v_{10}^{\mathrm{R}} - v_{0}^{\mathrm{R}}\right) - \left(v_{10}^{\mathrm{D}} - v_{0}^{\mathrm{D}}\right)$$

where v_{10}^{R} and v_{0}^{R} are values of RS variables in restored sites in the years 10 and 0, respectively, and v_{10}^{D} and v_{0}^{D} represent corresponding values in drained sites. Resp takes positive values if the change is positive in relation to change in drained sites and negative values if the change is negative in relation to change in drained sites.

Second, values for RS in drained and in restored sites may differ as they were not randomly selected. To assess the reliability of inferences of how RS variables respond to restoration, we calculated whether they differed at the beginning of the experiment between the drained and restored sites:

$$\mathrm{Diff1} = v_{0}^{\mathrm{R}} - v_{0}^{\mathrm{D}}$$

Third, we calculated whether the difference between restored and pristine control sites grew smaller (or larger) during the study period:

$$\mathrm{Diff2} = \mathrm{abs}\left(v_{10}^{\mathrm{R}} - v_{10}^{\mathrm{P}}\right) - \mathrm{abs}\left(v_{0}^{\mathrm{R}} - v_{0}^{\mathrm{P}}\right)$$

For all three measures, we calculated the median as well as the posterior probability for the median being larger than zero. We considered the measure to have high support for the median being positive/negative if the posterior probability is greater than 95% and moderate support if the posterior probability is greater than 80%. We calculated the same measures for abundance of each species, or PFT (probability of occurrence × cover given occurrence). As the species-specific responses to restoration merely reinforce the previous findings (Elo et al. 2024), we present them only in Fig. S4 together with the PFT-level information.

To answer whether RS variables improve predictive power of the species- or PFT-specific models, we first calculated twofold cross-validation. Then, we performed conditional cross-validation, where we used data from each RS variable, one at a time, and it's estimated associations with the species or PFTs to calculate the predictions. Finally, we compared whether including information on the RS variable yielded an improvement in predictive power by subtracting the cross-validated predictive power from the conditionally cross-validated predictive power (CCV). We did the cross-validations with parameter values based on thin = 10 due to the high computational demand of the calculations and because predictive powers tend to converge with a relatively low number of thinning. Furthermore, variance partitioning of the explanatory variables remained similar when thinning of 10 or 10,000 was used. Finally, we calculated association matrices, which represent the residual associations of RS variables and species, or PFTs, after controlling for the treatment, time, and their interaction.

Results

Effect of Restoration on Spectral Signatures

Almost all RS variables were affected by restoration (Fig. 2). Especially, both ES and MS red and NIR reflectance increased after restoration in most peatland types. Moreover, SAVI MS increased, whereas for SAVI ES, the response had low statistical support (posterior probability <95%). STR and NDMI decreased or showed no highly supported response to restoration, with STR showing highly supported response in more peatland types than NDMI. The only peatland type where no high support was seen in any of the RS variables was rich spruce mire forests, whereas the clearest effects were seen in pine mire forests and open mires. In pine mire forests and open mires, the red and NIR reflectance of restored sites had similar values than drained sites before restoration and approached those of pristine sites after restoration (Figs. 3 & 4). For other variables and peatland types, the temporal trends in restored, pristine, and drained sites were less clear, and the spectral signatures in restored sites did not clearly move closer to the signatures in pristine sites (Figs. 3–5).

Improvement in Predictive Power From RS Variables

For most species or PFTs, at least one of the RS variables improved the predictive power and resulted in a predictive power higher than 0 (Figs. 6 & S5). There were differences between species and peatland types, which RS variables improved the predictive power, and none of the variables was clearly better than the others (Fig. 7). The resulting predictive powers were generally relatively modest both for species and PFTs. The mean was typically circa 0.1–0.2, but for some species, CCV was very high (up to 0.65; Table S2). The same applied to the improvement in predictive power when including the best RS variable: typically, the improvement was small (<0.1), but for some species, it was very high (up to 0.52; Table S2).

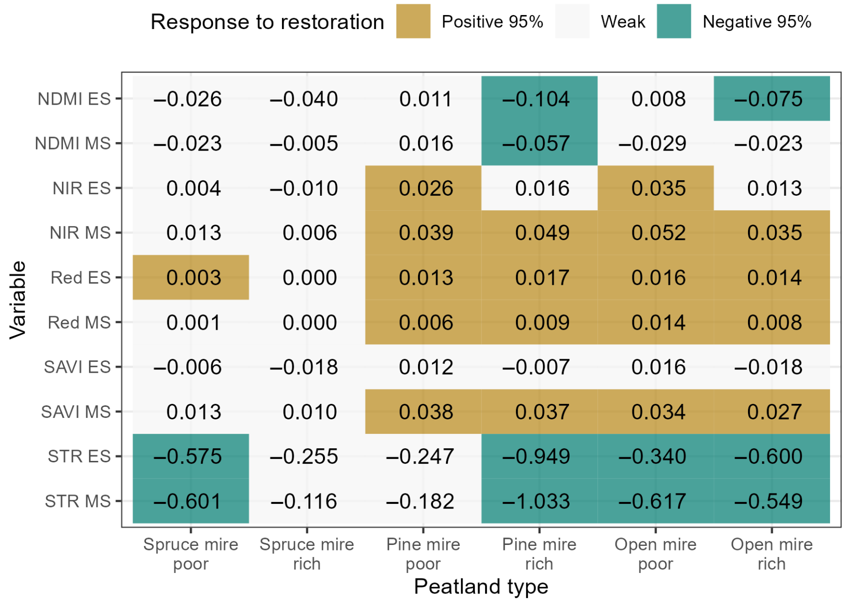

Figure 2. The response to restoration of remote sensing variables in different peatland types. Note that the values are based on the original values of each remote sensing variable; therefore, the range for shortwave infrared transformed reflectance (STR) is much larger than for non-transformed bands (STR is circa 50 and 1 for shortwave infrared reflectance of 1 and 26%, respectively). In the figure, NDMI refers to normalized difference moisture index, SAVI to soil-adjusted vegetation index, ES to early summer, and MS to midsummer. The statistical support is "Positive 95%" if the posterior probability of the median being larger than zero is greater than 95%; "Negative 95%" if the posterior probability of the median being smaller than zero is greater than 95%; and "Weak" if the posterior probability of the median being larger/smaller than zero is less than 95%.

Associations Between Species or PFTs and Remote Sensing Variables

When concentrating on those RS-species or RS-PFT linkages in which (1) restoration had an effect on both the RS variable and species or PFT and (2) incorporating RS variable increased predictive power (Figs. 8 & S6), the improvement in predictive power was typically small (<0.05 in improvement in cross-validated predictive power [CCV-CV]). The exceptions were mainly the negative associations of graminoids with NDMI and red reflectance (*Carex chordorrhiza* in poor pine mire forests and rich open mires, and also *C. lasiocarpa* cover in rich open mires; Fig. 8) and graminoid PFTs in rich open mires (Fig. S6). Additionally, a somewhat clear improvement (>0.05 in CCV-CV) was seen for *Vaccinium uliginosum* cover associated negatively with NDMI ES in rich pine mire forests. There were also other associations, both negative and positive, but in these cases, RS variables increased the predictive power little (<0.05 in CCV-CV).

Discussion

Our results show that (1) peatland restoration affects satellite-derived spectral signatures, (2) satellite image variables increase modestly species- or PFT-specific predictive power in joint species distribution models, and (3) there are few clear links between the changes in RS variables and the changes in post-restoration species or PFT occurrence and cover.

Restoration Effects on Spectral Signatures

Over time, the spectral signatures of restored sites moved closer to those of pristine sites. As pristine-like ecosystem structure and functioning is the goal for restoration, the result suggests that restoration can be successfully monitored with RS data. The trend toward pristine was particularly evident in red and NIR reflectance for sparsely treed pine mire forests and open mires, whereas for other tested variables and especially for densely treed spruce mire forests, the trends were not as clear. These findings align with Ball et al. (2023), who observed the convergence between restored and pristine sites with optical Sentinel-2 and synthetic aperture radar Sentinel-1 data. In their analysis, the similarity increased relatively strongly during the first 10–15 years after which the signatures between restored and pristine sites were close to each other. We could not verify this finding due to our 10-year post-restoration monitoring period but instead showed that during the first 10 years, the harmonization in variable values between restored and pristine sites was evident only for certain variables and peatland types. Ball et al. (2023) did not analyze the trends in different bands and indices but focused on overall spectral similarity using Mahalanobis distance and limited analysis to 1-year sampling of peatlands restored during different years. Therefore, our analysis complements the work by Ball et al. (2023) by showing (1) that there are differences between peatland types and RS variables and (2) what kind of trend is seen after restoration.

Our results indicate that reflectance of the red, NIR, and SWIR (STR is transformed SWIR reflectance and negatively correlated with it) increases after restoration, particularly in pine

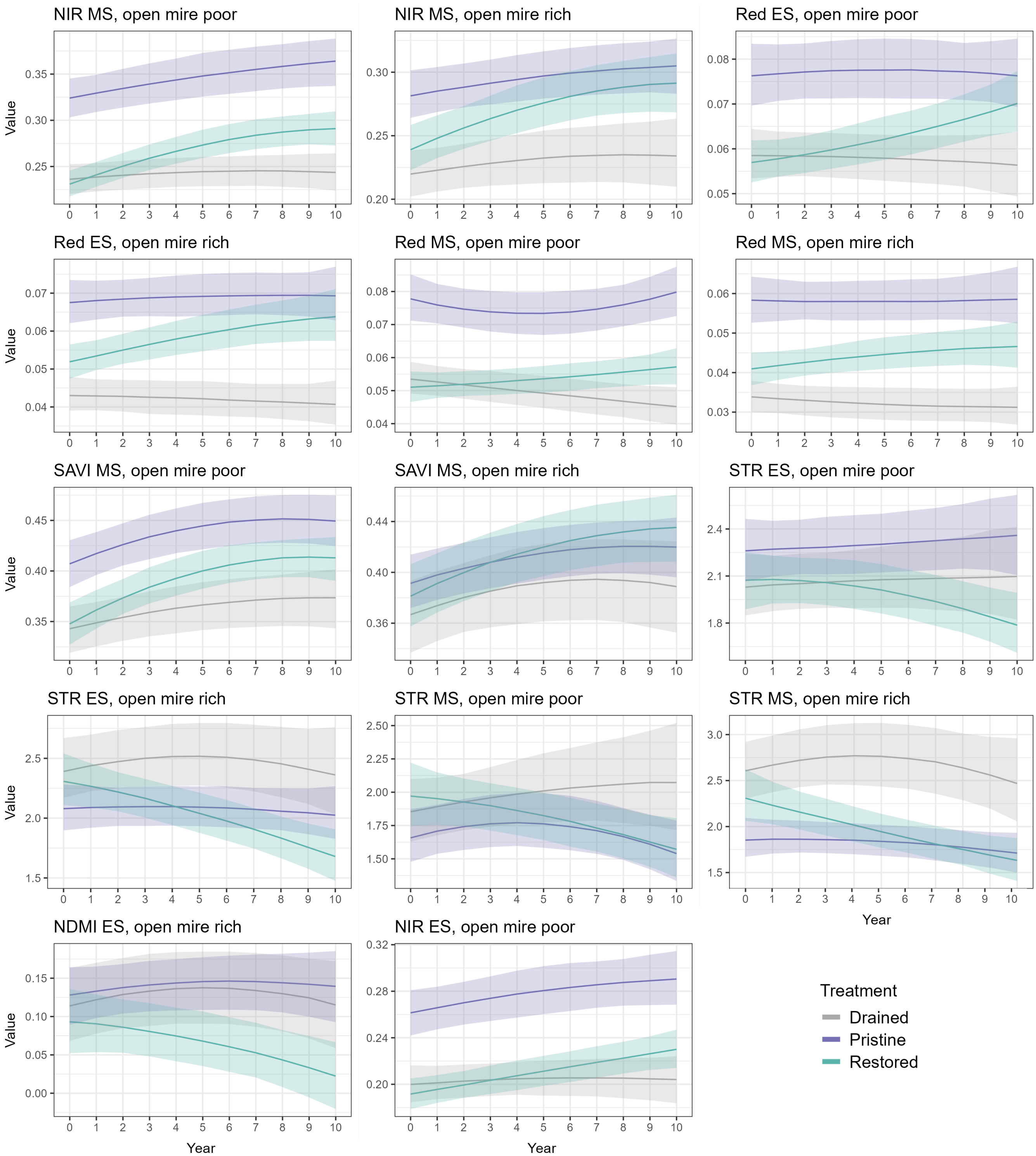

Figure 3. Changes in remote sensing variables over time in drained, pristine, and restored open mires. The plots are drawn only for those changes in remote sensing variables that responded either positively or negatively to restoration with a high support (a posterior probability of the median being larger/smaller than zero greater than 95%; Fig. 2). In the figure, NDMI refers to normalized difference moisture index, SAVI to soil-adjusted vegetation index, STR to shortwave infrared transformed reflectance, ES to early summer, and MS to midsummer.

mire forests and open mires. This is probably largely attributed to the felling of trees and increased openness in the landscape in these peatland types, as especially red reflectance and RS-measured albedo is negatively associated with woody canopy cover (Yang & Prince 1997; Kuusinen et al. 2016). Felling of trees is conducted during restoration to make room for

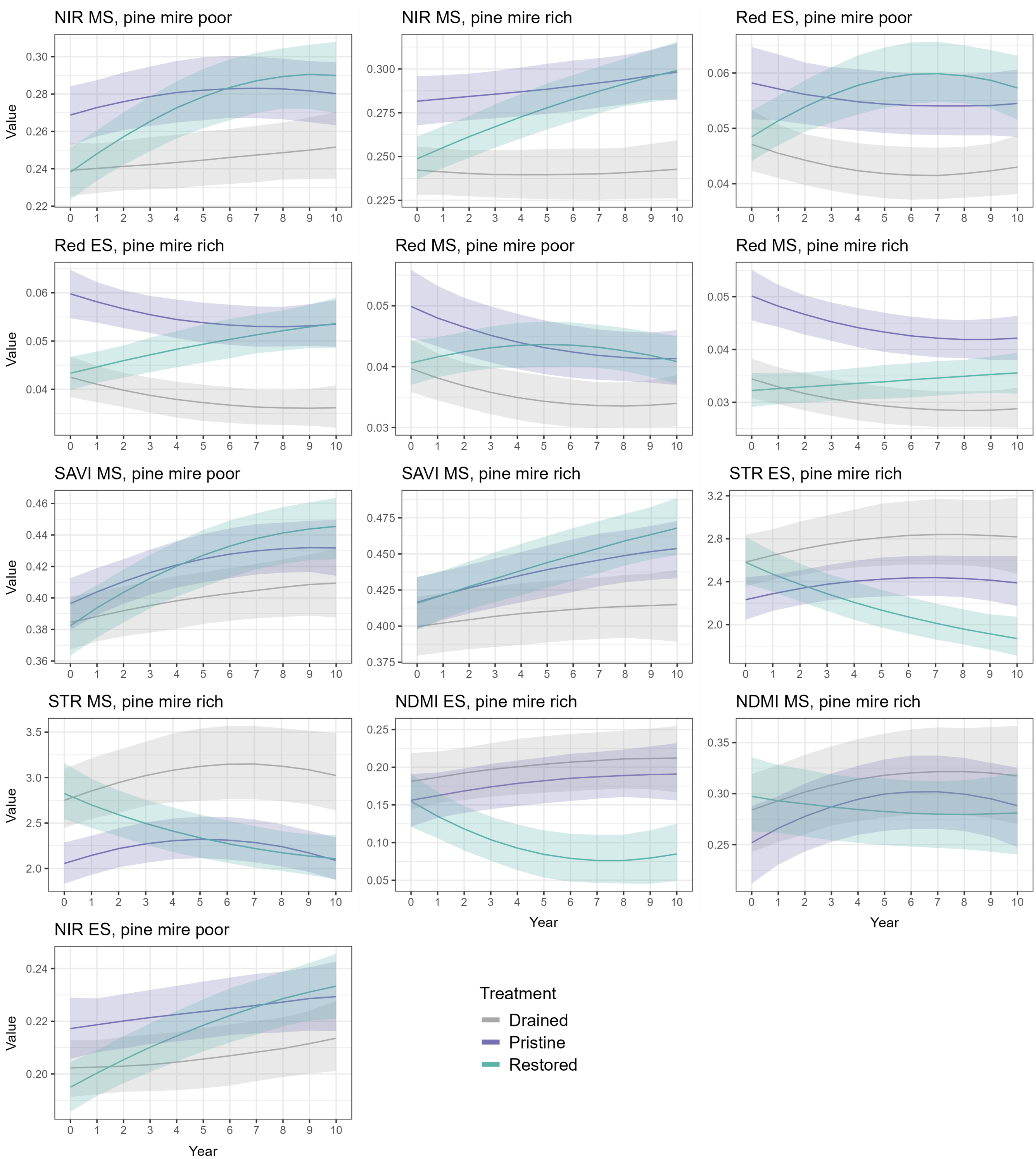

Figure 4. Changes in remote sensing variables over time in drained, pristine, and restored pine mire forests. The plots are drawn only for those changes in remote sensing variables that responded either positively or negatively to restoration with a high support (a posterior probability of the median being larger/smaller than zero greater than 95%; Fig. 2). In the figure, NDMI refers to normalized difference moisture index, SAVI to soil-adjusted vegetation index, STR to shortwave infrared transformed reflectance, ES to early summer, and MS to midsummer.

excavators along the ditches, bring back pristine-like canopy structure, and decrease evapotranspiration by trees. Although the effects of restoration occur short-term and are evident in 2 years after restoration data, our modeling approach, where time is used as a continuous variable, tends to extend this effect. However, the felling of trees during the time of restoration does

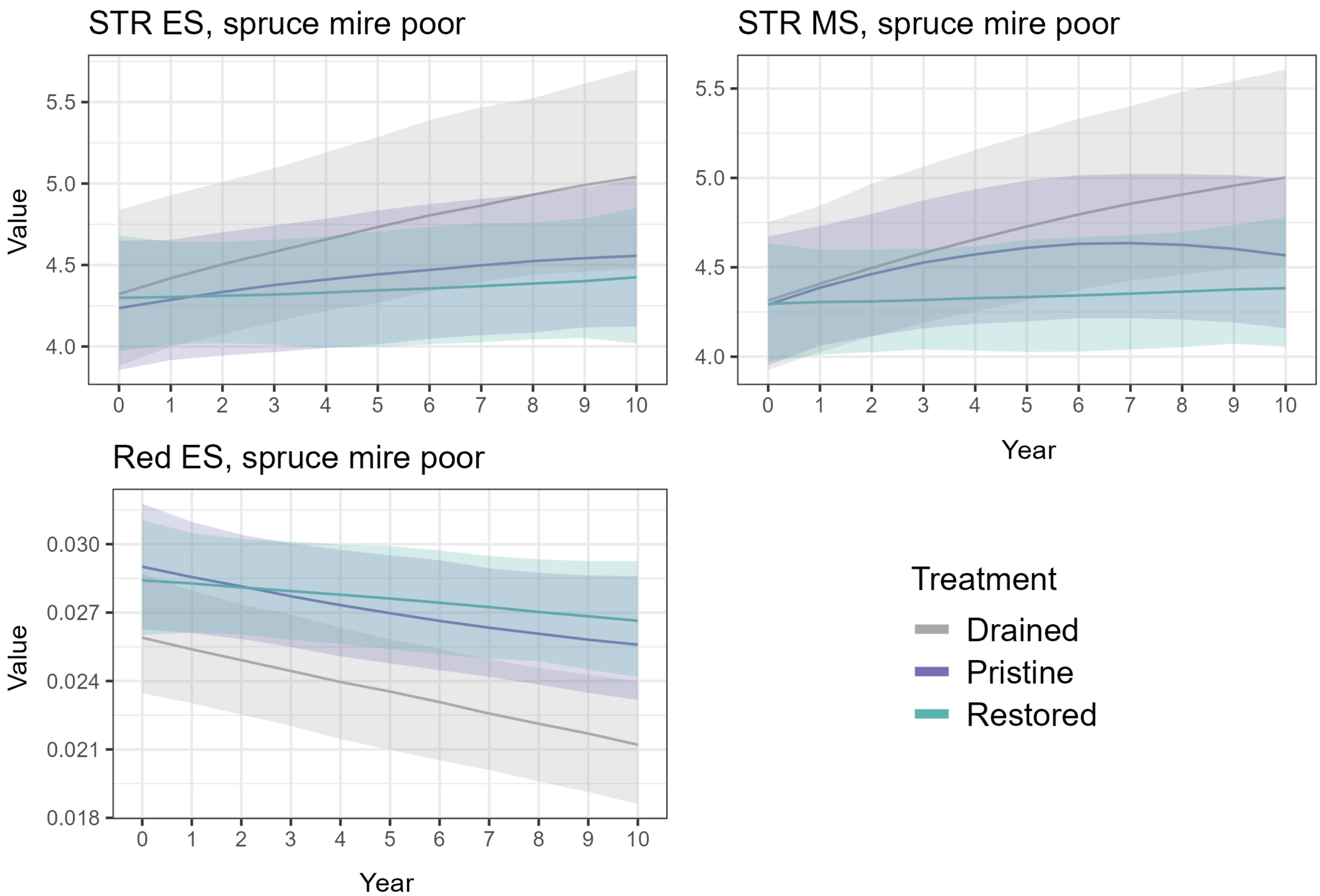

Figure 5. Changes in remote sensing variables over time in drained, pristine, and restored spruce mire forests. The plots are drawn only for those changes in remote sensing variables that responded either positively or negatively to restoration with a high support (a posterior probability of the median being larger/smaller than zero greater than 95%; Fig. 2). In the figure, STR refers to shortwave infrared transformed reflectance, ES to early summer, and MS to midsummer.

not probably fully explain the changes. Another possible reason is increased wetness, a key target of restoration, which, however, should decrease reflectance, as wetter peatland surfaces have lower reflectance than drier ones (Tahvanainen 2011; Kolari et al. 2022), and STR is lower during drier years in wet aapa mires (Jussila et al. 2024). Therefore, the changes are related probably also to other changes in land cover, such as filling of wet ditches and their gradual vegetation, and changes in ground vegetation composition, such as changes in floristic gradients, that are targeted for in restoration.

For the included indices utilizing two bands (SAVI and NDMI), the results were not as clear as for the indices based on the individual bands (Red, NIR, and STR). SAVI MS was weakly but positively affected by restoration in pine mire forests and open mires. In principle, greenness indices such as SAVI should correlate positively with vegetation biomass (Berner & Goetz 2022); therefore, the pre-restoration state with denser tree cover should have higher SAVI than the post-restoration state. However, there have been contradicting results on whether greenness indices correlate with vegetation biomass in open peatlands (McPartland et al. 2019; Räsänen et al. 2021). In addition, in our case, SAVI MS had a clearer relationship with restoration instead of SAVI ES that was observed to be important for predicting changes in floristic gradients. One possible reason for the positive SAVI-restoration relationship might also be the undesired outburst of *Betula pubescens* seedlings after restoration in some of the poorer sites (Haapalehto 2013), since strong growth in deciduous vegetation increases satellite-derived summertime greenness (Fiore et al. 2020). However, this cannot fully explain the SAVI changes, as seedling outburst does not happen in every restoration site.

NDMI, instead, should be positively correlated with soil moisture, an increase of which is targeted in restoration. In peatlands, a positive relationship has been found when utilizing SWIR reflectance of circa 1200 nm for index calculation (Meingast et al. 2014), but not when NDMI based on the SWIR band of circa 1800 nm, measured by Sentinel-2 and Landsat, has been utilized in water table modeling (Räsänen et al. 2022; Isoaho et al. 2024). In our results, the NDMI-restoration linkage was mostly negative but, in some cases, positive with low support. As the relationship between NDMI and restoration was unclear, no robust conclusion can be derived.

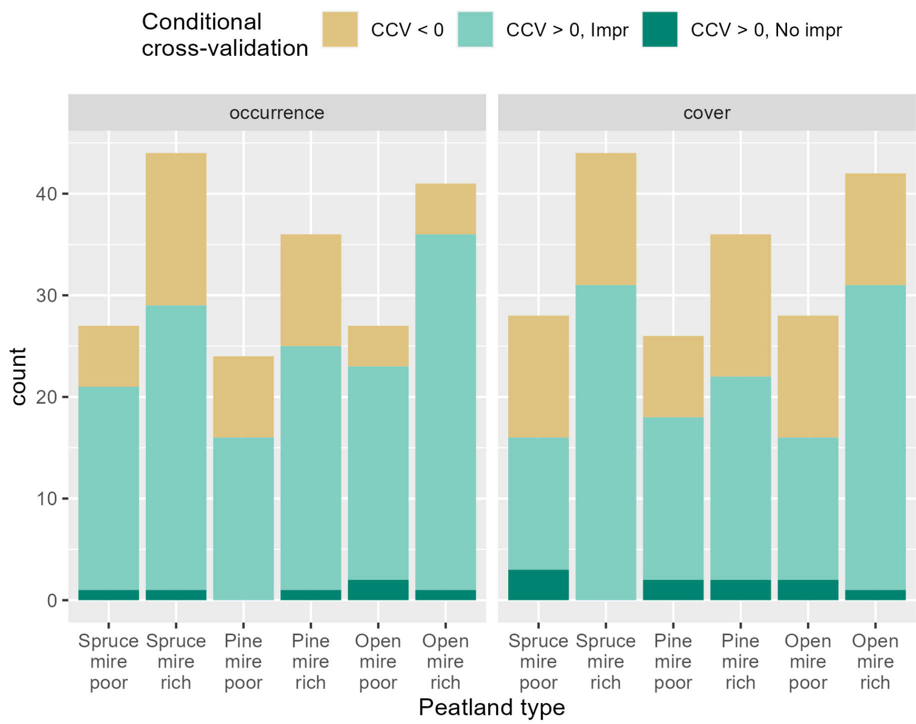

Figure 6. The number of species (*y*-axis), grouped according to whether their conditionally cross-validated predictive power (CCV) is lower or higher than 0, and whether in the latter case, CCV was larger than mere cross-validated predictive power, for at least one of the RS variables. The result is shown separately for predicting species occurrence and cover, given occurrence, and for different peatland types.

Remote Sensing of Single Species and Plant Functional Types

While RS variables moderately improved the predictive power of single species or PFT occurrence and cover, they were weakly linked to changes in species or PFT composition following restoration. This suggests that the changes in RS variables after restoration are related to general characteristics of land cover and plant communities rather than specific responses of individual species or PFTs.

We have examined the vegetation changes through Bayesian joint species distribution models, HMSC. Earlier, RS variables were used only a little in HMSC (e.g. Palmroos et al. 2023) while abundantly used in traditional species distribution models. While the interpretation of RS-species or RS-PFT associations in HMSC might be less intuitive than direct RS of species or PFTs, HMSC enables the analysis of residual correlations between RS variables and plants when the fixed effects (i.e. treatment, time, and their interactions) are accounted for. Therefore, HMSC should increase the possibilities for finding the linkages in cases of heterogeneous vegetation that is present in peatlands, but we have found only weak species-RS variable or PFT-RS variable linkages.

The problems of developing RS models for single species in peatland landscapes have been highlighted before (Pang et al. 2024). The difficulties are related to the spatially heterogeneous vegetation patterns, with different plant communities and species growing in various horizontal layers and co-occurring at similar spots. The problems are evident also due to the lack of studies developing reliable models for single species. The rare examples have mostly been very high-resolution studies for either very abundant species or relatively simple landscapes (Husson et al. 2014; Belcore et al. 2024; Simpson et al. 2024), or for species with unique spectral signatures (Kalacska et al. 2013).

Surprisingly, the RS variables had even fewer clear associations with PFTs than with species. This contradicts earlier studies that have indicated that PFTs are easier to detect with RS data than species (Pang et al. 2024). One of the reasons behind this surprising result might be the fact that there is no uniform response to restoration within a PFT, even though we further divided the PFTs based on species' habitat requirements. To be more precise, a single PFT can contain species that have positive, negative, and no responses to restoration. Therefore, the presence or cover of a specific PFT might not be an optimal indicator for monitoring peatland restoration success. One future research avenue could be to develop indicators of restoration-sensitive PFTs or functional traits that can be observed with RS data.

Furthermore, in future studies, change assessments of species or PFTs in restored peatlands could be conducted with repeated uncrewed aerial vehicle surveys targeting the most abundant species indicative of restoration. Alternatively, the focus could be on broader vegetation type or plant community changes in sites that have experienced clearly observable changes, such as a large increase of *Sphagnum* or sedge vegetation, or monitoring restoration in sites with clearer overall changes, such as peat extraction areas or agricultural

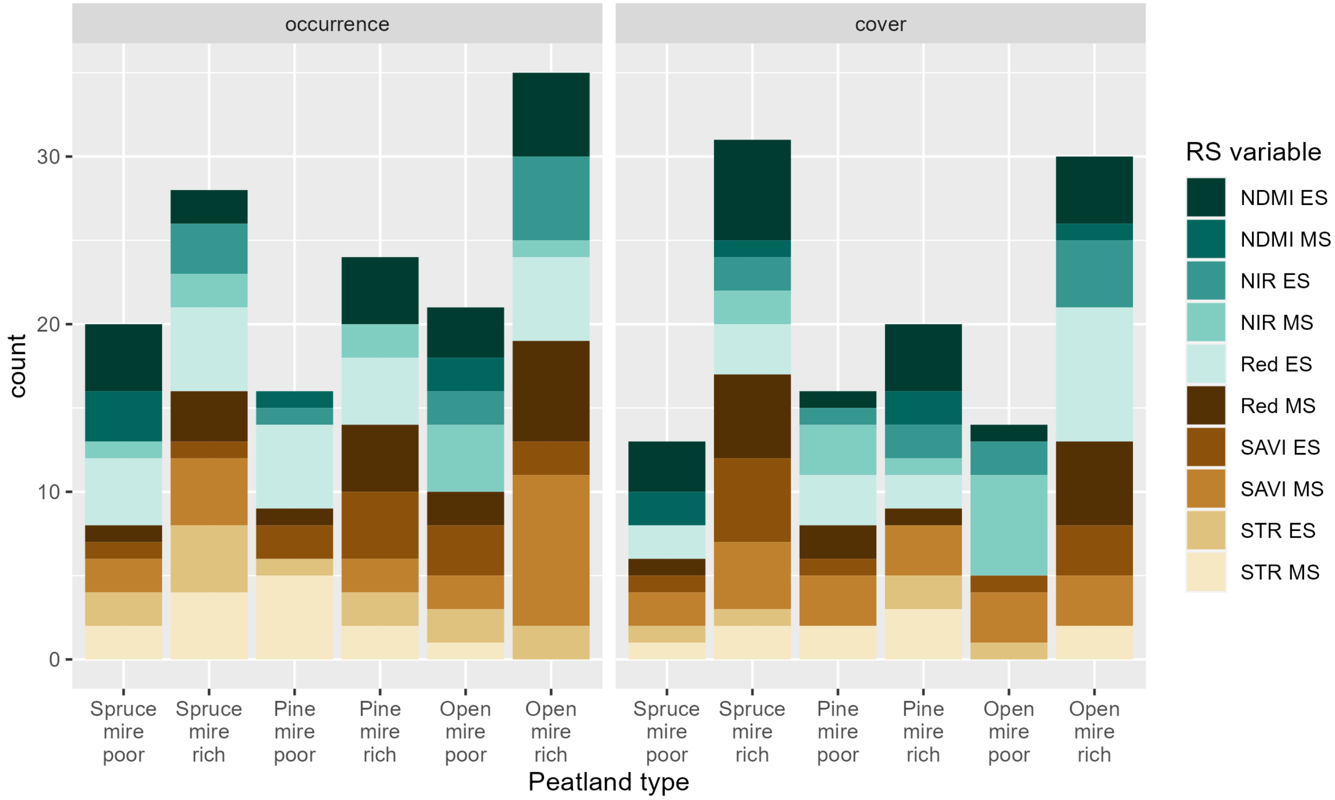

Figure 7. The number of species for which the RS variable (denoted by color) yields the highest conditionally cross-validated predictive power. Only the species with CCV greater than 0 and CCV greater than CV are shown. The result is shown separately for predicting species occurrence (presence/absence) and cover, given occurrence, and for different peatland types.

peatlands (e.g. Knoth et al. 2013). Our attempt was to generate generalizable models from a large sample of sites. It might be that evident changes in some sites cannot be seen in the data due to relatively large differences between and within peatland sites (e.g. Elo et al. 2016; Räsänen et al. 2020b, 2022), since the vegetation can drastically differ between peatland sites within one peatland type or even between vegetation plots at one site.

We had a spatial resolution mismatch: we linked satellite observations from a circa 700 m^2 circular area to 10 one-square meter vegetation plots within that area. While the vegetation plots constitute a reasonable sample within the circular area, they do not fully describe all vegetation within the area. On the one hand, it might be that there are also other land cover and vegetation changes within the area that are not captured in the sample. On the other hand, earlier studies have indicated that RS variables calculated from larger neighborhoods of vegetation sampling sites can provide better estimates than those from smaller neighborhoods (Palmroos et al. 2023). However, further studies should be conducted to test the impact of the scale of RS and field monitoring on model performance (c.f. Marignani et al. 2007).

Another possible reason for relatively weak results is the 10-year monitoring period, which is clearly not enough to allow full recovery of slowly recovering ecosystems, such as boreal peatlands (Elo et al. 2024). In 10 years, many species show responses to restoration, but in general, the changes in individual species abundance are rather small (Elo et al. 2024). Most notable exceptions are the rapid increase of several *Sphagnum* species and the decrease of some forest mosses such as *Pleurozium schreberi* and *Hylocomium splendens*, while the restoration responses within PFTs are heterogeneous. Altogether, to fully capture the species-specific responses to restoration, especially for the rare species with restricted dispersal, long-term monitoring is required. It might be that during the first 10 years, the changes in satellite imagery signatures are mostly driven by other land cover changes (wetness, tree canopy, and filling of ditches) rather than shifts in vegetation composition, while the situation might be reversed during longer monitoring periods. Long-term monitoring is required to test this assumption. Nevertheless, earlier research has shown that changes in spectral signatures in post-restoration peatlands during a 10-year monitoring period are connected to changes in floristic gradients. This suggests that ground vegetation change partially explains satellite-derived changes even within the first 10 years after restoration.

Even though the RS species relationships were mostly weak, there were some clearly observable changes. For instance, *Carex chordorrhiza* showed a negative association with NDMI in rich pine mire forests and open mires, as well as with red

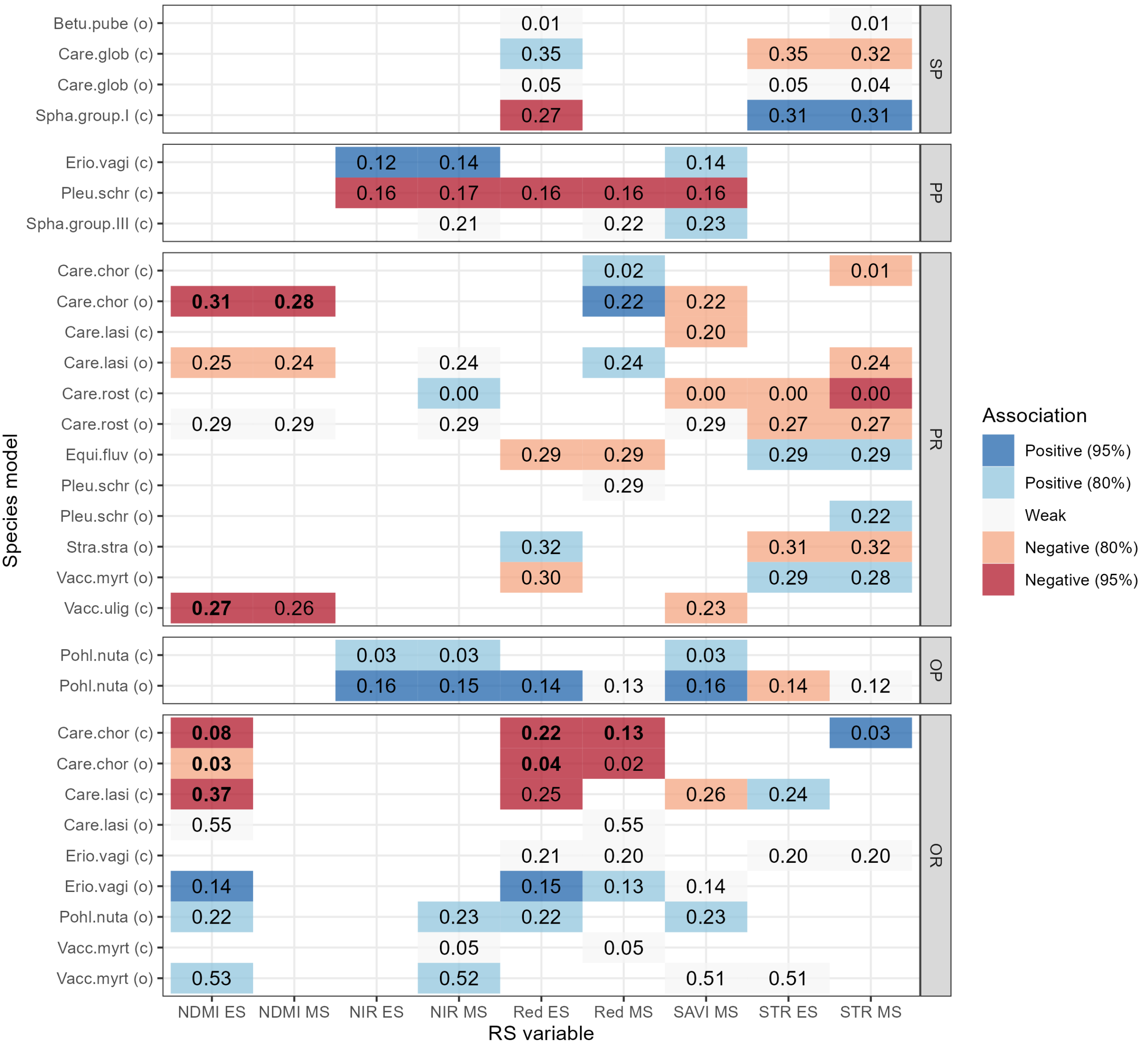

Figure 8. The combinations of the species and the remote sensing variables (ES, early summer; MS, midsummer; NDMI, normalized difference moisture index; SAVI, soil-adjusted vegetation index; STR, shortwave infrared transformed reflectance) that both responded to restoration in the given peatland type (OP, open mire poor; OR, open mire rich; PP, pine mire forest poor; PR, pine mire forest rich; SP, spruce mire forest poor) and for which including information on RS variable in conditional cross-validation yielded a better (and positive) predictive power in comparison to cross-validation only. The value shows the conditionally cross-validated predictive power (o = occurrence model, c = cover), and the values for which the improvement is larger than 0.05 are shown in bold. The color shows the sign of the association (negative, positive) and the level of statistical support ("Positive 95%"/"Negative 95%" if the posterior probability of the median being larger/smaller than zero is greater than 95%; "Positive 80%"/"Negative 80%" if the posterior probability of the median being larger/smaller than zero is greater than 80 but ≤95%; and "Weak" if the posterior probability of the median being larger/smaller than zero is ≤80%. Note that for spruce mire forest rich and SAVI ES, there was no response to restoration. Species' full names are given in Table S1.

reflectance in rich open mires. *Carex chordorrhiza* is a typical species for nutrient-rich wet flark areas, and it is positively associated with restoration in rich pine mire forests and open mires. Red reflectance has been found to be lower in wet flarks compared to drier peatland surfaces (Kolari et al. 2022), and it is positively associated with restoration in our data. Therefore, the negative red-*C. chordorrhiza* association might be related to the fact that red reflectance is not increased as much or even decreased after restoration in those sites that have wet flarks with abundant *C. chordorrhiza* cover. However, in sparsely treed pine mire forests, the *C. chordorrhiza*-red association was positive, but the predictive power was not largely improved by red reflectance, complicating the interpretation. NDMI, instead, had a negative relationship with restoration in these peatland types, pointing out that this relationship was less negative or even positive in the sites with *C. chordorhhiza*. Even though NDMI has had mixed evidence in tracking peatland wetness (Meingast et al. 2014; Räsänen et al. 2022; Isoaho et al. 2024), it can be useful for tracking changes in some species or environmental changes, suggesting that multiple RS variables should be tested in future studies.

Finally, our results indicate that increases in red and NIR reflectance can be used as RS-based indicators for monitoring peatland restoration success in open and sparsely treed peatlands. Their increases are attributed to increased openness of landscape (reflection of peatland surface instead of canopy and shadow), filling of ditches (more peat surfaces in the short term), increased wetness, and changes in ground layer vegetation (succession toward hydrophilic vegetation in the longer term). Future studies should test if the red-NIR reflectance changes can be used as universal indicators of restoration success and further test how the reflectance reacts to different types of post-restoration changes in land cover, wetness, and vegetation across climatic, topographic, and other environmental gradients. Furthermore, due to the weak linkages between RS variables and plant species, or PFTs, we cannot give definite suggestions for species- or PFT-specific restoration indicators trackable with RS. Therefore, more restoration monitoring studies of the associations between RS variables and plant species or vegetation traits are required to develop suitable indicators for tracking successful ecological restoration of boreal forestry-drained peatlands from space.

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Box and whiskers plots of elevation (m a.s.l.), mean temperature (°C), annual precipitation (mm), number of plant species, and plant species beta diversity gradients for different treatments and peatland types.
Figure S2. Convergence of beta and omega parameters for rich open mires, with thinning of 10,000.
Figure S3. Variance partitioning of explanatory variables for rich open mires, with thinning of 10,000.
Figure S4. Species and plant functional type median response to restoration, separately for each peatland type.
Figure S5. Analysis whether the remote sensing variables increased the conditionally cross-validated predictive power for different plant fuctional types.
Figure S6. The associations between the plant functional types and the remote sensing variables.
Table S1. Species abbreviations, full scientific names and plant functional types for each species.
Table S2. Conditionally cross-validated predictive power and the improvement in cross-validated predictive power when including the best performing remote sensing variable.

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