RESEARCH ARTICLE

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Functional diversity and trait composition of vascular plant and *Sphagnum* moss communities during peatland succession across land uplift regions

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Abstract

1. Most of the carbon accumulated into peatlands is derived from *Sphagnum* mosses. During peatland development, the relative share of vascular plants and *Sphagnum* mosses in the plant community changes, which impacts ecosystem functions. Little is known on the successional development of functional plant traits or functional diversity in peatlands, although this could be a key for understanding the mechanisms behind peatland resistance to climate change. Here we aim to assess how functionality of successive plant communities change along the autogenic peatland development and the associated environmental gradients, namely peat thickness and pH, and to determine whether trait trade-offs during peatland succession are analogous between vascular plant and moss communities.

2. We collected plant community and trait data on successional peatland gradients from post-glacial rebound areas in coastal Finland, Sweden and Russia, altogether from 47 peatlands. This allowed us to analyse the changes in community-weighted mean trait values and functional diversity (diversity of traits) during peatland development.

3. Our results show comparative trait trade-offs from acquisitive species to conservative species in both vascular plant and *Sphagnum* moss communities during peatland development. However, mosses had higher resistance to environmental change than vascular plant communities. This was seen in the larger proportion of intraspecific trait variation than species turnover in moss traits, while the proportions were opposite for vascular plants. Similarly, the functional diversity of *Sphagnum* communities increased during the peatland development, while the opposite occurred for vascular plants. Most of the measured traits showed a phylogenetic signal. More so, the species common to old successional stages, namely

Ericacae and Sphagna from subgroup Acutifolia were detected as most similar to their phylogenetic neighbours.

4. *Synthesis*. During peatland development, vegetation succession leads to the dominance of conservative plant species accustomed to high stress. At the same time, the autogenic succession and ecological engineering of Sphagna leads to higher functional diversity and intraspecific variability, which together indicate higher resistance towards environmental perturbations.

KEYWORDS

functional diversity, functional traits, intraspecific variability, peatland development, phylogenetic signal, plant economic spectrum, *Sphagnum*

1 | INTRODUCTION

In peatlands, accumulation of organic matter drives autogenic succession towards drier, more acidic and less fertile conditions as increasing peat thickness reduces the flow of mineral-rich waters to the peatland surface (Gignac & Vitt, 1990). Succession typically proceeds from fens dependent on catchment hydrology towards drier, nutrient-poor bogs (e.g. Bauer et al., 2003; Hughes & Barber, 2003; Kuhry & Turunen, 2006). The change in the vegetation and environmental conditions during the peatland succession modifies ecosystem functions, and the rate and vulnerability of the carbon (C) accumulation (e.g. Tuittila et al., 2013). Younger stages have been found to respond more readily to changing weather conditions while the annual variation in CH_4 and CO_2 dynamics is smaller in the older stages (Leppälä, Laine, et al., 2011; Leppälä, Oksanen, et al., 2011). Recent research from boreal peatlands implies that vegetation composition of the earlier successional stages that are dominated by vascular plants is more sensitive to environmental change, such as lower water availably, than later, *Sphagnum* moss-dominated stages (Kokkonen et al., 2019). However, the mechanism behind the resistance of later stages is so far unknown.

Trait-based ecology, with focus on quantitative plant properties, offers tools for mechanistic understanding on how vegetation responds to the changes in environmental conditions, and how vegetation change impacts ecosystem functions (Cornelissen & Makoto, 2014; Moor et al., 2017; Suding et al., 2008). Generally, decreasing resources are associated with environmental filtering of plant properties (i.e. functional traits) towards a combination that enhances resource-conservative growth strategy over resource-exploitative strategy (Reich, 2014). Over such gradients, properties that allow quick returns on resource investments, that is, high resource acquisition rates and high growth rates, such as high SLA and photosynthesis, are replaced with properties related to slow growth such as high leaf dry matter content (Eskelinen & Harrison, 2015). Although the combinations of nutrient and moisture conditions in peatlands complicate the bases of simple resource gradient (Moor et al., 2017), a pressure towards resource-conservative growth strategy over the peatland hydrosere succession from the relatively high resource habitats, such as rich fens, to the extremely resource-poor habitats, such as oligotrophic fens and bogs, can be expected.

During peatland succession, plant community dominance is known to shift from sedges and forbs to *Sphagnum* mosses and sedges to finally *Sphagnum* mosses and shrubs. While plant traits are yet little studied in peatlands, there is a strong evidence that the functional plant groups differ in their productivity, photosynthetic capacity (e.g. Hájek et al., 2011; Laine et al., 2016; Goud et al., 2017), decomposability (Bengtsson et al., 2018; Dorrepaal et al., 2005; Lang et al., 2009; Straková et al., 2012) and impact on methane emissions (Bubier et al., 1995; Gray et al., 2013). Therefore, successional changes in the functional group dominance are likely to impact the community trait composition and lead in the trait trade-offs from the high resource acquisition rates and rapid growth (typical to forbs and grasses) towards greater resource conservation (typical to evergreen shrubs), as has been found for vascular plant communities in different types of ecosystems (Chapin III et al., 1993; Diaz et al., 2004; Reich, 2014). While in peatlands the trait trade-offs have not been tested over large environmental gradients, the few existing studies imply that in bogs an artificial N enrichment has an ability to increase community-weighted leaf size, SLA and plant height, that is, cause a shift towards the more resource acquisitive trait composition (Lin et al., 2020), although a study by Bubier et al. (2011) found weak species-specific responses.

The *Sphagnum* moss traits are yet little studied, but there are findings indicating the trait trade-offs from acquisitive to conservative strategy also within Sphagna: Laine et al. (2011) found lower rates of photosynthesis and growth from species present at the bogs than from the younger peatlands, and Mazziotta et al. (2019) found a fast–slow economic spectrum among *Sphagnum* mosses growing along water level and shading gradients. Altogether, the successional changes in traits related to productivity and decomposability could be a way forward in understanding the differences in the rates of C accumulation between peatland types (e.g. Tuittila et al., 2013).

In addition to the direction of change in the plant properties, the trait-based approach can be used to evaluate the resistance of a plant community to an environmental change, that is, the ability of its functions to remain essentially unchanged despite species

turnover in response to the environmental change (see e.g. Robroek et al., 2017). One tool is to observe the relative contributions of species turnover (interspecific traits variability) versus intraspecific trait variation. A larger relative contribution of intraspecific variation implies greater community resistance as species are able to adapt to changing conditions by modifying their traits according to the new environmental requirements (Albert et al., 2011; Lepš et al., 2011; Violle et al., 2012). In addition, functional diversity can be used in evaluating resistance, as greater trait dispersion within a community implies higher resistance (Dıaz & Cabido, 2001). Consequently, the recently observed lower community resistance in the fens than in the bogs (Kokkonen et al., 2019) gives us a reason to expect increased intraspecific variation in traits and/or increased functional diversity during peatland succession.

Primary paludification and the following peatland development occur in the areas of ongoing post-glacial rebound, namely along the coast of Bothnian Bay in Finland and Sweden, the Hudson Bay lowlands in Canada and along the White Sea in Russia, regions where the ice sheet was thickest during the last glaciation. The phenomenon creates chronosequences that can be used in addressing both the compositional and the functional change over long-term succession (e.g. Tuittila et al., 2013), which is not possible with experimental or palaeoecological approach.

We take advantage on the successional gradients found in the rebound areas in Finland, Sweden and Russia to (a) quantify if succession leads in a trait trade-off from acquisitive to conservative strategy that relates to low decomposition rates, a prerequisite of C accumulation in peatlands, at both vascular plant and moss communities; (b) evaluate how the resistance of successive vascular plant and moss communities develop based on the relative contributions of species turnover, intraspecific trait variation and functional diversity; and (c) quantify if succession leads in the phylogenetic conservatism strategy at both vascular plant and *Sphagnum* traits. We hypothesize that (a) traits indicating acquisitive strategy (i.e. high values of SLA, leaf N content and *Sphagnum* moss capitulum size) and competition over light rather than nutrients (high values of plant height) are replaced by traits of conservative strategy (low values of SLA, high C:N ratio and *Sphagnum* moss capitulum size) and of increased competition over nutrient rather than light (low values of height) as succession proceeds; (b) based on the observed increasing resistance of ecosystem functions during peatland succession, the resistance in vascular plant and moss communities increase during succession; and (c) decreasing resources during succession leads to phylogenetic conservatism strategy at both vascular plant and *Sphagnum* traits.

2 | MATERIALS AND METHODS

2.1 | Study areas

We sampled four study areas located in the regions with ongoing post-glacial rebound: Sävar on the west coast of Bothnian Bay (63°50′N, 20°40′E, Sweden), Siikajoki (64°45′N, 24°43′, Finland) and Hailuoto island (65°07′N, 24°71′E, Finland) on the east coast of Bothnian Bay, and Belomorsk-Virma (63°90′N, 36°50′E, Russia) on the coast of the White Sea (Figure 1). Within each area, we selected peatlands with differing elevation and consequently different age and developmental stage. The peatlands are assumed to have initiated via primary paludification immediately after the uplift exposed new coastal land, except in Sävar where most of the sites emanate from lake ingrowth. The number of sampled sites varied from 17 in Siikajoki to 7 in Hailuoto, with 47 sites in total. The climatic conditions were quite uniform across the study areas, with mean annual temperature ranging from 2.8 to 4.6°C, mean annual precipitation from 542 to 579 mm, coldest month temperatures ranging from −8.2 to −9.6°C and warmest month from 15.5 to 16.2°C.

2.2 | Plant community and environmental measures

At each site, we determined the plant community composition by visually estimating the projection cover of each species separately for field (vascular plants) and moss layer using the scale 0.1%, 0.25%, 0.5%, 1%, 2%, 3%, etc (e.g. Sottocornola et al., 2009). There were fifteen 50×50 cm plots in each peatland at Siikajoki and Belomorsk-Virma, and 10 at Sävar and Hailuoto. The sample plots were located 5 m apart along a transect starting from the generally treeless peatland margin and heading towards the peatland centre. For smaller peatlands, we had several transects crossing the site. Siikajoki sites were sampled in August 2016, Sävar sites at the end of June 2017, Hailuoto sites during July 2017 and Belomorsk sites at the end of August 2017.

Peat thickness was measured with a Russian corer except in Hailuoto where an iron rod with a rounded head was used. pH was measured from peat water samples with a YSI Professional Plus (Pro Plus; YSI Incorporated). A small hole was dug to peat and water was allowed to collect at the hole and stabilize for at least half an hour before pH measurement. Site location and elevation were recorded with a GPSMAP 64s (Garmin Ltd.; precision ± 3.65 m). To estimate the average moisture conditions in the sites, we calculated a moisture index for each site as a weighted average based on the species Ellenberg moisture index values and average species cover. Ellenberg moisture indices were attained from the studies of Hill et al. (1999, 2007) and Ellenberg et al. (1991). In our dataset, the species-vice index ranged from 5 (*Vaccinium vitis-idaea*, *Pleurozium shreberii*) to 12 (*Utricularia intermedia*), that is, from a moist-site indicator, mainly on fresh soils of average dampness (5) to a submerged plant, permanently or almost constantly under water (12).

2.3 | Functional trait measurements

Functional traits were measured during the plant community measurement campaigns. At each site, we selected the most common (on average 80% coverage) vascular and moss species for trait
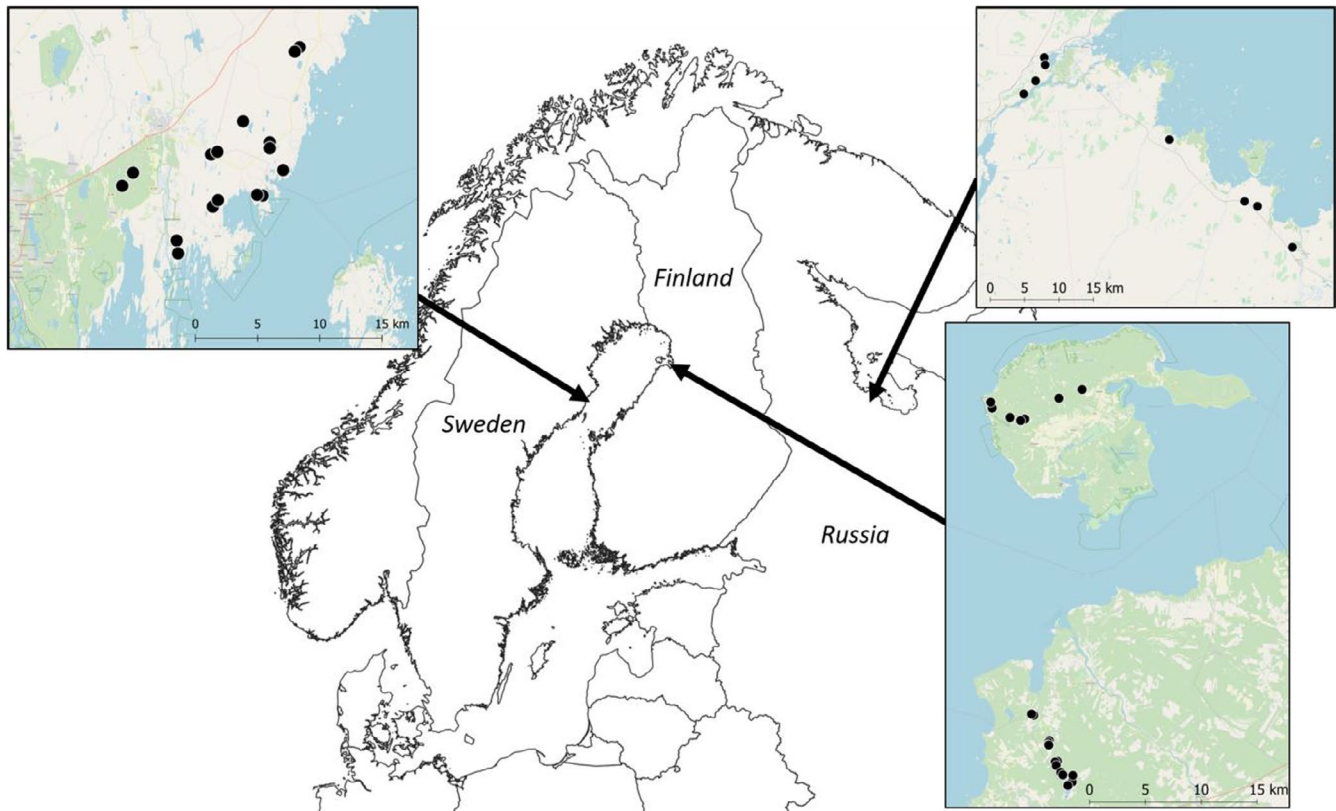
FIGURE 1 Location of the studied peatlands along the three land uplift regions: on the west coast of Bothnian Bay (Sävar, Sweden), east coast of Bothnian Bay (Siikajoki and Hailuoto Island, Finland) and on the coast of the White Sea (Belomorsk-Virma, Russia)

measurements (Tables S1.1). Plant height was measured from 10 individuals per vascular species per site, while other traits were measured from half of these plants, and three replicates per species per site were used for mosses.

We measured the following vascular plant traits: plant height, leaf size (LS), SLA and leaf carbon (C) and nitrogen (N) contents. These traits were selected as they are known to correlate with ecosystem functions, that is, productivity and decomposability, and with plant strategies. Increase in plant height has been linked to switch from nutrient competition to competition from light, while the selected leaf traits are associated with leaf economy. The measurements were made according to the study by Pérez-Harguindeguy et al. (2016), and we sampled only fully grown plants and fresh and undamaged leaves. Plant height (cm) was measured as the shortest distance between the upper boundary of the main photosynthetic tissues (excluding inflorescences) and the ground level. To measure SLA (i.e. the one-sided area of a fresh leaf divided by its oven-dry mass, cm^2/g), the freshly picked leaf or a sample of three leaves in case of shrubs with small leaves was pressed flat between a board and a glass, and a standardized photograph was taken. The LS (cm^2) was analysed from the photographs with ImageJ software (Schindelin et al., 2015; Schneider et al., 2012). The leaf samples were stored in paper bags and dried at 60°C for a minimum of 48 hr. The dried samples were weighed, and SLA was calculated. The SLA samples were used for C and N content analysis. Leaves from each species from each site were pooled into one sample, which was milled (Retsch MM301

mill) and analysed for C and N concentrations and for C:N ratio on a CHNS/O Elemental analyzer (EA1110; University of Oulu).

Sphagnum moss samples were collected with a corer (7 cm diameter, area 38 cm^2, height at least 8 cm) to maintain the natural density of the stand. The collection was targeted to single species stands. Samples were stored in plastic bags in a cool room or frozen until measured. Unlike for the vascular plants, there are no established set of traits for *Sphagnum* mosses. Therefore, we selected such properties that our recent study linked to the capacity to remain moist and, consequently, to photosynthesize (Gong et al., 2020). We defined the following *Sphagnum* traits: stand density (number of shoots cm^{-2}), capitulum width (cap_width, mm) and dry weight (cap_dw, mg), fascicle density (number cm^{-1}), capitulum dry matter content (CDMC, mg/g), capitulum water content (cap_wc, g/g) and capitulum C and N contents and C:N ratio. Stand density was measured as the number of mosses in the sample. From 10 individuals we measured the width of the capitula and counted the number of fascicles from a 5-cm segment below capitulum. We separated the 10 moss individuals into capitulum and stem (5 cm below capitula), wetted them and allowed to dry on top of tissue paper for 2 min before weighing them for water-filled fresh weight. Samples were placed on paper bags and dried at 60°C for at least 48 hr after which the dry mass of capitula and stems were measured. CDMC and cap_wc were calculated from the fresh and dry weight. We used the capitulum samples for analyses of C and N concentrations and for C:N ratio, and treated them similar to vascular plant samples.

2.4 | Data analysis

2.4.1 | Plant community data

To visualize the variation in peatland vegetation along the successional gradients in the four areas we applied non-metric multidimensional scaling (NMDS) ordination via the metaMDS function in the R package VEGAN (Oksanen et al., 2015). Our ordination was based on the Bray–Curtis dissimilarity matrix of the vegetation datasets with 47 sites. Significance of the effect of peat thickness, pH and moisture index on vegetation composition was tested with a permutational multivariate analysis of variance (PERMANOVA, adonis in vegan) on the same dissimilarity matrix (999 permutations). Envfit function (also from the VEGAN package) was used to visualize the correlation of peat thickness, pH and moisture index with NMDS ordination. To evaluate how the studied sites fitted within previous interpretation on primary peatland succession from the intensively studied Siikajoki area (e.g. Laine et al., 2011; Leppälä et al., 2008; Tuittila et al., 2013), we used a combination of CLUSTER analysis with Bray–Curtis similarities matrix and group average algorithm, and 'Similarity profile' (SIMPROF) tests, using the CLUSTSIG package (Whitaker et al., 2014) in the R environment (R Development Core Team, 2011). The most common species and average environmental conditions of each cluster are given in Tables S1.2. and S1.3. respectively. Finally, Generalized Additive Models (GAM) were used to evaluate the dependency of moss and vascular plant cover on the peat thickness, pH and moisture gradient. Vascular plants were reduced to three groups, namely shrubs, sedges and grasses plus forbs, and mosses to two groups, *Sphagnum* mosses and 'others'. The analyses were performed with Canoco 5.11.

In all analyses we considered each site as a unit by averaging the sample plot data. Rare species that were present in less than three (of 47) sites were removed from the analysis.

2.4.2 | Functional trait data

Vascular plant and *Sphagnum* moss data were analysed separately as mostly different traits were used for each community. Community-weighted mean (CWM) trait values were calculated for each site using two differing trait datasets. The first set, called 'site-specific', included site-specific average trait values for those common species, generally covering ~80% of the vegetation, that were measured from the particular site. For the remaining rare species, present at the plant community but not measured from the site, we used an average trait value calculated from the full dataset covering all sites. In the second dataset called 'fixed', the average trait values calculated from the full data were used for all species. Community-weighted mean traits were calculated using the FD package (Laliberté et al., 2014) in the R environment (R Development Core Team, 2011). We used principal component analysis (PCA) to examine the covariation between site-specific CWM traits with centred and standardized trait values. To examine how main variation in traits relate to environmental variation, peat thickness and pH were included as

supplementary variables with the envfit function. The analyses were performed using package VEGAN in R. We complemented the analyses with Horn's Test of Principal Components with Package PARAN in R environment. To relate individual traits with peat thickness and pH, we used linear mixed effect models with study area as a random factor with the NLME package in the R environment.

To assess vegetation resistance to environmental gradients, peat thickness and pH, associated with peatland succession, we evaluated the relative contributions of species turnover and intraspecific trait variation along the gradients for both vascular plant and *Sphagnum* moss communities using a method presented by Lepš et al. (2011). In this method, between-site differences in CWM trait values based on fixed trait values can only be caused by differences in species composition (i.e. species turnover). The between-site differences in CWM trait values based on site-specific trait values can be caused either by differences in species composition or/and intraspecific trait variation, while the difference between site-specific and fixed averages can be caused solely by intraspecific trait variation. For this we ran three generalized linear model regressions for each trait, using either 'site-specific', 'fixed' or 'intraspecific' CWM site averages with peat thickness or pH as an explanatory variable. The 'intraspecific' being the difference between 'site-specific' and 'fixed' estimates. From each model, the sum of squares (SS specific, SS fixed and SS intraspecific respectively) was extracted and finally, the SS cov component, which is the effect of covariation between inter- and intraspecific trait variability, was calculated by subtracting SS fixed and SS intraspecific from SS specific. Models were run in the R environment.

To complement the analysis of the vegetation resistance to environmental gradients, we evaluated the dependence of functional diversity on pH and peat thickness gradients with PCA including peat thickness and pH as supplementary variables with the envfit function. We complemented the analyses with Horn's Test of Principal Components with Package PARAN in R environment. We used Rao's quadratic entropy from FD package in R (Botta-Dukát, 2005) as a measure of functional diversity and calculated it for both vascular plant and *Sphagnum* moss communities using (a) all measured traits and (b) each trait separately.

2.4.3 | Testing for phylogenetic signal in vascular and *sphagnum* traits

We reconstructed the phylogenetic tree of vascular plants using the V.PHYLOMAKER package in R (Jin & Qian, 2019) that generates phylogenies for vascular plants based on two recent large phylogenetic trees (Smith & Brown, 2018; Zanne et al., 2014). The resulting mega-tree includes 10,587 genera and 74,533 species of vascular plants. When the species are missing from the mega-tree, V.Phylomaker uses species that are sister to or closely related with some species or genera in the mega-tree to accurately attached species to their relatives in the phylogenetic tree. As bryophytes are missing from V.Phylomaker, we used gene sequence from the ribosomal non-coding protein *trnL* intron and *trnL-F* intergenic spacers to build *Sphagnum* phylogeny (Piatkowski & Shaw, 2019). We selected these loci as they were the

FIGURE 2 Ordination based on non-metric multidimensional scaling (NMDS) with plant species composition of the 47 mires and peat thickness and pH as supplementary environmental variables. Ordination has two dimensions and the Stress value is 0.16. Non-metric fit, R2 0.976, linear fit, R2 0.893. (a) Ordination of species with the largest contribution to the analysis, and (b) peatland sites clustered, based on their vegetation, into 10 groups (different symbols) with SIMPROF. The most common vascular and moss species per group are given in Tables S1.2. Five of the sites from Siikajoki chronosequence, which were previously divided into different successional stages, namely wet meadows, mesotrophic fens, oligotrophic fens, fen/bog transition and bog (Laine et al., 2011), are marked with arrows
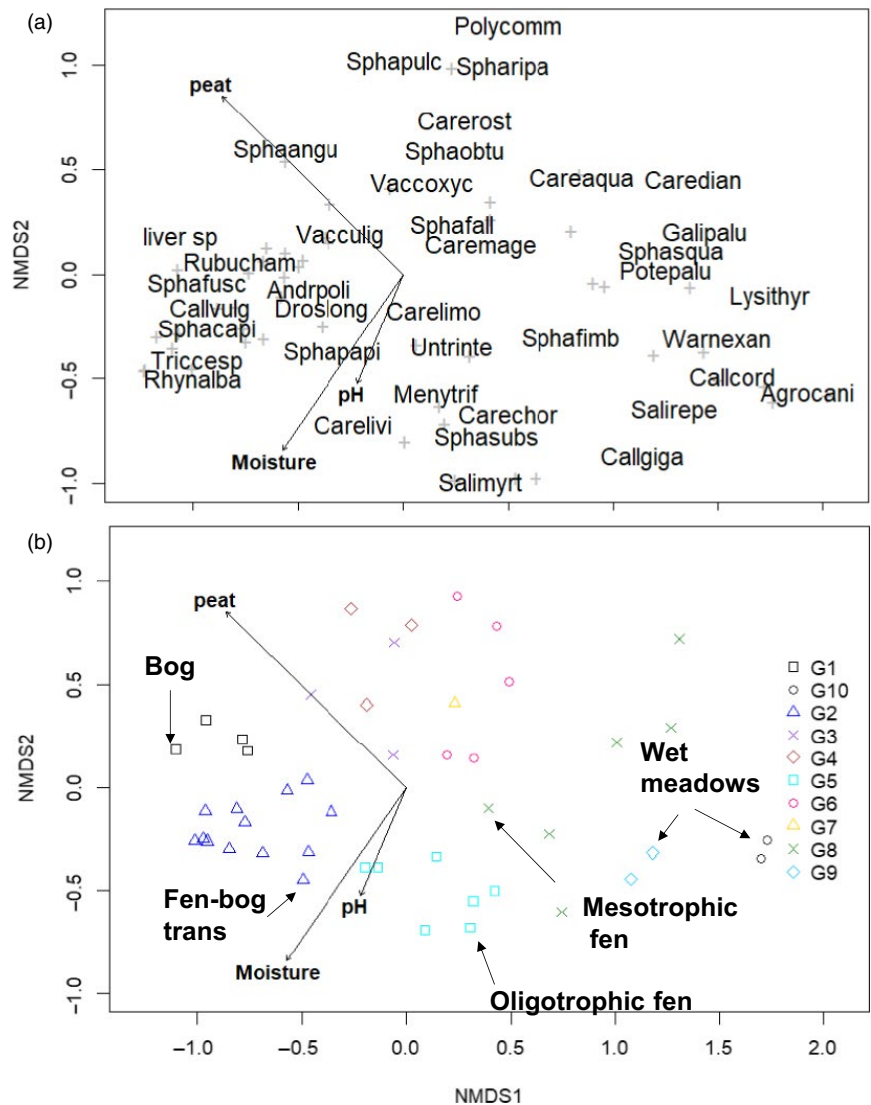
only available sequences for all *Sphagnum* species in our species list in the GeneBank database. Each locus was aligned using MAFFT for multiple alignments (Katoh & Standley, 2013). Then, phylogenetic inference was performed using NGphylogeny.fr (Lemoine et al., 2019). The resulting *Sphagnum* phylogenetic tree was supported by the high-resolution tree recently built for *Sphagnum* mosses and based on 16 loci (Piatkowski & Shaw, 2019).

We assessed the phylogenetic signal within vascular and *Sphagnum* traits under the Brownian Motion model (BM). BM predicts that the variance in trait increases at a constant rate proportionate to evolutionary distance, with more closely related species having more similar values, indicating that the trait has a phylogenetic signal (Felsenstein, 1985). We used three indices to evaluate the phylogenetic signal within plant traits: Abouheif's C_{mean}, Pagel's λ and Blomberg's K (Münkemüller et al., 2012). These indices build on the concept of autocorrelation. Each index has been tested for the null hypothesis of absence of the phylogenetic signal, that is, trait values are randomly distributed in the phylogenetic tree. This is achieved by randomization for K and C_{mean} (1,000 permutations), and by likelihood ratio test for λ. While these indices give precious information

about the general presence of a phylogenetic signal within a phylogenetic tree, these approaches assume that traits evolve similarly across the phylogeny. However, the phylogenetic signal likely varies across clades, and additional local statistics are needed to highlight local trait patterns within the phylogenetic tree. To do so, we used the Local Indicators of Phylogenetic Association (LIPA) index that allow to detect hotspot of autocorrelation within the phylogenetic trees between species and their neighbours. The PHYLOSIGNAL R package was used to run these analyses (Keck et al., 2016).

3 | RESULTS

3.1 | Vegetation composition

The transects covered the successional trend from mesotrophic fen mosses and herbs (e.g. *Warnstorfia exannulata*, *Sphagnum squarrosum*, *Potentilla palustris*) to mosses and shrubs typical for ombrotrophic bogs (e.g. *Sphagnum fuscum*, *Calluna vulgaris*) seen in the variation in the species composition along the first NMDS ordination
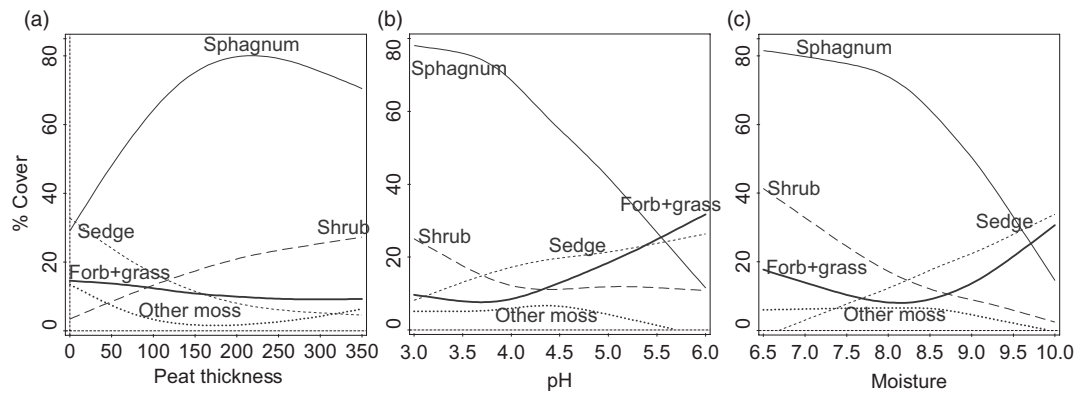
FIGURE 3 Fitted Generalized Additive Models (using a Gaussian distribution with smoothness term of 2.0 *df*) for different plant functional types with (a) peat thickness (*Sphagnum*, sedge, shrub and other moss models had r^2 of 0.37, 0.48, 0.46 and 0.31, respectively, and $p < 0.0005$; grass + forb model was insignificant), (b) pH (*Sphagnum*, shrub and grass + forb models had r^2 of 0.29, 0.24 and 0.26, respectively, and $p < 0.005$; sedge and other moss models were insignificant) and (c) moisture index (*Sphagnum*, sedge, shrub and grass + forb models had r^2 of 0–28, 0.30, 0.56 and 0.26, respectively, and $p < 0.005$; other moss model was insignificant). Functional type-wise plots including the measured data points are shown in Figure S1.1

axis (Figure 2a). SIMPROF clustering of the sites into 10 groups based on their vegetation that ranged from wet meadows to ombrotrophic bogs, largely followed the site ordering along the NMDS axis 1 (Figure 2b). Permutational multivariate analysis of variance (PERMANOVA) test showed that the variation in vegetation composition was significantly related to peat thickness, pH and moisture index gradients ($p < 0.005$). The species with the highest moisture index values are a combination of those most common for young periodically flooded fens (*Carex aquatilis*, *Equisetum fluviatile*, *Lysimachia thyrsiflora*, *P. palustris*, *Calliergon cordifolia*, *Carex rostrata*) and those most common in the pools of older relatively nutrient-poor peatlands (*Carex limosa*, *Scheuchzeria palustris*, *Sphagnum majus*, *Warnstorfia fluitans* and *Utricularia intermedia*), which leads to an intermediate position of the moisture in the NMDS ordination (Figure 2).

Based on their estimated cover, *Sphagnum* mosses became the most important component of vegetation when peat thickness was more than 50 cm (Figure 3a), and pH lower than 4.5 (Figure 3b). In here we estimated peatland moisture conditions based on the Ellenberg's indicator values and therefore the response of different plant groups to moisture is a sum of species expected affinity towards moisture. All peatland species have high (>6) moisture index, but shrubs and many *Sphagnum* mosses are accustomed to drier conditions than sedges and grasses (Figure 3c).

3.2 | Trade-offs in community-weighted mean functional plant traits

As expected, the CWM of vascular plant trait composition formed a successional gradient from the young fen communities to the old oligotrophic fens and bogs, with decrease in the plant height, SLA, LS and leaf N content and increase in the leaf C content and C:N along the PC axis 1. Along this trait composition, gradient peat thickness increased and pH decreased (Figures 4a and 5). Average trait values per vascular plant species are given in Table S1.4.
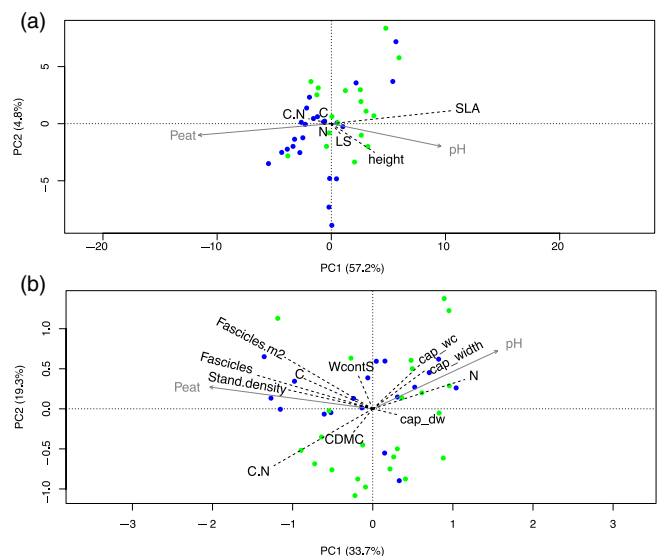

FIGURE 4 Ordination of site-specific community-weighted mean (CWM) plant traits based on principal component analysis (PCA), with peat thickness and pH as supplementary variables (grey arrows); (a) vascular plant traits; Eigenvalues of Axis 1 and Axis 2 were 3.724 and 1.103 respectively. Supplementary variables peat thickness and pH were significant ($p = 0.001$; b) *Sphagnum* moss traits; Eigenvalues of Axis 1 and Axis 2 were 4.423 and 2.904 respectively. Supplementary variables peat thickness and pH were significant ($p < 0.004$). Sites with a high proportion of species with a phylogenetic signal are shown by blue points, while green points are sites with a low proportion of species with a phylogenetic signal

Similar to vascular plant traits, CWM traits of *Sphagnum* mosses formed a successional gradient. Along this gradient capitulum width, N content and water content decreased and capitulum C content, capitulum C:N, moss stand density and the amount of fascicles per stem and per stand increased from the youngest to the oldest peatlands. Along this gradient, peat thickness increased and pH
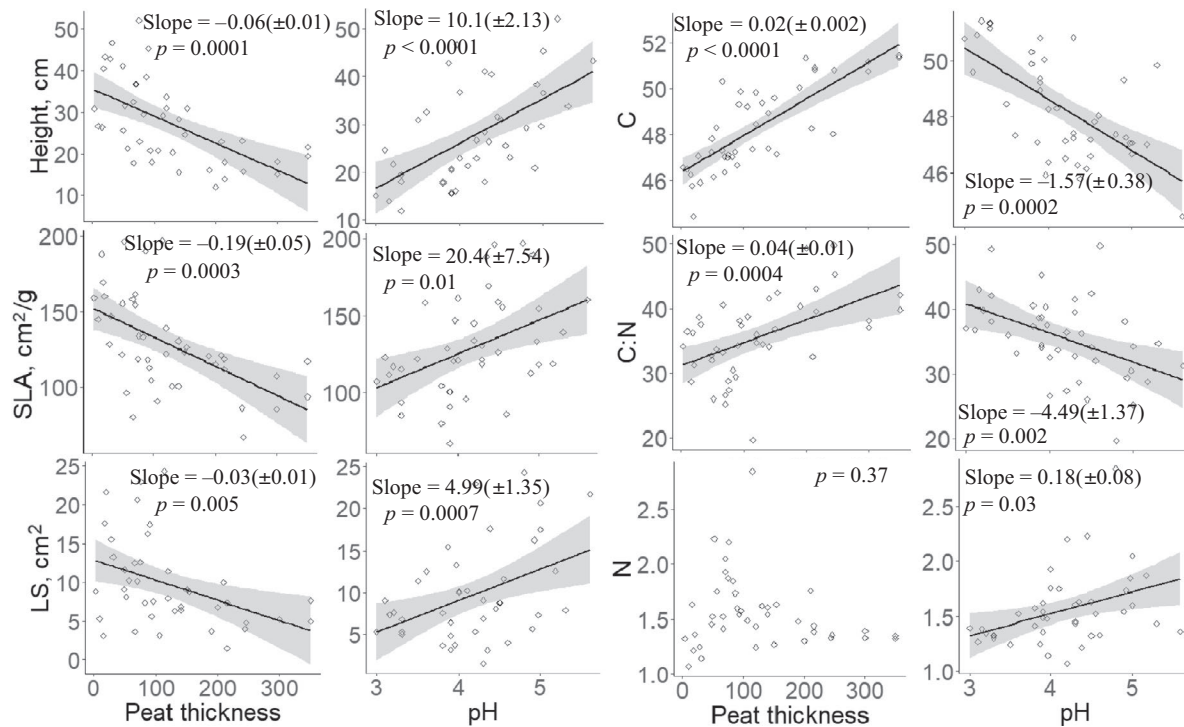
FIGURE 5 Relationship between community-weighted mean traits of vascular plants and peat thickness or pH; slope and *p*-value denote for linear mixed effect model results

decreased (Figures 4b and 6). Average traits values per *Sphagnum* species are given in Table S1.5.

3.3 │ Resistance of successive plant communities

The importance of species turnover versus intraspecific CWM traits variability along the peat thickness and pH gradients differed between vascular plant and *Sphagnum* communities (Table 1). For vascular plants, the changes in CWM traits were due to species turn-over (with exception of plant height along pH gradient), while for Sphagna also the intraspecific variability was significant for most traits. As an example, for fascicle density and C content the intraspecific variability was equally strong as variance caused by species turnover. For Sphagna, the covariation was always positive, indicating that sites dominated by species with larger value of a trait were also dominated by individuals of these species having larger than average value of the trait.

The response of functional diversity, expressed as Rao's quadratic entropy (RaoQ), to peat thickness and pH gradients was contrasting for vascular plant and moss communities (Figure 7a,b). For vascular plant communities, RaoQ increased along with pH (Figure 7a), that is, towards the early succession sites, while for the *Sphagnum* moss communities, RaoQ increased along with peat thickness, that is, towards the older stages (Figure 7b). The pattern was similar for RaoQ calculated based on all traits (FD(Rao)) and based on the individual traits. The only exceptions were RaoQ for C:N and C of vascular plant communities, which increased along the peat thickness gradient.
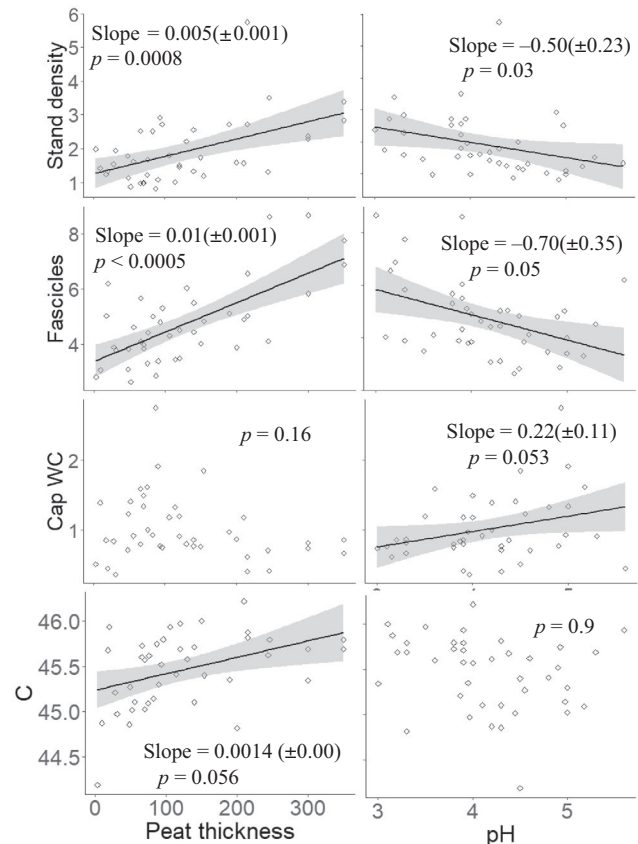

FIGURE 6 Relationship between community-weighted mean traits of *Sphagnum* mosses and peat thickness or pH; slope and *p*-value denote for linear mixed effect model results

TABLE 1 Percentage of variance of each CWM trait that is due to species turn-over, intraspecific trait variability and the covariation between the two along peat thickness and pH gradients. A positive covariation means that sites dominated by species with larger values of a trait are also dominated by individuals of these species having larger than average values of the trait. A negative covariation means that plots dominated by species with larger values of a trait are dominated by individuals of these species having smaller than average values of the trait. The different levels of statistical significance are expressed as $p < 0.05′$, $p < 0.01^*$, $p < 0.001^{**}$, $p < 0.0001^{***}$

| Vascular traits	Species turn-over; Peat thickness/pH	Intraspecific; Peat thickness/pH	Covariation; Peat thickness/pH
Height	28.1***/21.7***	0.4/1.6′	6.8/11.7
SLA	33.0***/20.7***	0.01/0.000	−1.5/−0.01
LS	21.5**/24.4***	0.017/0.005	−3.8/−0.07
C:N	39.6***/25.8**	1.1/0.002	−12.9/−4.6
C	56.6***/33.8***	0.2/0.003	6.3/6.8
N	10.1**/13.7**	2.1/0.000	−9.2/0.01
Sphagnum traits	**Changes in community composition; Peat thickness/pH**	**Intraspecific trait variation; Peat thickness/pH**	**Covariation; Peat thickness/pH**
Capitulum width	3.8/8.7′	0.7′/0.000	3.3/1.05
Stand density	20.4**/10.6′	0.3/0.000	4.8/0.27
Fascicles indiv	11.8**/4.5′	11.1**/4.8′	22.8/9.3
Fascicles m²	23.4***/9.66′	3.1**/0.94	17.0/6.04
C:N	8.7*/8.46*	4.2′/6.33*	12.1/14.65
C	4.4/0.68	4.0′/28.36′	8.4/8.78
N	9.0*/5.13′	3.3′/5.31*	10.9/10.43
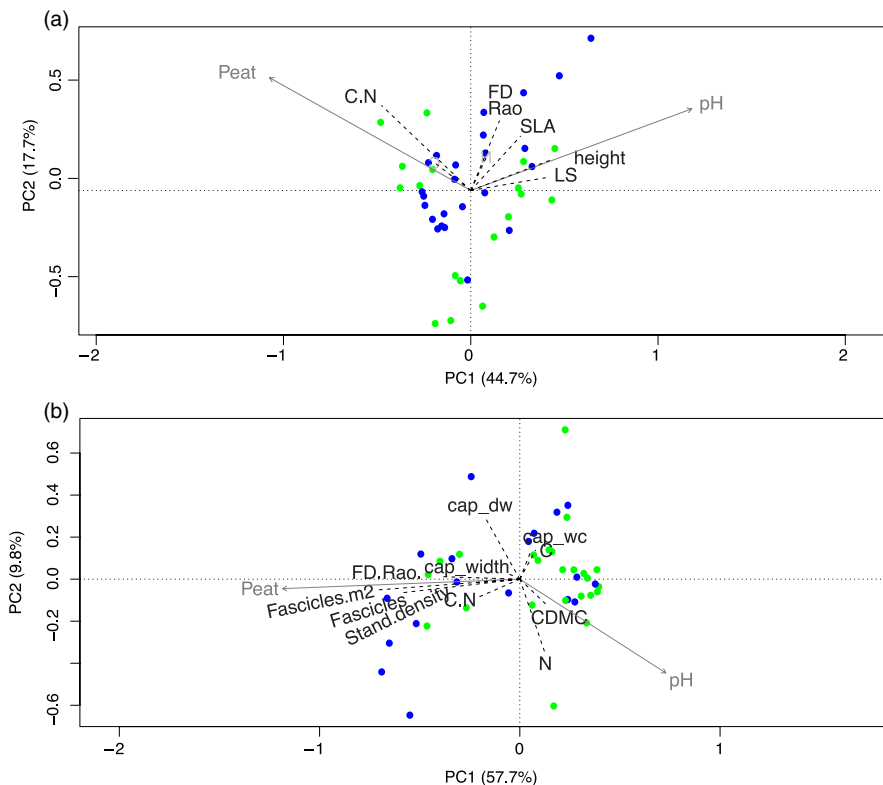
FIGURE 7 Ordinations based on principal component analysis (PCA) of functional diversity (RaoQ) of each study site, with peat thickness and pH as supplementary variables (grey arrows). A RaoQ index is calculated for each site based on all traits (FD(Rao)) and separately for each trait. (a) Analysis based on vascular plant communities; Eigenvalues of Axis 1 and Axis 2 were 3.088 and 1.751 respectively. Supplementary variables peat thickness and pH were significant ($p < 0.003$). (b) Analysis based on *Sphagnum* communities; Eigenvalues of Axis 1 and Axis 2 were 6.337 and 1.425 respectively. Supplementary variable peat thickness was significant ($p = 0.004$). Sites with a high proportion of species with a phylogenetic signal are shown by blue points, while green points are sites with a low proportion of species with a phylogenetic signal

3.4 | Phylogenetic signal in plant traits

Vascular plant traits showed a strong phylogenetic signal (Table 2), plant height being the only trait without the phylogenetic signal. *Sphagnum* mosses showed more contrasted results as phylogenetic signal was absent for Cap_wc, Cap_dw, C and N contents (Table 2). LIPA analyses on vascular plants revealed a significant local phylogenetic signal within Ericacae for all traits (Figure 8a), while among *Sphagnum* traits phylogenetic signal was local and significant within subgenus Acutifolia (Figure 8b). These two species groups were particularly associated with older successional stages (Figure 2), and therefore the sites with higher proportion of species with significant phylogenetic signal were more common at conditions with acidic pH and high peat thickness (Figure 4a,b).

TABLE 2 Summary of tests for phylogenetic signal in vascular plant and *Sphagnum* traits. Tests were computed under a Brownian motion model. The different levels of statistical significance are expressed as $p < 0.05^*$, $p < 0.01^{**}$, $p < 0.001^{***}$
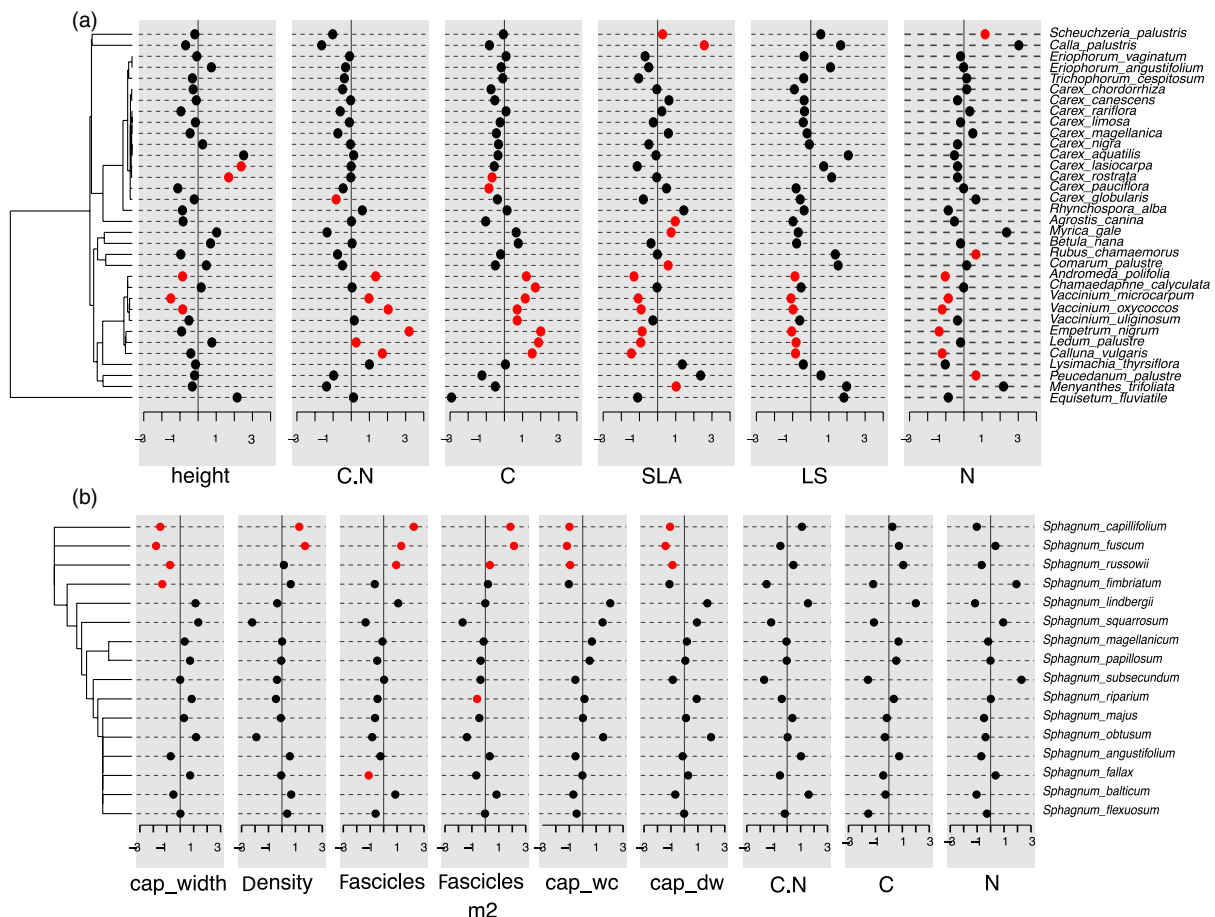
Trait	Phylogenetic signal	K.star (significance)	Cmean (significance)	Lambda (significance)
Vascular plants				
Height	Absent	0.035 (ns)	0.192 (*)	0.000049 (ns)
SLA	Present	0.193 (**)	0.236 (*)	0.929 (**)
LS	Present	0.043 (ns)	0.290 (**)	0.748 (**)
C:N	Present	0.274 (**)	0.385 (**)	0.884 (**)
C	Present	0.733 (**)	0.527 (**)	0.988 (**)
N	Present	0.334 (**)	0.224 (*)	0.978 (**)
Sphagnum				
Stand density	Present	0.0000738 (*)	0.181 (ns)	0.754 (***)
Fascicles	Present	0.000000211 (ns)	0.243 (*)	1.184 (***)
Fascicles m^2	Present	0.000000680 (ns)	0.352 (**)	1.000 (***)
Cap_width	Present	0.000000201 (ns)	0.305 (*)	0.880 (***)
Cap_wc	Absent	0.0000117 (ns)	0.148 (ns)	0.725 (**)
Cap_dw	Absent	0.0000252 (ns)	0.122 (ns)	0.601 (**)
C:N	Present	0.00108 (**)	−0.182 (ns)	1.000 (***)
C	Absent	0.0000119 (ns)	−0.118 (ns)	0.136 (ns)
N	Absent	0.0000119 (ns)	−0.135 (ns)	1.000 (***)

FIGURE 8 Local Indicators of Phylogenetic Association (LIPA) index showing the hotspot of autocorrelation within phylogenetic trees between species and their neighbours. Red colour indicates significant Local Moran's index. (a) Vascular plants (traits: plant height, C:N ratio, C content, SLA, leaf size (LS) and N content) and (b) *Sphagnum* mosses (traits: capitulum width (cap_width), stand density, amount of fascicles per stem, amount of fascicles per m^2, capitulum water content (cap_wc), capitulum dry weight (cap_dw), C:N ratio, C content and N content)

4 | DISCUSSION

Our study assessed the change in plant traits and their plasticity during peatland succession. The sampling that encompassed a wide primary successional gradient of peatlands ranging from the coastal wet meadows through the sedge fens to the ombrotrophic bogs agreed with earlier literature on peatland succession (e.g. Bauer et al., 2003; Elina & Kuznetsov, 1996; Hughes & Barber, 2003; Klinger & Short, 1996). Peatland plant community dominance shifted from forb and graminoid to shrub and *Sphagnum* moss, following the gradient formed by increasing peat thickness and decreasing pH, that is, development towards the less fertile habitats (Gignac & Vitt, 1990). A turning point in peatland succession occurs when *Sphagnum* mosses become an important component of the vegetation (Magyari et al., 2001). In our study *Sphagnum* moss projection cover exceeded that of vascular plants already at sites with shallow peat (50 cm) and at pH of 4.8.

4.1 | Trait trade-offs during peatland succession

The trait trade-off from the acquisitive to the conservative resource use strategy is generally linked with ecosystem functions so that the communities with acquisitive species have higher productivity, rapid litter decomposition, high N turnover and availability, while high litter accumulation, resistance to herbivory and soil C accumulation are related characteristics of conservative strategy (Garnier et al., 2004; Lavorel & Grigulis, 2012). In peatlands, lower productivity but nevertheless also greater net C sequestration is connected to slow-growing species with low litter decomposability, commonly occurring in nutrient-poor peatlands (Freschet et al., 2012; Moor et al., 2015; Turetsky et al., 2008). Our trait-based results support this view as we found a similar vascular plant trait trade-off from acquisitive to conservative resource use strategy along the successional peatland gradient, as has been described from fertility and successional gradients in grasslands and forests (e.g. De Deyn et al., 2008; Garnier et al., 2004; Reich, 2014; Sterck et al., 2006; Wright et al., 2004) and along an experimental N gradient in an ombrotrophic peatland (Lin et al., 2020). To the best of our knowledge, this is the first study focusing on the trait trade-offs along peatland succession, the community-weighted SLA and LS decreased with increasing peat thickness and decreasing pH (decreasing nutrient status), agreeing with the study by Lin et al. (2020) who found SLA and LS to increase along with increasing N loading (increasing nutrient status). In general, high values of these leaf-level traits enhance light capture and leaf cooling and enable high photosynthetic capacity and growth rates (Pérez-Harguindeguy et al., 2016; Poorter & Evans, 1998; Walker et al., 2014). However, leaf N content, which is integral to the proteins of photosynthetic machinery, especially Rubisco (Lambers et al., 2008), showed a less clear association with the successional gradient. It has been shown that in low SLA leaves (i.e. plants with a conservative strategy), a larger share of N is bound to cell wall

proteins per unit leaf area, leading to a smaller allocation of N to the photosynthetic machinery (Onoda et al., 2004; Takashima et al., 2004). Therefore, it is not self-evident that high N content should be an indicator of high acquisition rates but may, as well, be related to longer leaf life span, supporting a conservative strategy (Hikosaka, 2004). Plant height affects plants ability to capture light (Westoby et al., 2002) and varies independently from the leaf-level traits (Diaz et al., 2004). In our study, the plant height showed strong negative dependency on the peat thickness. This pattern occurred although all the sites were open or only sparsely treed peatlands, so it was not related to strong shading from tree stand. The CWM plant height was overall low, and varied relatively little (average 28 cm, range 12–52 cm). The only measured vascular plant traits positively associated with the increasing peat thickness were leaf C content and C:N ratio, which high values are good predictors for slow litter decomposition rates (e.g. Pérez-Harguindeguy et al., 2000).

In mosses, there was a trait trade-off from acquisitive to conservative species that can be considered analogous to that of vascular plants. In earlier studies, the high acquisition strategy of *Sphagnum* species has been associated with large capitula (apical growing part), low stand density, higher N content and greater rates of photosynthesis, growth and litter mass loss, while species with small capitula and densely packed stands coupled with slow ecosystem processes are considered conservative (Bengtsson et al., 2016; Laine et al., 2011; Laing et al., 2014; Mazziotta et al., 2019; Moor et al., 2015; Rice et al., 2008). In most of these studies, the trait trade-off has been related to a water-table and/or shade gradient, but here we show a strong correlation with peatland succession associated with peat thickness and pH gradients. We found a clear trend from early successional fens to ombrotrophic bogs. Early successional peatlands support capitula with high N content and loose stands that allow deeper light penetration and likely have greater vertical distribution of photosynthesis, metabolically inexpensive tissues that photosynthesize and elongate rapidly (Rice et al., 2008). Ombrotrophic bogs, on the contrary, are dominated by *Sphagnum* species that tolerate environmental stress by high investment in water holding capacity, high carotenoid concentrations and larger C allocation to main structural carbohydrate polymers (Elumeeva et al., 2011; Limpens et al., 2017; Rice et al., 2008). In our study, capitulum size was an exception: similar to older bogs, early succession wet meadows that have unstable hydrology (Laine et al., 2016) support hummock-forming *Sphagnum* species with small capitula, such as *Sphagnum fimbriatum*. Therefore, the species with the largest capitula occurred at fens at the middle of the successional gradient.

At the early successional sites with a thin layer of peat, mineral nutrients from the underlying soil and incoming flow of water and nutrients enable the 'acquisitive strategy' that involves high use of resources (nutrients and water) to rapidly acquire C (Wright et al., 2004). At the other end of the successional gradient, thick peat layer creates an extremely restrained growth environment, poor in mineral nutrients and often with either limited (hummock) or excess (hollow) water availability (Rydin & Jeglum, 2013). In addition, these

sites are usually exposed to direct sunlight, as vascular plant cover is low. Under such conditions, resource conservation enhances survival and plants with a conservative strategy thrive.

4.2 | Resistance of peatland plant communities

With our trait dataset we were able evaluate if the resistance of peatland plant communities agrees with the finding of higher resistance of the later successional stages (bog) than earlier stages (fens) by analysing the relative contributions of inter- versus intraspecific trait variation and the rate of functional diversity along the successional gradient. We observed different responses for vascular plants and *Sphagnum* mosses: for vascular plant traits, the interspecific variability dominated, indicating low resistance of the community structure to the changes in peat thickness and pH (Albert et al., 2011; Lepš et al., 2011; Violle et al., 2012). Supporting this, Bubier et al. (2011) and Lin et al. (2020) observed only modest intraspecific response of bog vascular plants to increased N levels. Many of the *Sphagnum* moss traits, however, showed equally high and significant contributions of inter- and intraspecific variation. As an example, greater peat thickness, which favours the occurrence of *Sphagnum* species with a large number of fascicles, also favours moss individuals with a large number of fascicles. The significant contribution of intraspecific trait variation indicates greater resistance of plant community structure to environmental perturbations (e.g. Lepš et al., 2011). Therein, our results indicate *Sphagnum* moss community to be more resistant to change compared to vascular plant community.

In addition, we found increasing functional diversity in *Sphagnum* communities during peatland succession, while functional diversity in vascular plant communities was higher at younger peatlands with low peat thickness and high pH. Studies addressing functional diversity in peatlands are yet rare; however, in a study by D'astous et al. (2013), a secondary succession following cut-over peatland restoration led to a corresponding decrease in vascular plant functional diversity in few years after an initial peak. The pattern found here for *Sphagnum* mosses supports the plant community assembly theory on the shift of control from abiotic to biotic filtering with diminishing resources. While not previously tested in peatlands, the theory has found support from several other ecosystems (e.g. Leibold et al., 2004; Lohbeck et al., 2012; Mason et al., 2011; Purschke et al., 2013). During early successional stages, moss species with similar traits are selected due to their shared adaptation to a particular environment, causing low functional diversity. Later, as mosses create their own microenvironment, biotic filtering through competitive exclusion and resource partitioning selects functionally different species, which increases functional diversity (Weiher et al., 2011; Weiher & Keddy, 1995). Contrastingly, it seems that in peatlands the abiotic filtering for vascular plants is strongest in older oligotrophic minerogenic and ombrotrophic peatlands. The harsh conditions created by Sphagna favour functionally similar vascular species, mostly stunted ericoid shrubs. This finding was further supported by the significant local phylogenetic signal within Ericacae for all traits, indicating abiotic filtering in older successional stages where this species group

is the most abundant. Our results give support to a study by Robroek et al. (2017) who found that within the oldest successional stage, that is, bogs, vascular plant species turnover along a climatic gradient was associated with deterministic replacement of functionally similar species. Such apparent decoupling of taxonomic and functional turnover may be an important mechanism underlying the capability of bog ecosystems to maintain functioning under environmental change. Our results, however, imply that the same may not be the case for more fertile fens.

4.3 | Phylogenetic signal of peatland plant traits

We found a phylogenetic signal for most of the measured vascular plant and moss traits indicating phylogenetic conservatism, that is, the tendency for closely related species to share similar ecological and biological attributes (Blomberg et al., 2003). The signal was particularly strong for the late successional species groups such as Ericoid shrubs and Sphagna belonging to subgroup Acutifolia (e.g. *S. fuscum*, *S. capillifolium*). Based on this, the harsh environmental conditions of bogs cause strong abiotic filtering selecting evolutionary-related species with similar traits. The strong phylogenetic signal of vascular plant traits could allow the prediction of trait values for unstudied species and communities (de Bello et al., 2015) and offer a basic for creating predictive models on the response of peatland plant community functions to climate change.

4.4 | Consequences of climate change on peatlands

Climate change that increases evaporative demand (Helbig et al., 2020) and likely reduces spring water excess in the northern peatland-dominated landscapes (Teutschbein et al., 2015) is suggested to accelerate peatland hydrosere succession, such that fens are more rapidly overgrown by bog vegetation (e.g. Väliranta et al., 2017). Both wet and warm periods, which induce greater peat growth rates (e.g. Hughes, 2000), and drier conditions with water-table drawdown, which lead to surface isolation and support *Sphagnum* growth (e.g. Tahvanainen, 2011), steer towards ombrotrophication. Our study shows that such shift from a fen to a bog community is connected to a trait trade-off from acquisitive to conservative strategy and changes in community resistance, which may strongly influence peatland C and nutrient cycling, with potential feedbacks to future climate via plant–soil microbe feedbacks (Bragazza et al., 2013; Jassey et al., 2013). Through the Holocene, fen to bog transitions induced by warmer and dryer climate have been connected to a sharp increase in rates of C accumulation (Loisel & Yu, 2013; Loisel et al., 2014). Consequently, accelerated succession towards bogs, which are more stable in their trait and species composition as found here, and in their C sink function (Leppälä et al., 2008; Wu & Roulet, 2014) could have a major effect on the climate-related impact of peatlands, potentially creating a cooling feedback. The persistence of *Sphagnum* mosses as the elemental part of the plant community seems, however,

crucial for this positive development. Low functional diversity and low intraspecific variability in the bog vascular vegetation found in our study indicate that alternative development, that is, climate change-induced large-scale shrubification (e.g. Sturm et al., 2001; Tape et al., 2006) at the expense of mosses, could lead to reduced resistance of peatlands. Such ecosystem change has been shown to lead to a decreased peat accumulation (Turetsky et al., 2012).

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AUTHORS' CONTRIBUTIONS

A.M.L., E.-S.T. and M.N. conceived the ideas and designed the methodology; A.M.L., T.L. and O.K. collected the data; A.M.L. analysed the data, except analysis of phylogenetic signal of plant traits that was carried out by V.E.J.J.; A.M.L. and E.-S.T. led the writing of the manuscript, while all the authors contributed critically to the drafts and gave final approval for publication.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Primary data are stored at the Pangaea Data Library https://doi.org/10.1594/PANGAEA.926827 (Laine et al., 2021).

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REFERENCES

Albert, C. H., Grassein, F., Schurr, F. M., Vieilledent, G., & Violle, C. (2011). When and how should intraspecific variability be considered in trait-based plant ecology? *Perspectives in Plant Ecology, Evolution and Systematics*, *13*(3), 217–225. https://doi.org/10.1016/j.ppees.2011.04.003

Bauer, I. E., Gignac, L. D., & Vitt, D. H. (2003). Development of a peatland complex in boreal western Canada: Lateral site expansion and local variability in vegetation succession and long-term peat accumulation. *Canadian Journal of Botany*, *81*(8), 833–847. https://doi.org/10.1139/b03-076

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

Bengtsson, F., Rydin, H., & Hájek, T. (2018). Biochemical determinants of litter quality in 15 species of Sphagnum. *Plant and Soil*, *425*(1–2), 161–176. https://doi.org/10.1007/s11104-018-3579-8

Blomberg, S. P., Garland, T. Jr, & Ives, A. R. (2003). Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. *Evolution*, *57*(4), 717–745. https://doi.org/10.1111/j.0014-3820.2003.tb00285.x

Botta-Dukát, Z. (2005). Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *Journal of Vegetation Science*, *16*(5), 533–540. https://doi.org/10.1111/j.1654-1103.2005.tb02393.x

Bragazza, L., Parisod, J., Buttler, A., & Bardgett, R. D. (2013). Biogeochemical plant–soil microbe feedback in response to climate warming in peatlands. *Nature Climate Change*, *3*(3), 273. https://doi.org/10.1038/nclimate1781

Bubier, J. L., Moore, T. R., & Juggins, S. (1995). Predicting methane emission from bryophyte distribution in northern Canadian peatlands. *Ecology*, *76*(3), 677–693. https://doi.org/10.2307/1939336

Bubier, J. L., Smith, R., Juutinen, S., Moore, T. R., Minocha, R., Long, S., & Minocha, S. (2011). Effects of nutrient addition on leaf chemistry, morphology, and photosynthetic capacity of three bog shrubs. *Oecologia*, *167*(2), 355–368. https://doi.org/10.1007/s00442-011-1998-9

Chapin III, F. S., Autumn, K., & Pugnaire, F. (1993). Evolution of suites of traits in response to environmental stress. *The American Naturalist*, *142*, 78–92. https://doi.org/10.1086/285524

Cornelissen, J. H., & Makoto, K. (2014). Winter climate change, plant traits and nutrient and carbon cycling in cold biomes. *Ecological Research*, *29*, 517–527. https://doi.org/10.1007/s11284-013-1106-1

D'Astous, A., Poulin, M., Aubin, I., & Rochefort, L. (2013). Using functional diversity as an indicator of restoration success of a cut-over bog. *Ecological Engineering*, *61*, 519–526. https://doi.org/10.1016/j.ecoleng.2012.09.002

de Bello, F., Berg, M. P., Dias, A. T., Diniz-Filho, J. A. F., Götzenberger, L., Hortal, J., Ladle, R. J., & Lepš, J. (2015). On the need for phylogenetic 'corrections' in functional trait-based approaches. *Folia Geobotanica*, *50*(4), 349–357. https://doi.org/10.1007/s12224-015-9228-6

De Deyn, G. B., Cornelissen, J. H., & Bardgett, R. D. (2008). Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecology Letters*, *11*(5), 516–531. https://doi.org/10.1111/j.1461-0248.2008.01164.x

Dıaz, S., & Cabido, M. (2001). Vive la difference: Plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, *16*(11), 646–655.

Diaz, S., Hodgson, J. G., Thompson, K., Cabido, M., Cornelissen, J., Jalili, A., Montserrat-Martí, G., Grime, J. P., Zarrinkamar, F., Asri, Y., Band, S. R., Basconcelo, S., Castro-Díez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Pérez-Harguindeguy, N., Pérez-Rontomé, M. C., Shirvany, F. A., … Zak, M. R. (2004). The plant traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science*, *15*(3), 295–304. https://doi.org/10.1111/j.1654-1103.2004.tb02266.x

Dorrepaal, E., Cornelissen, J. H., Aerts, R., Wallen, B. O., & Van Logtestijn, R. S. (2005). Are growth forms consistent predictors of leaf litter quality and decomposability across peatlands along a latitudinal gradient? *Journal of Ecology*, *93*(4), 817–828. https://doi.org/10.1111/j.1365-2745.2005.01024.x

Elina, G. A., & Kuznetsov, O. L. (1996). Paleovegetation and Paleogeography of Holocene of Pribelomorskaya lowland in Karelia; prognosis for 1000 years. *Aquilo, Series Botanica*, *36*, 9–20.

Ellenberg, H., Arndt, U., Bretthauer, R., Ruthsatz, B., & Steubing, L. (1991). Biological monitoring. In *Signals from the environment* (p. 318). Vieweg.

Elumeeva, T. G., Soudzilovskaia, N. A., During, H. J., & Cornelissen, J. H. (2011). The importance of colony structure versus shoot morphology for the water balance of 22 subarctic bryophyte species. *Journal of Vegetation Science*, *22*(1), 152–164. https://doi.org/10.1111/j.1654-1103.2010.01237.x

Eskelinen, A., & Harrison, S. P. (2015). Resource colimitation governs plant community responses to altered precipitation. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(42), 13009–13014. https://doi.org/10.1073/pnas.1508170112

Felsenstein, J. (1985). Phylogenies and the comparative method. *The American Naturalist*, *125*, 1–15.

Freschet, G. T., Aerts, R., & Cornelissen, J. H. (2012). A plant economics spectrum of litter decomposability. *Functional Ecology*, *26*(1), 56–65. https://doi.org/10.1111/j.1365-2435.2011.01913.x

Garnier, E., Cortez, J., Billès, G., Navas, M., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C., & Toussaint, J. (2004). Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, *85*, 2630–2637. https://doi.org/10.1890/03-0799

Gignac, L. D., & Vitt, D. H. (1990). Habitat limitations of Sphagnum along climatic, chemical, and physical gradients in mires of western Canada. *Bryologist*, *93*, 7–22. https://doi.org/10.2307/3243541

Gong, J., Roulet, N., Frolking, S., Peltola, H., Laine, A. M., Kokkonen, N., & Tuittila, E. S. (2020). Modelling the habitat preference of two key *Sphagnum* species in a poor fen as controlled by capitulum water content. *Biogeosciences*, *17*(22), 5693–5719.

Goud, E. M., Moore, T. R., & Roulet, N. T. (2017). Predicting peatland carbon fluxes from non-destructive plant traits. *Functional Ecology*, *31*(9), 1824–1833. https://doi.org/10.1111/1365-2435.12891

Gray, A., Levy, P. E., Cooper, M. D. A., Jones, T., Gaiawyn, J., Leeson, S. R., Ward, S. E., Dinsmore, K. J., Drewer, J., Sheppard, L. J., Ostle, N. J., Evans, C. D., Burden, A., & Zieliński, P. (2013). Methane indicator values for peatlands: A comparison of species and functional groups. *Global Change Biology*, *19*(4), 1141–1150. https://doi.org/10.1111/gcb.12120

Hájek, T., Ballance, S., Limpens, J., Zijlstra, M., & Verhoeven, J. T. (2011). Cell-wall polysaccharides play an important role in decay resistance of Sphagnum and actively depressed decomposition in vitro. *Biogeochemistry*, *103*(1–3), 45–57. https://doi.org/10.1007/s10533-010-9444-3

Helbig, M., Waddington, J. M., Alekseychik, P., Amiro, B., Aurela, A., Barr, A. G., Black, T. A., Blanken, P. D., Carey, S. K., Chen, J., Chi, J., Desai, A. R., Dunn, A., Euskirchen, E., Friborg, T., Flanagan, L. B., Forbrich, I., Grelle, A., Harder, S., … Wofsy, S. (2020). Peatland-dominated boreal ecoregions at risk of drying in a warmer climate. *Nature Climate Change*. https://doi.org/10.1038/s41558-020-0763-7

Hikosaka, K. (2004). Interspecific difference in the photosynthesis–nitrogen relationship: Patterns, physiological causes, and ecological importance. *Journal of Plant Research*, *117*(6), 481–494. https://doi.org/10.1007/s10265-004-0174-2

Hill, M. O., Mountford, J. O., Roy, D. B., & Bunce, R. G. H. (1999). *Ellenberg's indicator values for British plants. ECOFACT Volume 2 Technical Annex*. Institute of Terrestrial Ecology. 46 pp. (ECOFACT, 2a).

Hill, M. O., Preston, C. D., Bosanquet, S. D. S., & Roy, D. B. (2007). *BRYOATT: Attributes of British and Irish mosses, liverworts and hornworts*. Centre for Ecology and Hydrology.

Hughes, P. D. M. (2000). A reappraisal of the mechanisms leading to ombrotrophy in British raised mires. *Ecology Letters*, *3*(1), 7–9. https://doi.org/10.1046/j.1461-0248.2000.00118.x

Hughes, P. D. M., & Barber, K. E. (2003). Mire development across the fen–bog transition on the Teifi floodplain at Tregaron Bog, Ceredigion, Wales, and a comparison with 13 other raised bogs. *Journal of Ecology*, *91*, 253–264.

Jassey, V. E., Chiapusio, G., Binet, P., Buttler, A., Laggoun-Défarge, F., Delarue, F., Bernard, N., Mitchell, E. A., Toussaint, M. L., & Francez, A. J., & Gilbert, D. (2013). Above-and belowground linkages in Sphagnum peatland: Climate warming affects plant-microbial interactions. *Global Change Biology*, *19*(3), 811–823.

Jin, Y., & Qian, H. (2019). V. PhyloMaker: An R package that can generate very large phylogenies for vascular plants. *Ecography*, *42*(8), 1353–1359.

Katoh, K., & Standley, D. M. (2013). MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. *Molecular Biology and Evolution*, *30*, 772–780.

Keck, F., Rimet, F., Bouchez, A., & Franc, A. (2016). phylosignal: An R package to measure, test, and explore the phylogenetic signal. *Ecology and Evolution*, *6*(9), 2774–2780. https://doi.org/10.1002/ece3.2051

Klinger, L. F., & Short, S. K. (1996). Succession in the Hudson Bay lowland, Northern Ontario, Canada. *Arctic and Alpine Research*, *28*(2), 172–183. https://doi.org/10.2307/1551757

Kokkonen, N. A., Laine, A. M., Laine, J., Vasander, H., Kurki, K., Gong, J., & Tuittila, E. S. (2019). Responses of peatland vegetation to 15-year water level drawdown as mediated by fertility level. *Journal of Vegetation Science*, *30*(6), 1206–1216. https://doi.org/10.1111/jvs.12794

Kuhry, P., & Turunen, J. (2006). The postglacial development of boreal and subarctic peatlands. In R. K. Wieder & D. H. Vitt (Eds.), *Boreal peatland ecosystems* (pp. 25–46). Springer Berlin Heidelberg.

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., Lindholm, T., Nilsson, M., Kutznetsov, O., Jassey, V. E. J., & Tuittila, E.-S. (2021). Data from: Functional diversity and trait composition of vascular plant and *Sphagnum* moss communities during peatland succession across land uplift regions. *Pangaea*, https://doi.org/10.1594/PANGAEA.926827

Laine, A. M., Tolvanen, A., Mehtätalo, L., & Tuittila, E. S. (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

Laing, C. G., Granath, G., Belyea, L. R., Allton, K. E., & Rydin, H. (2014). Tradeoffs and scaling of functional traits in Sphagnum as drivers of carbon cycling in peatlands. *Oikos*, *123*(7), 817–828.

Laliberté, E., Legendre, P., Shipley, B., & Laliberté, M. E. (2014). *Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology*. R package version 1.0–11. Retrieved from http://cran.r-project.org/web/packages/FD/FD.pdf

Lambers, H., Chapin III, F. S., & Pons, T. L. (2008). *Plant physiological ecology* (p. 540). Springer Science & Business Media, Springer-Verlag.

Lang, S. I., Cornelissen, J. H., Klahn, T., Van Logtestijn, R. S., Broekman, R., Schweikert, W., & Aerts, R. (2009). An experimental comparison of chemical traits and litter decomposition rates in a diverse range of subarctic bryophyte, lichen and vascular plant species. *Journal of Ecology*, *97*(5), 886–900. https://doi.org/10.1111/j.1365-2745.2009.01538.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

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J. B., Law, R., Tilman, D., Loreau, M., & Gonzalez, A. (2004). The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters*, *7*(7), 601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x

Lemoine, F., Correia, D., Lefort, V., Doppelt-Azeroual, O., Mareuil, F., Cohen-Boulakia, S., & Gascuel, O. (2019). NGPhylogeny. fr: New generation phylogenetic services for non-specialists. *Nucleic Acids Research*, *47*(W1), W260–W265.

Leppälä, M., Kukko-Oja, K., Laine, J., & Tuittila, E. S. (2008). Seasonal dynamics of CO2 exchange during primary succession of boreal mires as controlled by phenology of plants. *Ecoscience*, *15*(4), 460–471.

Leppälä, M., Laine, A., Seväkivi, M.-L., & Tuittila, E.-S. (2011). Differences in CO_2 dynamics between successional mire plant communities during wet and dry summers. *Journal of Vegetation Science*, *22*, 357–366. https://doi.org/10.1111/j.1654-1103.2011.01259.x

Leppälä, M., Oksanen, J., & Tuittila, E.-S. (2011). Methane flux dynamics during mire succession. *Oecologia*, *165*, 489–499. https://doi.org/10.1007/s00442-010-1754-6

Lepš, J., de Bello, F., Šmilauer, P., & Doležal, J. (2011). Community trait response to environment: Disentangling species turnover vs

intraspecific trait variability effects. *Ecography*, *34*(5), 856–863. https://doi.org/10.1111/j.1600-0587.2010.06904.x

Limpens, J., Bohlin, E., & Nilsson, M. B. (2017). Phylogenetic or environmental control on the elemental and organo-chemical composition of Sphagnum mosses? *Plant and Soil*, *417*(1–2), 69–85. https://doi.org/10.1007/s11104-017-3239-4

Lin, G., Zeng, D. H., & Mao, R. (2020). Traits and their plasticity determine responses of plant performance and community functional property to nitrogen enrichment in a boreal peatland. *Plant and Soil*, *449*(1-2), 151–167. https://doi.org/10.1007/s11104-020-04478-4

Lohbeck, M., Poorter, L., Paz, H., Pla, L., van Breugel, M., Martínez-Ramos, M., & Bongers, F. (2012). Functional diversity changes during tropical forest succession. *Perspectives in Plant Ecology, Evolution and Systematics*, *14*(2), 89–96. https://doi.org/10.1016/j.ppees.2011.10.002

Loisel, J., & Yu, Z. (2013). Recent acceleration of carbon accumulation in a boreal peatland, south central Alaska. *Journal of Geophysical Research: Biogeosciences*, *118*(1), 41–53. https://doi.org/10.1029/2012JG001978

Loisel, J., Yu, Z., Beilman, D. W., Camill, P., Alm, J., Amesbury, M. J., Anderson, D., Andersson, S., Bochicchio, C., Barber, K., Belyea, L. R., Bunbury, J., Chambers, F. M., Charman, D. J., De Vleeschouwer, F., Fiałkiewicz-Kozieł, B., Finkelstein, S. A., Gałka, M., Garneau, M., ... Zhou, W. (2014). A database and synthesis of northern peatland soil properties and Holocene carbon and nitrogen accumulation. *The Holocene*, *24*(9), 1028–1042. https://doi.org/10.1177/0959683614538073

Magyari, E., Sümegi, P., Braun, M., Jakab, G., & Molnár, M. (2001). Retarded wetland succession: Anthropogenic and climatic signals in a Holocene peat bog profile from north-east Hungary. *Journal of Ecology*, *89*(6), 1019–1032. https://doi.org/10.1111/j.1365-2745.2001.00624.x

Mason, N. W., Carswell, F. E., Richardson, S. J., & Burrows, L. E. (2011). Leaf palatability and decomposability increase during a 200-year-old post-cultural woody succession in New Zealand. *Journal of Vegetation Science*, *22*(1), 6–17. https://doi.org/10.1111/j.1654-1103.2010.01223.x

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., Hylander, K., & Norberg, J. (2015). Predicting climate change effects on wetland ecosystem services using species distribution modeling and plant functional traits. *Ambio*, *44*, 113–126. https://doi.org/10.1007/s13280-014-0593-9

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

Münkemüller, T., Lavergne, S., Bzeznik, B., Dray, S., Jombart, T., Schiffers, K., & Thuiller, W. (2012). How to measure and test phylogenetic signal. *Methods in Ecology and Evolution*, *3*(4), 743–756. https://doi.org/10.1111/j.2041-210X.2012.00196.x

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., & Wagner, H. (2015). *vegan: Community ecology package*. R package version, 2, 2-1. Retrieved from http://vegan.r-forge.r-project.org/

Onoda, Y., Hikosaka, K., & Hirose, T. (2004). Allocation of nitrogen to cell walls decreases photosynthetic nitrogen-use efficiency. *Functional Ecology*, *18*, 419–425. https://doi.org/10.1111/j.0269-8463.2004.00847.x

Pérez-Harguindeguy, N., Díaz, S., Cornelissen, J. H., Vendramini, F., Cabido, M., & Castellanos, A. (2000). Chemistry and toughness predict leaf litter decomposition rates over a wide spectrum of functional types and taxa in central Argentina. *Plant and Soil*, *218*(1–2), 21–30.

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., de Vos, A. C., ... Cornelissen, J. H. C. (2016). Corrigendum to: New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, *64*(8), 715–716. https://doi.org/10.1071/BT12225_CO

Piatkowski, B. T., & Shaw, A. J. (2019). Functional trait evolution in *Sphagnum* peat mosses and its relationship to niche construction. *New Phytologist*, *223*(2), 939–949. https://doi.org/10.1111/nph.15825

Poorter, H., & Evans, J. R. (1998). Photosynthetic nitrogen-use efficiency of species that differ inherently in specific leaf area. *Oecologia*, *116*(1–2), 26–37. https://doi.org/10.1007/s004420050560

Purschke, O., Schmid, B. C., Sykes, M. T., Poschlod, P., Michalski, S. G., Durka, W., Kühn, I., Winter, M., & Prentice, H. C. (2013). Contrasting changes in taxonomic, phylogenetic and functional diversity during a long-term succession: Insights into assembly processes. *Journal of Ecology*, *101*(4), 857–866. https://doi.org/10.1111/1365-2745.12098

Reich, P. B. (2014). The world-wide 'fast–slow' plant economics spectrum: A traits manifesto. *Journal of Ecology*, *102*(2), 275–301. https://doi.org/10.1111/1365-2745.12211

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

Robroek, B. J. M., Jassey, V. E. J., Payne, R. J., Martí, M., Bragazza, L., Bleeker, A., Buttler, A., Caporn, S. J. M., Dise, N. B., Kattge, J., Zając, K., Svensson, B. H., van Ruijven, J., & Verhoeven, J. T. A. (2017). Taxonomic and functional turnover are decoupled in European peat bogs. *Nature Communications*, *8*(1), 1161. https://doi.org/10.1038/s41467-017-01350-5

R Development Core Team. (2011). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. ISBN 3-900051-07-0. Retrieved from http://www.R-project.org/

Rydin, H., & Jeglum, J. K. (2013). *The biology of peatlands* (2nd ed., p. 400). Oxford University Press.

Schindelin, J., Rueden, C. T., Hiner, M. C., & Eliceiri, K. W. (2015). The ImageJ ecosystem: An open platform for biomedical image analysis. *Molecular Reproduction and Development*, *82*(7-8), 518–529. https://doi.org/10.1002/mrd.22489

Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, *9*(7), 671–675. https://doi.org/10.1038/nmeth.2089

Smith, S. A., & Brown, J. W. (2018). Constructing a broadly inclusive seed plant phylogeny. *American Journal of Botany*, *105*(3), 302–314. https://doi.org/10.1002/ajb2.1019

Sottocornola, M., Laine, A., Kiely, G., Byrne, K. A., & Tuittila, E. S. (2009). Vegetation and environmental variation in an Atlantic blanket bog in South-western Ireland. *Plant Ecology*, *203*(1), 69–81. https://doi.org/10.1007/s11258-008-9510-2

Sterck, F. J., Poorter, L., & Schieving, F. (2006). Leaf traits determine the growth-survival trade-off across rain forest tree species. *The American Naturalist*, *167*(5), 758–765. https://doi.org/10.1086/503056

Straková, P., Penttilä, T., Laine, J., & Laiho, R. (2012). Disentangling direct and indirect effects of water table drawdown on above-and below-ground plant litter decomposition: Consequences for accumulation of organic matter in boreal peatlands. *Global Change Biology*, *18*(1), 322–335. https://doi.org/10.1111/j.1365-2486.2011.02503.x

Sturm, M., Racine, C., & Tape, K. (2001). Climate change: Increasing shrub abundance in the Arctic. *Nature*, *411*(6837), 546. https://doi.org/10.1038/35079180

Suding, K. N., Lavorel, S., Chapin, F. S., Cornelissen, J. H. C., Díaz, S., Garnier, E., Goldberg, D., Hooper, D. U., Jackson, S. T., & Navas, M.-L. (2008). Scaling environmental change through the community-level: A trait-based response-and-effect framework

for plants. *Global Change Biology*, *14*(5), 1125–1140. https://doi.org/10.1111/j.1365-2486.2008.01557.x

Tahvanainen, T. (2011). Abrupt ombrotrophication of a boreal aapa mire triggered by hydrological disturbance in the catchment. *Journal of Ecology*, *99*, 404–415. https://doi.org/10.1111/j.1365-2745.2010.01778.x

Takashima, T., Hikosaka, K., & Hirose, T. (2004). Photosynthesis or persistence: Nitrogen allocation in leaves of evergreen and deciduous Quercus species. *Plant, Cell & Environment*, *27*(8), 1047–1054. https://doi.org/10.1111/j.1365-3040.2004.01209.x

Tape, K. E. N., Sturm, M., & Racine, C. (2006). The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Global Change Biology*, *12*(4), 686–702. https://doi.org/10.1111/j.1365-2486.2006.01128.x

Teutschbein, C., Grabs, T., Karlsen, R. H., Laudon, H., & Bishop, K. (2015). Hydrological response to changing climate conditions: Spatial streamflow variability in the boreal region. *Water Resources Research*, *51*(12), 9425–9446. https://doi.org/10.1002/2015WR017337

Tuittila, E., Juutinen, S., Frolking, S., Väliranta, M., Laine, A., Miettinen, A., Seväkivi, M., Quillet, A., & Merilä, P. (2013). Wetland chronosequence as a model of peatland development: Vegetation succession, peat and carbon accumulation. *Holocene*, *23*, 25–35. https://doi.org/10.1177/0959683612450197

Turetsky, M. R., Bond-Lamberty, B., Euskirchen, E., Talbot, J., Frolking, S., McGuire, A. D., & Tuittila, E. S. (2012). The resilience and functional role of moss in boreal and arctic ecosystems. *New Phytologist*, *196*(1), 49–67. https://doi.org/10.1111/j.1469-8137.2012.04254.x

Turetsky, M. R., Crow, S. E., Evans, R. J., Vitt, D. H., & Wieder, R. K. (2008). Trade-offs in resource allocation among moss species control decomposition in boreal peatlands. *Journal of Ecology*, *96*(6), 1297–1305.

Väliranta, M., Salojärvi, N., Vuorsalo, A., Juutinen, S., Korhola, A., Luoto, M., & Tuittila, E.-S. (2017). Key plant species and succession patterns associated to past fen-bog transitions – future perspectives. *Holocene*, *27*, 752–764.

Violle, C., Enquist, B. J., McGill, B. J., Jiang, L., Albert, C. H., Hulshof, C., Jung, V., & Messier, J. (2012). The return of the variance: Intraspecific variability in community ecology. *Trends in Ecology & Evolution*, *27*(4), 244–252. https://doi.org/10.1016/j.tree.2011.11.014

Walker, A. P., Beckerman, A. P., Gu, L., Kattge, J., Cernusak, L. A., Domingues, T. F., Scales, J. C., Wohlfahrt, G., Wullschleger, S. D., & Woodward, F. I. (2014). The relationship of leaf photosynthetic traits–Vcmax and Jmax–to leaf nitrogen, leaf phosphorus, and specific leaf area: A meta-analysis and modeling study. *Ecology and Evolution*, *4*(16), 3218–3235.

Weiher, E., Freund, D., Bunton, T., Stefanski, A., Lee, T., & Bentivenga, S. (2011). Advances, challenges and a developing synthesis of ecological community assembly theory. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1576), 2403–2413.

Weiher, E., & Keddy, P. A. (1995). The assembly of experimental wetland plant communities. *Oikos*, *73*, 323–335. https://doi.org/10.2307/3545956

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*(1), 125–159. https://doi.org/10.1146/annurev.ecolsys.33.010802.150452

Whitaker, D., Christman, M., & Whitaker, M. D. (2014). *Package 'clustsig'. R package*. Retrieved from https://cran.r-project.org/web/packages/cluster/cluster.pdf

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., ... Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, *428*(6985), 821. https://doi.org/10.1038/nature02403

Wu, J., & Roulet, N. T. (2014). Climate change reduces the capacity of northern peatlands to absorb the atmospheric carbon dioxide: The different responses of bogs and fens. *Global Biogeochemical Cycles*, *28*(10), 1005–1024. https://doi.org/10.1002/2014GB004845

Zanne, A. E., Tank, D. C., Cornwell, W. K., Eastman, J. M., Smith, S. A., FitzJohn, R. G., & Royer, D. L. (2014). Three keys to the radiation of angiosperms into freezing environments. *Nature*, *506*(7486), 89–92.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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