



## RESEARCH ARTICLE

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# Drivers on Carbon Accumulation Vary Along the Hydrological Gradient of a Subarctic Patterned Peatland

### Key Points:

- Carbon accumulation rates across different peatland habitats are likely to respond differently to climate changes
- Plant functional types and water-table depth exert strong controls on carbon accumulation for intermediately wet lawns
- Decreasing moisture directly leads to lower carbon accumulation and indirectly through limiting *Sphagnum* growth at lawns

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### Supporting Information:

Supporting Information may be found in the online version of this article.

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**Abstract** Peatlands are important climate change mitigation agents as they store large amounts of carbon (C). Yet, their C sink capacity is vulnerable to environmental changes, which is however uncertain in a changing climate. Here, we examined potential habitat-specific C accumulation drivers over the past ~1,000 years, using replicate peat records sampled from dry strings and wetter lawns of a subarctic patterned peatland. We found that at both habitats water-table depth impacted the plant functional types and/or peat properties, but they impacted the C accumulation significantly only at lawns. Specifically, the plant functional type and water-table depth had stronger controls on C accumulation than peat properties. Our data suggest that drying-induced C accumulation decrease maybe compensated by *Sphagnum* expansion in wetter areas. This implies that peatland C accumulation at different habitats is likely to respond to climate changes in varying ways. Thus, quantification of the climatic links to habitat-specific succession and C processes is needed before peatland C sink capacity can be predicted.

**Plain Language Summary** Peatlands are valuable ecosystems that store large amounts of carbon, helping to mitigate climate change. However, their ability to continue storing carbon is uncertain as the climate changes. In this study, we investigated how carbon accumulation has been influenced by different environmental factors over the past ~1,000 years in two types of habitats within a subarctic peatland: drier areas (strings) and wetter areas (lawns). We found that water-table depth affected plant types and peat properties in both habitats, but only in the wetter lawns did these factors significantly influence carbon accumulation. Among the factors, plant types and water-table depth were more important for carbon storage than peat properties. Interestingly, our data suggest that even if drying reduces carbon accumulation, this loss could be offset by the expansion of *Sphagnum* moss, a key peat-forming plant in wetter areas. These findings emphasize that different parts of peatlands may respond differently to climate change. Understanding how specific habitats react to environmental changes is essential for predicting how much carbon peatlands will store in the future.

## 1. Introduction

Peatlands cover ~3% of Earth's surface but store more than 30% of soil organic carbon (C) (Leifeld & Menichetti, 2018; UNEP, 2022; Xu et al., 2018; Yu et al., 2010). It is suggested that depending on the land use practices and overall response to climate change, peatlands could either partially mitigate climate change or create a positive feedback challenge (Gallego-Sala et al., 2018; Günther et al., 2020). Thus, maintaining peatland C storage and sink capacity is crucial when pursuing C neutrality targets set by the Paris Agreement (UNEP, 2022). The peat C accumulation rate (CAR) is the net balance of photosynthetic C uptake and C release through aerobic and anaerobic respiration, and through leaching. It could represent the C sink capacity of peatlands. All processes involved in the C sink capacity potential as mentioned above are dynamic and highly sensitive to climatic and environmental changes (Laine et al., 2019; Zhang et al., 2021). Peatland environmental conditions, such as vegetation and water table, are altering (i.e., habitat succession) in divergent ways in a changing climate (Kokkonen et al., 2019; Kolari et al., 2021; Ma et al., 2022; Zhang et al., 2022), which in turn challenges the

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predictions of peat C accumulation trajectories. Therefore, it is important to understand the interactions between peatland C sink processes and environmental variables.

Climate impacts peatland C accumulation directly by steering photosynthesis and respiration processes, and indirectly by influencing peatland biological communities and environmental conditions, such as hydrology and nutrient availability (Huang et al., 2021; Kokkonen et al., 2022; Magnan et al., 2022; Piilo et al., 2022; Wyatt et al., 2021). Previous studies have detected linkage between peat C accumulation and certain abiotic drivers. For instance, peatland surface drying, that is, water level drawdown (Sim et al., 2021; Zhang et al., 2020), and warmer temperatures during the nongrowing season were linked to reduced C accumulation using peat core data (Liu et al., 2022). Moreover, *Sphagnum* expansion possibly reflecting nutrient limiting and a certain degree of surface drying (Kuuri-Riutta et al., 2024) was linked to increased C accumulation over recent centuries (Magnan et al., 2022), which was also inferred by Piilo et al. (2022). However, such studies only investigated the effect of one single factor on C accumulation without considering the complex causal links between various factors operating simultaneously in natural ecosystems. For example, modern carbon flux studies suggest that peatland physicochemical variables (e.g., water table, peat depth, and carbon content) could directly impact peatland carbon emissions or via changing plant communities and functional traits (Laine et al., 2022). Complex interactions are likely to restrict holistic understandings of the causality between the abiotic drivers and C accumulation (Zhang et al., 2018).

In this study, we aimed to quantify direct and indirect effects of environmental changes, namely water-table depth (WTD), peat properties, peatland vegetation, on peat C accumulation over the past ~1,000 years. The structural equation modeling approach, which is increasingly used in modern ecological studies (Perez-Quezada et al., 2024; Wang et al., 2023), was applied to estimate the cause-effect relationships between these environmental variables and past C accumulation. We investigated four peat profiles, two from dry strings and two from intermediately wet lawns, collected from a patterned fen in northern Finland. Previous studies have shown divergent responses of peatland hydrology and C accumulation to past climate changes (Sim et al., 2021; Zhang et al., 2020, 2022). Therefore, we expect to detect different causal links between the studied environmental factors and C accumulation in the two habitats where hydrology and accordingly plant communities varied.

## 2. Materials and Methods

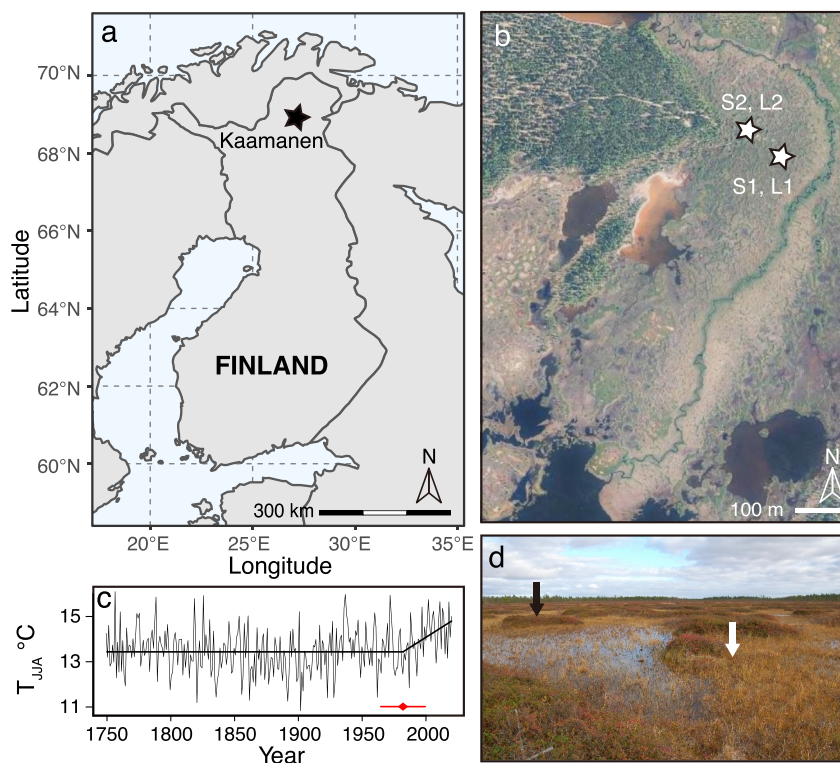
### 2.1. Study Site and Sampling

The studied Kaamanen peatland (69.14°N, 27.27°E, 155 m a.s.l.) is a subarctic patterned flark fen (ca. 43 ha) located in northern Finland (Figure 1). The long-term mean annual air temperature and the precipitation sum of the region are  $-0.4^{\circ}\text{C}$  and 472 mm, respectively, while the long-term mean summer air temperature and precipitation sum are  $12^{\circ}\text{C}$  and 192 mm, respectively (Pirinen et al., 2012; <https://en.ilmatieteenlaitos.fi>). The dominating vegetation communities vary over the different parts of the peatland and according to microtopographic features (Piilo et al., 2020). Strings are dominated by feather mosses common for forests and dry habitats, such as *Dicranum* spp. and *Pleurozium schreberi*; lichens; and dwarf shrubs, such as *Rhododendron tomentosum*, *Empetrum nigrum*, *Vaccinium uliginosum*, *V. vitis-idaea*, and *Rubus chamaemorus*. Intermediate lawn vegetation is composed of *Sphagnum* mosses and dwarf shrubs. Flark vegetation is mainly composed of sedges *Carex* spp., *Trichophorum cespitosum*, and *Eriophorum angustifolium*; forb *Menyanthes trifoliata*; and brown mosses (typically *Scorpidium scorpioides*).

Four peat cores (length ~60 cm) were collected using a box corer ( $7 \times 4 \times 65$  cm) in September 2016 (Piilo et al., 2020). Two cores (S1 and S2) were sampled from dry strings with *Ericales-Pleurozium* vegetation. In those locations, water table was not reached when sampling. The other two cores (L1 and L2) were sampled from intermediate lawns with *Betula-Sphagnum* vegetation, where the WTD was around 18 cm (Figure 1d). Profiles were cut into 1-cm slices for the analyses.

### 2.2. Chronology

A total of 12 samples were selected for accelerator mass spectrometry (AMS)  $^{14}\text{C}$  analysis. The top sections (~40 cm) of the profiles were dated with the  $^{210}\text{Pb}$  method. We revised the previous chronologies published in Piilo et al. (2020) using the *Plum* model (Aquino-López et al., 2018) with “*rplum*” package in R version 4.2.2 (R Core Team, 2011). *Plum* includes the raw  $^{210}\text{Pb}$  activity data and  $^{14}\text{C}$  data, which avoids remodeling of the  $^{210}\text{Pb}$



**Figure 1.** Study site information. (a) Study site map (Natural Earth map data). (b) Aerial photo of the peatland (National Land Survey of Finland) with white stars indicating coring locations. (c) Summer (June–July–August) temperature of Finland since 1750 (Berkeley Earth data, v2021). The red symbol indicates a significant warming change point year (est.  $\pm$  SE;  $1982 \pm 8.8$ ) detected using a segmented linear approach. (d) The microtopographic features of the study site. Black arrow: dry string; white arrow: intermediate lawn.

data as happens when processed using the Bacon model (Piilo et al., 2020). The updated age-depth models are presented in Figure S1 in Supporting Information S1. The time period focused in this study is the past  $\sim$  1000 years.

### 2.3. Environmental Variables

Plant macrofossil analysis was conducted to reconstruct past vegetation changes at the coring locations throughout the deposition history. Plant macrofossil analysis followed the protocol described in Valiranta et al. (2007). Plant remains were grouped into six functional types, that is, *Sphagnum*, non-*Sphagnum* moss, sedge, shrub, lichen, and unidentified organic matter (UOM). The full history (maximum of  $\sim$ 3,000 years) of the plant compositional variations of the studied peat sections were published in Piilo et al. (2020).

Testate amoeba analysis was carried out to reconstruct past WTD changes. Testate amoeba sample processing followed a modified version of the standard method (Booth et al., 2010), and the assemblages were first published in Zhang et al. (2022). Testate amoebae-based WTD reconstructions were performed using the transfer function developed by Amesbury et al. (2016) with weak silicic idiosomic tests excluded (Swindles et al., 2020). The absolute WTD values were normalized to  $z$  scores over the length of each profile.  $Z > 0$  indicates drier conditions than the profile's average;  $z < 0$  indicates conditions wetter than the average.

Peat bulk density (BD;  $g\ cm^{-3}$ ) was determined using the dry mass of a known fresh volume for every 1-cm slice. C and nitrogen (N) contents were measured at 4-cm intervals using a LECO TruSpec elemental determinator. These results were used to calculate average values for the layers between the measurements. The C/N ratio was calculated using the C and N content data (Piilo et al., 2020).

## 2.4. Apparent and Non-Autogenic C Accumulation

Apparent CAR ( $\text{g C m}^{-2} \text{ yr}^{-1}$ ) were calculated by multiplying the BD, C content, and the corresponding peat growth rate that was derived from the age-depth model. Due to different decomposition levels through a profile, it is very likely that the observed apparent CARs of the top sections are higher than those of the deep sections (Young et al., 2021). To estimate the effect of environmental variables on CARs, we first excluded the impact of different decomposition levels through time, that is, removed the autogenic trend. This was done by using the Clymo peat accumulation model (Clymo, 1984). The model was first applied on cumulative peat mass (BD) data to derive peat addition rate ( $p$ ) and peat decay coefficient ( $\alpha$ ) parameters using a curve fitting method (Figure S2 in Supporting Information S1) (Loisel & Yu, 2013). After this, the derived parameters  $p$  and  $\alpha$  together with carbon content were used to model autogenic CAR under constant conditions. The difference (non-autogenic CAR, presented as CAR  $z$  scores) between apparent CAR and autogenic CAR is therefore interpreted to be driven by allogenic forcing (Charman et al., 2013). Further analyses and discussions of C accumulation are based on the CAR  $z$  scores. For each core, the model was first fitted to the whole studied peat profile. If there were large deviations of data points from the Clymo equation curve, as in L1, L2, and S1, the peat profile was divided into two sections (top and bottom) based on BD, C/N value variations, and the instantaneous rate of change of the age-depth models (Zhang et al., 2018). The model was then fitted to these two sections separately. For the lawn cores, the boundary separating these two sections was generally consistent with the on-site observed contemporary WTD.

## 2.5. Statistical Analyses

Firstly, ordination analyses were carried out to reduce data dimensions, with the nonmetric multidimensional scaling (NMDS) for plant functional type (*Sphagnum*, non-*Sphagnum* moss, sedge, shrub, lichen, and UOM) percentages and principal component analysis (PCA) for peat properties (BD, C content, N content, C/N ratio). The scores of the NMDS1 and PCA1 were then considered as the controlling factors representing each group in the following partial correlation analysis.

Secondly, partial correlation analysis, an effective method that explores the correlation between two variables after controlling the effects of other variables, was used to study the relationships of C accumulation (CAR  $z$  score) with potential drivers (WTD, plant functional type, peat property) for all records combined and separately for dry strings and intermediate lawns. When a specific environmental variable was included as the explaining variable, all other variables were considered as covariates.

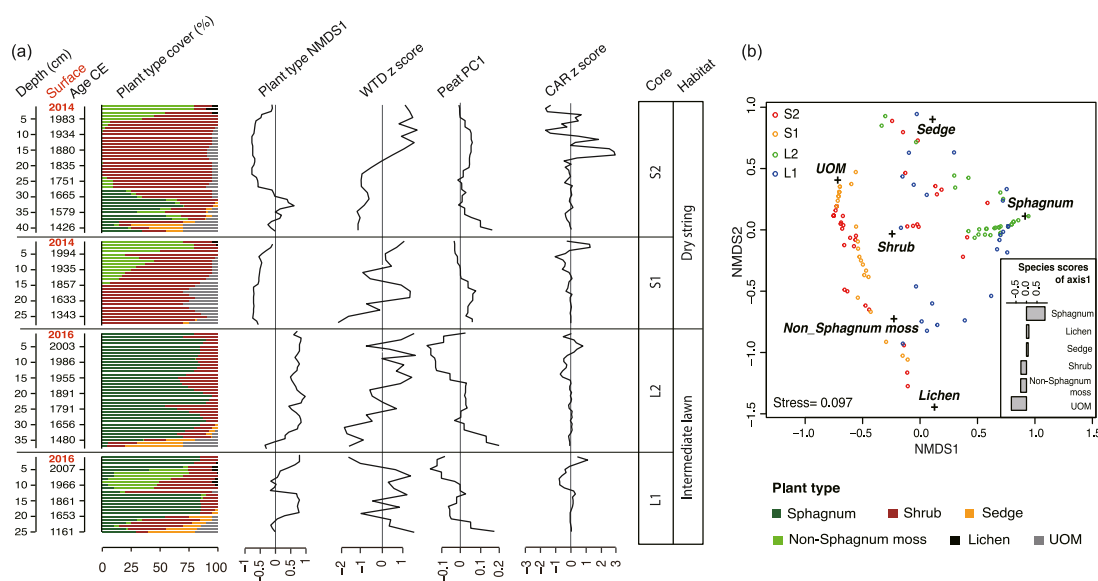
Thirdly, we performed partial least squares path modeling (PLS-PM) to detect the direct and indirect effects of the above factors (WTD, peat properties, and plants) on C accumulation for the full data set of four cores, and separately for dry strings and intermediate lawns. Here, the direct effect means the pathway from a factor to C accumulation, while the indirect effect describes the pathway from a factor to C accumulation through some mediators (other factors). The method was selected because it exhibits higher tolerance to data distribution, sample size, and collinearity (Fan et al., 2016). We constructed the PLS-PM based on the following assumptions: WTD, peat properties, and plants directly impact C accumulation, possibly by controlling decomposition and photosynthesis processes (Magnan et al., 2022; Yang et al., 2023; Zhang et al., 2020). WTD also indirectly influences C accumulation by altering peat properties and plant growth or succession (e.g., Kokkonen et al., 2019). Peat properties could also indirectly affect C accumulation by altering plant growth or succession (e.g., Kokkonen et al., 2019). BD, C content, N content, and C/N ratio were all set as the formation variables of peat properties in the initial model. Goodness of Fit (GoF) was calculated to evaluate whether these formation variables should be included. The final model, which has the largest GoF, included BD, N, and CN for peat properties; NMDS1 of plant macrofossil data for plants; and testate amoebae-based WTD reconstruction for WTD.

All statistical analyses were conducted in R using packages “vegan” (Oksanen et al., 2022), “ppcor” (Kim, 2015), and “plspm” (Bertrand et al., 2024).

## 3. Results

### 3.1. Variation in Peat C Accumulation as Linked to Key Factors

The CAR  $z$  scores, that is, standardized non-autogenic CARs, demonstrated spatiotemporal variations in external forcing on peat C accumulation (Figure 2a). S2 showed large fluctuations of CAR  $z$  scores after ca. 1850 CE. The



**Figure 2.** Peat carbon accumulation and the studied factors. (a) Diagram showing plant functional type (see the legend on the right) coverage, non-autogenic carbon accumulation (CAR  $z$  score), and the potential controlling factors, that is, plant functional types (plant type NMDS1), standardized testate amoebae (TA)-based water-table depth reconstruction (WTD  $z$  score), and peat properties (Peat PC1) for the studied four cores. Plant functional types and peat properties were expressed using the sample scores of the first axes of NMDS and PCA conducted within the corresponding variables. UOM: unidentified organic matter. (b) NMDS of plant functional types. The inset plot shows the species scores of the axis 1.

other records exhibited a decrease after *ca.* 1900 CE, which was particularly pronounced in L1, followed by a peak over the past decades.

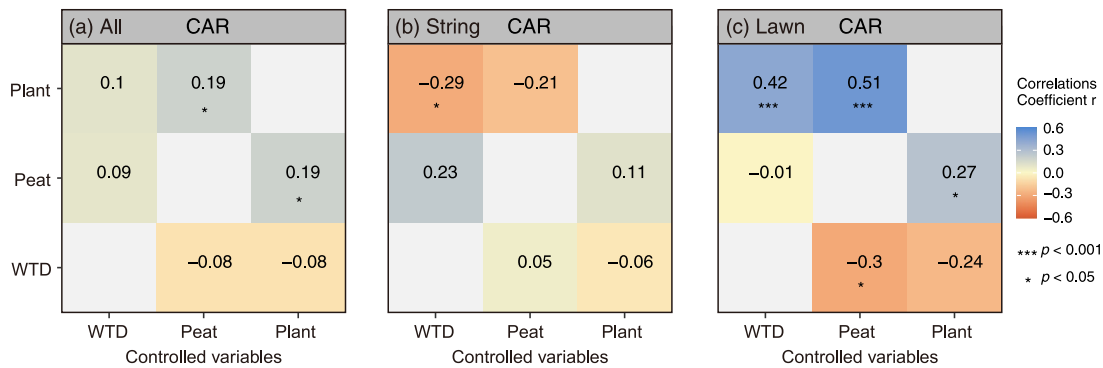
Vegetation history of the records for the studied  $\sim 1,000$  years differed by habitats (Figure 2a). S1 and S2 that were collected from dry strings were generally dominated by shrubs, while L1 and L2 that were collected from wetter intermediate lawns were mostly dominated by mosses, mainly *Sphagnum* spp. The NMDS of plant functional types yielded large scores of the axis 1 for samples dominated by *Sphagnum* mosses (Figure 2b). NMDS axis 2 arranged the samples from sedges typical to wet habitats to lichens characteristic to the top of dry strings. Testate amoebae-based WTD reconstructions suggested a general drying trend for S1, S2, and L2, while L1 exhibited a wetting trend toward recent years. Peat properties of L1 and L2 showed a similar decreasing trend of PC1 scores toward recent years, while S1 and S2 had relatively little variation, with C content (positive) and the C/N ratio (negative) being the dominating two variables of the axis 1 (Figures 2a and Figure S3 in Supporting Information S1). Scores of NMDS axis 1 and PCA axis 1, used in the following analyses, represent *Sphagnum*-other plants, and C-C/N ratio gradients (positive-negative scores), respectively.

### 3.2. Dominant Controls on C Accumulation

Partial correlation analysis indicated that significant ( $p < 0.05$ ) correlations between the environmental drivers and C accumulation varied between different habitats. Plant functional type composition was the most significant control for C accumulation for both habitats, while WTD was significant only at intermediate lawns. In addition, the correlation coefficients and significance levels changed when different controlling factors were considered (Figure 3). For example, the correlation coefficient of plant functional types and C accumulation for strings was significant when the impact of WTD was accounted for (coefficient =  $-0.29$  and  $p < 0.05$ ), but the correlation was insignificant when the impact of peat properties was accounted for.

When considering all the factors together in PLS-PM, no significant effect on C accumulation was observed for the data set combining all records (Figure 4a) and for dry strings (Figure 4b), which contradicts the partial analysis that revealed a link between plant functional type composition and C accumulation.

Although in general, our simple model that included limited formation factors did not show a very high performance (GoF = 0.46), PLS-PM for intermediate lawns showed plant functional types and WTD as direct controls for C accumulation, with positive (standardized path coefficient (refer to coef. hereafter) = 0.40) and



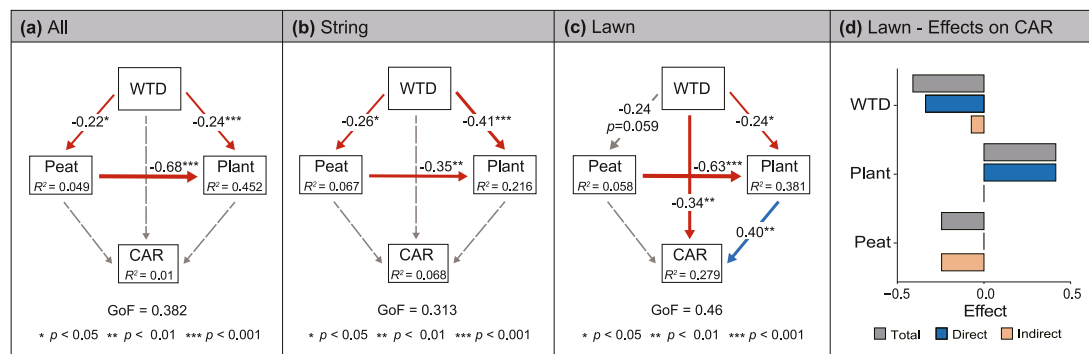
**Figure 3.** Partial correlations between the non-autogenic carbon accumulation rate (CAR) and water-table depth (WTD), peat properties (Peat), and plant functional types (Plant) for (a) all records, (b) dry strings, and (c) intermediate lawns. Peat and Plant represent the sample scores of the first axes of PCA and NMDS conducted for the corresponding variables, reflecting the C-C/N ratio (positive-negative scores) and *Sphagnum*-other plants gradients, respectively. Larger WTD values mean drier conditions. Differences in color between controlled factors indicate the level of dependency of the correlations between CAR and the examined factor on the controlled variable (increase/decrease in color intensity = gain/loss of correlation).

negative (coef. =  $-0.34$ ) effects, respectively. In addition to these two direct controls, WTD and peat properties had indirect effects on C accumulation through influencing plants. WTD was negatively correlated with NMDS1 of plant functional types, suggesting that drier conditions reduce *Sphagnum* abundance at lawns. Peat properties, including BD, N content, and C/N ratio as formation variables, were also negatively related to NMDS1 of plant functional types. The loading values (i.e., the correlations between the latent variable and the observed variables) of these formation variables were 0.89, 0.97, and 0.95, respectively. When calculating the significant direct and indirect effects together, plant functional types (coef. = 0.40) and WTD (coef. =  $-0.43$ ) had stronger controls on C accumulation than peat properties (coef. =  $-0.25$ ).

#### 4. Discussion

Our plant macrofossil data suggest that generally the current habitat types, dry strings, and intermediate lawns had prevailed at the coring locations throughout the deposition history and over the studied time period, which enabled us to test the differences of habitat-specific C accumulation drivers. In line with our expectations, as revealed by the partial correlation and PLS-PM analyses, the causal links between reconstructed peatland WTD, plant functional types, peat properties, and C accumulation varied between the two habitats.

Significant effects on C accumulation were found for lawn records. The positive effect of higher *Sphagnum* abundance (NMDS axis 1) on C accumulation suggests that *Sphagnum* domination promotes C accumulation.



**Figure 4.** Partial least squares path modeling showing the direct and indirect effects of water-table depth (WTD), peat properties (Peat), and plant functional types (Plant) on non-autogenic carbon accumulation rate (CAR). (a) All records, (b) dry strings, (c) intermediate lawns, and (d) significant effects of factors on CAR for lawns. Peat includes bulk density, N content, and C/N ratio as formation variables. Plant represents the sample scores of the first axis of NMDS conducted for the plant macrofossil data, reflecting *Sphagnum*-other plants gradients (positive-negative scores). Larger WTD values mean drier conditions. Blue and red arrows indicate significance ( $p < 0.05$ ) of the positive and negative relationship, respectively. Dot lines indicate non-significant relationships. The numbers on the arrows reflect the strength of the relationships.

Corresponding with this study, previous studies have reported recent changes in peat C accumulation and attributed it to the changes in *Sphagnum* expansion (Loisel & Yu, 2013; Magnan et al., 2022; Piilo et al., 2022; Yang et al., 2023). This might largely be due to the higher decay resistance of the *Sphagnum* mosses than vascular plant litter (Lang et al., 2009). This explanation is further supported by the detected negative effect of peat properties on plant functional type in the PLS-PM results of the lawn records. In other words, the results suggest higher C/N ratios that reflect low decomposition levels correspond with a higher *Sphagnum* proportion. In addition, *Sphagnum* mosses could promote higher acidity conditions (Mandal et al., 2018), which could also restrict peat decomposition (Rousk et al., 2010).

Peatland WTD is suggested to be a strong driver on vegetation composition, biomass production, net ecosystem exchange, and thus vegetation-related C balance (Evans et al., 2021; Laine et al., 2019; Mäkiranta et al., 2018). Consistently, as in our PLS-PM for lawns that implied significant drivers on C accumulation, drying could directly decrease C accumulation and indirectly limit C accumulation by decreasing *Sphagnum* abundances. However, these two processes may exhibit temporal decoupling due to the inherent inertia of peatland ecosystems. For instance, vegetation communities demonstrate considerable resilience to WTD fluctuations, which could result in delayed abundance responses that lag behind hydrological modifications (Waddington et al., 2015). While it is predicted that the suitable habitat and abundance of *Sphagnum* mosses will increase extensively in peatlands located north of 50°N under a warmer climate (Ma et al., 2022), and recent *Sphagnum* establishment has been observed in high-latitude regions (e.g., Cleary et al., 2024; Juselius et al., 2022), our results indicate that hydrology could be a limiting factor for *Sphagnum* expansion at lawns in a warming climate, particularly in non-permafrost peatlands. This might imply a nonlinear impact of peatland hydrology on *Sphagnum* expansion/growth. The detected negative effect of drying on C accumulation has been previously indicated from two other peatlands in Southern Finland (Zhang et al., 2020). Even so, if investigating records from larger temperature gradients, a stronger temperature impact on C accumulation might be expected (e.g., Gallego-Sala et al., 2018).

Our study is the first attempt that revealed the two mechanisms of WTD impacting on past C accumulation simultaneously, even though similar causality through which WTD concurrently controls C dynamics have been recognized previously for modern C cycling (Kokkonen et al., 2022). Concerning peat addition and decomposition processes, the peat addition rates for top layers (*Sphagnum*-dominated lawns: 174.2 and 181.9 g m<sup>-2</sup> yr<sup>-1</sup>) detected in this study are relatively similar across different locations. In contrast, they showed larger variations (*Sphagnum*-dominated low hummocks and high lawns: 139.4–472.5 g m<sup>-2</sup> yr<sup>-1</sup>) in Southern Finland (Zhang et al., 2020). Notably, rates exceeding 500 g m<sup>-2</sup> yr<sup>-1</sup> in *Sphagnum*-dominated locations were reported in central Alaska (Loisel & Yu, 2013). Among those records, peat decay coefficients in central Alaska (0.02–0.04 years<sup>-1</sup>) are several times higher than most Finnish records (0.003–0.01 years<sup>-1</sup>), but comparable to one Finnish record (0.022 years<sup>-1</sup>) associated with the highest peat addition rate (472.5 g m<sup>-2</sup> yr<sup>-1</sup>). In general, higher peat addition rates are coupled with high decay coefficients, but both parameters could vary regionally and likely at the habitat level (Zhang et al., 2018), highlighting the functional complexity of peatlands. Nevertheless, current modeling studies suggest drying-induced decreases in C accumulation might generally work for northern peatlands (Chaudhary et al., 2020; Qiu et al., 2020), which highlights the vulnerability of peatland C sink capacity in a drying and warming climate.

Unlike lawn records, we did not detect any significant main drivers of carbon accumulation for dry strings, even though similar correlations between the studied environmental factors were derived for both habitats. Our 60-cm string peat profiles did not reach the current water table level, and the plant macrofossil analysis revealed a long-term shrub-dominated vegetation history at the coring locations. This suggests that the water table might not be an active control on peat/C accumulation for these habitats, as shrubs can survive with limited water (e.g., Kokkonen et al., 2019), which is also indicated in our PLS-PM for dry strings. Higher gross ecosystem productivity of shrubs allowed the ongoing peat accumulation at these dry strings (Ratcliffe et al., 2019). Similarly, a weak correlation between ecosystem respiration and water table was reported in a dry bog with water table varying between 30 and 75 cm below the hummock tops (Lafleur et al., 2005). Moreover, a previous study did not find any relationship between C accumulation and WTD for habitats wetter than the lawn habitats studied here (Zhang et al., 2020). Thus, it is possible that other variables, which were not studied here, such as microbial factors (Buttler et al., 2023; Wang et al., 2021), play a more important role in C accumulation at extreme ends of the hydrological gradient. One possible assumption of C accumulation drivers in dry strings is that the microbial biomass representing decomposition ability might be more important than the variables studied here. We therefore tested this

assumption for dry strings using testate amoebae concentration data in the PLS-PM, yet a non-significant ( $p = 0.09$ ) correlation of  $-0.21$  with C accumulation emerged. As testate amoebae are not decomposers themselves but harvest decomposing fungi and bacteria (Jassey et al., 2013), further analysis using enlarged microbiological approaches to quantify the whole peat microbial biomass is needed to better test this assumption.

Nevertheless, our study suggested that C accumulation responses to environmental changes differ between peatland habitats. Peatlands are complex ecosystems that have distinctly variable features. Many predictive studies concerning future peatland C sink capacity have been carried out in a rough spatial resolution, sometimes using single record per site (Gallego-Sala et al., 2018; Qiu et al., 2022). It is evident that these cannot capture the heterogeneity of peatland C dynamics (Kou et al., 2022). Recent studies have shown the highly sensitive nature of peatland vegetation and water table to environmental changes (Kolari et al., 2021; Ma et al., 2022; Zhang et al., 2022). Currently, many peatland processes, such as vegetation and peat property changes, cannot be appropriately simulated so far by large-scale peatland models (Qiu et al., 2022). Therefore, most of the Earth system models have not incorporated peatlands as an active feedback agent (Canadell et al., 2021), which to some extent has restricted accurate estimations of the global terrestrial carbon budget (Todd-Brown et al., 2013). Yet, our results show complicated responses of peatland carbon accumulation to environmental changes even in a habitat scale, making peatland modeling even more challenging. More efforts on detecting controlling factors on C dynamics for typical peatland habitats, and quantifying future peatland habitat succession pathways are needed in order to accurately predict their future C dynamics and mitigation potential.

## 5. Conclusions

In this study, we investigated the causal links between environmental factors and peat C accumulation for different peatland habitats. We found that while various environment variables impact peatland habitat dynamics, and also C accumulation, the causal relationships varied between dry strings and intermediate lawns. WTD could impact peat properties and plant functional type compositions. However, significant control of these factors on C accumulation was detected only for lawns. Specifically, plant functional type and WTD were stronger controls on C accumulation than peat properties. Our findings imply that well-established knowledge of peatland successional features and related C processes could promote development of more accurate C sink capacity prediction models for the future.

## Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

## Data Availability Statement

The data that support the findings of this study are available on Figshare via <https://doi.org/10.6084/m9.figshare.27907830> (Zhang, 2025).

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