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RESEARCH ARTICLE

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A deepened water table increases the vulnerability of peat mosses to periodic drought

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Abstract

1. Here we address the combined impact of multiple stressors that are becoming more common with climate change. To study the combined effects of a lower water table (WT) and increased frequency of drought periods on the resistance and resilience of peatlands, we conducted a mesocosm experiment. This study evaluated how the photosynthesis of lawn *Sphagnum* mosses responds to and recovers from an experimental periodic drought after exposure to the stresses of a deep or deepened WT (naturally dry and 17-year-long water level drawdown [WLD] in fen and bog environments).

2. We aimed to quantify if deep WTs (1) support acclimation to drought, or (2) increase the base-level physiological stress of mosses or (3) exacerbate the impact of periodic drought.

3. There was no evidence of acclimation in mosses from drier environments; periodic drought decreased the photosynthesis of all *Sphagnum* species studied. WLD decreased the photosynthesis of bog-originating mosses prior to periodic drought, indicating that these mosses were stressed by the hydrological change. Deep WTs exacerbated *Sphagnum* vulnerability to periodic drought, indicating that the combination of drying habitats and increasing frequency of periodic drought could lead to a rapid transition in lawn vegetation. Water-retaining traits may increase *Sphagnum* resilience to periodic drought. Large capitula size was associated with a higher resistance; the bog originating species studied here lacked large capitula or dense carpet structure and were more vulnerable to drought than the larger fen originating species. Consequently, lawns in bogs may become threatened.

4. Recovery after rewetting was significant for all mosses, but none completely recovered within 3 weeks. The most drought-resilient species had fen origin, indicating that fens are less likely to undergo a sudden transition due to periodic drought.

5. *Synthesis*: Water level drawdown associated with climate change increases the sensitivity of *Sphagnum* mosses to periods of drought and moves them closer to

their tipping point as species on the edge of their ecological envelope rapidly shut down photosynthesis and recover poorly.

KEYWORDS
drought stress, functional traits, global change ecology, peatland, photosynthesis, plant-climate interactions, recovery, resilience, *Sphagnum* moss, water table change

1 | INTRODUCTION

Peatlands store up to one third of soil carbon globally (Ratcliffe et al., 2021; Yu et al., 2011) and the fate of this carbon is of great concern in the predicted future warmer climate with increased frequency of extreme climatic events. Due to warming-induced increases in evapotranspiration, boreal peatlands are already facing dryer surface conditions (Gong et al., 2012; Gorham, 1991; Helbig et al., 2020; Rinne et al., 2020; Roulet et al., 1992; Swindles et al., 2019). Additionally, precipitation patterns are expected to become more extreme and growing-season droughts are occurring more frequently (Donat et al., 2016; IPCC, 2023). As hydrology is the major control of peatland structure and function, such changes are likely to alter peatland vegetation, particularly through mosses from the genus *Sphagnum* that are a fundamental part of most peatland types (Gunnarsson, 2005; Jassey & Signarbieux, 2019; Kokkonen et al., 2019b; Korrensalo et al., 2017; Kuiper et al., 2014; Laine, Lindholm, et al., 2021; McNeil & Waddington, 2003; Radu, 2017; Strack & Price, 2009). Pivotal ecosystem shifts where ecosystems have moved to a new stable state due to climate change are already documented in marine and terrestrial environments (Hoegh-Guldberg & Bruno, 2010; Parmesan & Yohe, 2003) and peatlands are also likely to reach a tipping point and undergo significant changes in structure and function.

Sphagnum mosses are a particularly important species group in boreal peatlands where they cover an estimated $1.5 \times 10^6 \, km^2$ (Rydin, Jeglum, et al., 2006). These mosses form extensive carpets and, despite having lower photosynthetic capacity than vascular plants, account for a significant proportion of the carbon sequestered in these systems (Korrensalo et al., 2016; Martin & Adamson, 2001). Lacking a root system or stomatal control, mosses are forced to develop alternative mechanisms to withstand drought; terrestrial and epiphytic mosses are adapted to frequently undergoing drying and re-wetting cycles. *Sphagnum* species do not have a well-developed mechanism to tolerate extreme fluctuations and instead, tend to avoid drought by inhabiting moist environments such as peatlands (Gerdol et al., 1996; Schipperges & Rydin, 1998; Titus & Wagner, 1984; Winnicka et al., 2018). Therefore, *Sphagnum* productivity is strongly dependent on water availability (Graham & Vitt, 2016; Granath et al., 2010; McNeil & Waddington, 2003; Murray et al., 1989) and drought-induced reduction of peatland CO_2 uptake is predominantly related to the reduced *Sphagnum* photosynthesis (Gerdol et al., 1996; Kuiper et al., 2014; Schipperges & Rydin, 1998; Silvola, 1991; Titus & Wagner, 1984; Winnicka et al., 2018).

Very few *Sphagnum* species can survive complete desiccation (where cell turgor is lost) and recover their photosynthetic function (Hájek & Vicherová, 2014; Sagot & Rochefort, 1996; Schipperges & Rydin, 1998). To avoid desiccation, *Sphagnum* species have developed drought avoidance traits that are related to the moss carpet structure such as density (Gong et al., 2020; Laine, Lindholm, et al., 2021) and the ability of individual mosses to store water between their branches and leaves, and within specialized hyaline cells (Bengtsson et al., 2020; Jassey & Signarbieux, 2019; Laine, Lindholm, et al., 2021; Laing et al., 2014). While trait differences between species are well known, the within-species trait plasticity and capacity for acclimation to changing water availability in short (Hájek & Beckett, 2008; Jassey & Signarbieux, 2019; Silvola, 1991) and longer timeframes (Laine, Korrensalo, et al., 2021) are far less known. Lawn mosses are most likely to be forced to acclimate to periodic drought as they lack the moisture-conserving dense structure of hummocks and the water availability in hollows (Hájek & Vicherová, 2014).

Climate change is projected to have a two-fold impact on peatland hydrology: first, by the gradual drying caused by increased evapotranspiration over a longer growing season, and second by the increasing frequency and severity of extreme climate events, such as droughts during the summers 2018 and 2021 in Europe (FMI, 2021; Rinne et al., 2020). There are three alternative hypotheses about how peatland ecosystems could potentially respond to drying. First, gradual drying may allow mosses to acclimate through structural changes in individuals or as a carpet and thereby increase their ability to avoid desiccation during drought events (Hájek & Vicherová, 2014). Second, long-term gradual drying could cause lower photosynthesis rates by stressing mosses towards the edge of their ecological envelope even without periodic drought. Third, exposure to long-term deep or deepened water tables may increase the vulnerability of Sphagna as the stress of dry habitats may have a cumulative impact when combined with periodic drought. This would increase the ecosystem's vulnerability to extreme events by moving the ecosystem closer to its tipping point where its structure and function irreversibly change (Köster et al., 2023; Thormann et al., 1997).

While there are contradicting results supporting all these hypotheses (Clymo, 1973; Hájek & Beckett, 2008; Kokkonen et al., 2022; Luken, 1985; Robroek et al., 2009; Rydin, 1985; Rydin & McDonald, 1985; Titus & Wagner, 1984; Winnicka et al., 2018, 2020), previous studies suggest that the response pathway to drought depends on the peatland site type. Bogs that receive their moisture and nutrients solely from rainwater show little response in their species composition to long-term drying (Kokkonen et al., 2019b). More

fertile fens may follow the second pathway and go through extensive species turnover after water level drawdown (WLD) that reduces the inflow of minerogenic groundwater (Kokkonen et al., 2019b). However, none of the studies so far has directly addressed the combined pressures of long-term WLD and periodic drought.

In this study, we aimed to address the three contrasting hypotheses namely, deep and deepened WTs (1) diminish the impact of periodic drought suggesting acclimation, (2) increase the base-level physiological stress seen as lower photosynthesis, which is further decreased by a drought period (i.e. an additive effect) and (3) exacerbate the impact of the periodic drought due to accumulate d stress.

As the previous studies indicate fens and bogs responding differently to hydrological changes, we test the three contrasting hypotheses on lawn mosses originating from the two types of peatlands, fens and bogs.

We apply traits related to water holding capacity to better understand the underlying mechanisms supporting response to and recovery from drought.

Our focus was on the response to drought (resistance) and recovery of photosynthesis after drought (resilience). We collected mesocosms for an experimental study in a greenhouse from three different WT histories to quantify the impact of WT history on the response of *Sphagnum* to periodic drought.

2 | MATERIALS AND METHODS

2.1 | Source peatlands and mesocosm collection

To get *Sphagnum* samples with different water level histories, we collected mesocosms from Lakkasuo peatland complex located in Southern Finland (61°47′ N; 24°18′ E), which contains both natural and experimental spatial variation in water level. Lakkasuo peatland complex is approximately 130 ha in size with nutrient status varying from fen (minerogenic) to bog (ombrogenic) areas as well as natural variation in WT, resulting in wet, open peatland habitats as well as drier habitats with naturally generated tree stands (Table S1). In both the wet open fen and bog areas within Lakkasuo, a WLD experiment was established in 2000 (see

Kokkonen et al., 2019b). Ditching was installed in 2001 and has been intermittently maintained since, causing a moderate WLD of 10 to 15 cm (Table S1; Kokkonen et al., 2019b), as well as tree canopy development on the fen but not on the bog. Permission for this field experiment in Lakkasuo was granted to Hyytiälä Forest Research Station and additional permission was not required for this research.

In this study, we collected a total of 96 cylindrical moss surface samples with a diameter of 15 cm and a depth of 10 cm (mesocosm), originating from six subsites. Within the origin peatland types, fen and bog (site), we collected mosses from three subsites differing in their WT history: (1) subjected to shallow WT (undrained wet open, "wet"), (2) subjected to 17 years of continuous moderate WLD (experimentally drained, "WLD") and (3) subjected to naturally deep WT (undrained treed, "dry"), resulting in 16 mesocosms per subsite. For the experimental WLD, we assumed that 17 years is long enough to allow morphological adaptation of *Sphagnum* species. WT history thus integrates the impact of WT on species composition as well as on physiological and morphological state of the mosses.

At each subsite, we collected two carpet-forming *Sphagnum* species, with eight replicates each. One species was common within either the fen (*Sphagnum recurvum* coll.) or the bog (*Sphagnum balticum*), while the second was a dominant species characteristic to each subsite. Altogether, seven unique species were used in the experiment (Table 1). We collected the mesocosms into PVC cylinders in early May 2018, carefully preserving the natural moss carpet structure and density. Mesocosms were chosen to have at least 90% cover of the target species. Mesocosms were stored for 2 months at 6°C over the exceptionally hot summer of 2018 until the initiation of the experiment in August of that year. This storage period may have had an impact on the absolute function of the Sphagna, but we focussed on the relative changes in photosynthesis resulting from a drought treatment, giving a valid comparison between control and treated mesocosms.

2.2 | Experimental design

Mesocosms were placed in the greenhouse in WT-controlled cylinders constructed following the design outlined in Nijp et al. (2014;

TABLE 1 Mesocosm source areas with mean (and range) water table (WT) on lawn habitats in 2016 and the two sampled moss species for each subsite. From each subsite, we selected a common and characteristic species. Common species was defined as a widely present species on lawn surfaces across each particular peatland origin, that is generalist. The characteristic species was a lawn species distinctively widespread on that individual subsite but not necessarily on others, that is specialist. Note that *Sphagnum recurvum* coll. includes closely related species *Sphagnum fallax* and *Sphagnum flexuosum*.

Subsite	2016 WT mean (and range; cm)	Common species	Characteristic species
Wet fen	−7 (+7 to −19)	*S. recurvum coll.*	*Sphagnum teres*
Dry fen	−18 (−8 to −36)	*S. recurvum coll.*	*Sphagnum divinum*
WLD fen	−13 (−1.8 to −25)	*S. recurvum coll.*	*S. divinum*
Wet bog	−4 (+6.8 to −17)	*Sphagnum balticum*	*Sphagnum rubellum*
Dry bog	−16 (−5 to −31)	*S. balticum*	*Sphagnum angustifolium*
WLD Bog	−4 (+4 to −17)	*S. balticum*	*Sphagnum tenellum*

Figure 1). In this design, the WT is controlled by reservoirs fitted with overflow vents set to a pre-determined height so that a connection is maintained between the mesocosm and the reservoirs. Reservoirs are refilled from above by Mariotte bottles to maintain a constant WT and replace evaporative losses from the mesocosms. Overflow vents in the control reservoirs allow excess water to escape after precipitation, which prevents flooding and keeps mesocosm WTs at set levels.

Prior to placement in the greenhouse on 14 August 2018, all vascular plants were clipped from the moss surface, and some peat was removed from the bottom of each mesocosm to ensure a consistent sample depth of approximately 8 cm. WT depth was set to 10 cm below the moss surface to replicate the WT at the field source sites (Kokkonen et al., 2019b), which was within the optimum range for the Sphagna studied (Laine et al., 2019). The chemistry of the supplied groundwater was adjusted to match the source site groundwater (Tables S2 and S3). Precipitation was added in the form of weekly overhead watering (18.1 mm or 320 mL per mesocosm based on the 30-year average growing season monthly rainfall at Hyytiälä weather station; FMI, 2021) during the acclimatization and recovery periods. During the drought period only the control mesocosms received precipitation. Mesocosms were left to acclimatize to greenhouse conditions for 7 weeks (Blodau et al., 2004; Nijp et al., 2014), after which the drought treatment was initiated on 1 October. Greenhouse environmental monitoring is detailed in the Supporting Information.

Of the eight mesocosms from each origin peatland type × WT history × species combination, half were designated to drought treatment, where the WT was lowered to 30 cm below the surface based on an observed large-scale drought experienced in 2018 by North European peatlands (Rinne et al., 2020) while the other half were left as a control with WT at 10 cm below surface. For comparison, during the drought of 2018, the WT in Lakkasuo fen dropped ca. 23 cm below pre-drought levels and in the bog a ca. 33 cm drop was observed (unpublished data). The drought treatment was maintained for 43 days, which exceeds the longest rainless period in the area since 1986, that is 36 days. This is a reasonable period assuming increased extremes in precipitation from climate change (Donat et al., 2016) and is based on historical climate records at Hyytiälä Forestry Station approximately 10 km North from Lakkasuo (FMI, 2021; Table S4). After this, the three-week recovery period was initiated, and the WT of the drought mesocosms was readjusted back to 10 cm below the surface and the mesocosms were moistened using the precipitation treatment described above. Moisture within the moss stand in each mesocosm was measured using cigarette filters of a known mass made of cellulose acetate buried to the depth of ca. 5 cm and reweighed at the end of the drought and after 3 weeks of recovery. See Table 2 for the detailed course of the experiment.

2.3 | Photosynthesis measurements

Photosynthesis was measured from the moss mesocosms using the closed chamber method which utilized an infrared CO_2 analyser (EGM-5, PP Systems) attached to an airtight glass chamber equipped with an internal light source (Figure S2). Five campaigns were completed during the experiment, namely before the initiation of the drought period, 6 weeks after the start of the drought period, and 1, 2 and 3 weeks after the start of the recovery period (Table 2).

FIGURE 1 (a) Mesocosms in the water table (WT) control cylinders constructed following the design outlined in Nijp et al. (2014) with (b) WLD of 20 cm introduced by lowering the position of control reservoirs. Mesocosms were organized into four rows containing a complete set of experimental variables (treatment × species × origin peatland type × WT history) and four complete blocks along the length of the table.

TABLE 2 Timeline of the experiment, detailing the timing of the carbon dioxide flux measurement campaigns and the number of mesocosms studied during each campaign. Note that untreated control mesocosms were not measured during campaigns three and four.

Campaign	Dates	# weeks since start	# mesocosms	Experimental stage
I	18.9.–28.9.	6	96	After 6 weeks of acclimatization
II	5.11.–12.11.	12	96	After 6 weeks of drought
III	19.11.–21.11.	14	48	After 1 week of recovery
IV	26.11.–29.11.	15	48	After 2 weeks of recovery
V	7.12.–13.12.	16	96	After 3 weeks of recovery

To quantify the photosynthetic light response and obtain light response curve parameters, CO_2 flux (i.e. net ecosystem exchange) of each mesocosm was measured at four different PPFD (photosynthetic photon flux density, $\mu mol\,m^{-2}\,s^{-1}$) levels: high (PPFD 1000–800), medium (PPFD 600–300), low (PPFD 100–20) and darkness (PPFD 0) to obtain respiration rate. Photosynthesis rates were calculated from these measurements using the hyperbolic light response curve (Equation 1) as part of non-linear mixed-effects models described in the data analysis section below. The different light levels were monitored using a light sensor (Apogee Sunlight Quantum Sensor, PP systems) placed level with the moss surface inside the chamber (Figure S2). A blackout curtain was used for dark measurements. Photosynthetic processes were allowed to adapt for 1.5–5 min at each light level, and then the chamber was vented before the measurement began. During the 1.25–3 min measurement, the CO_2 concentration and PPFD were recorded every 15 s. The CO_2 flux (mg CO_2 $m^{-2}\,day^{-1}$) at each of the four light levels was calculated from the linear change in the CO_2 concentration in the chamber headspace as a function of time, accounting for the chamber headspace volume and mesocosm surface area as well as the mean chamber air temperature during the measurement. The photosynthesis rates measured prior to the drought treatment fell within the range recorded for *Sphagnum* mosses (Bengtsson et al., 2016; Gerdol et al., 1996; Granath et al., 2009; Hájek et al., 2009; Harley et al., 1989; Kangas et al., 2014; Korrensalo et al., 2016; Laine et al., 2016; Nijp et al., 2015; Rydin & McDonald, 1985; Schipperges & Rydin, 1998; Tuittila et al., 2004). Over the course of the experiment, both photosynthesis (P_{max}) and respiration (R) showed a slow but significant decrease, irrespective of drought treatment along the number of days since the beginning of the experiment, similarly to daily PAR and ambient temperature (Figure 2, Table SM1).

2.4 | Trait measurements

To explain the differences in the response to drought, we measured morphological functional traits of the mosses. Non-destructive measurements were done before initiating the drought period (campaign one), after 6 weeks of drought (campaign 2), and after 3 weeks of recovery (campaign 5). These traits included moss density (CapDen, number of capitula cm^{-2}, measured as the number of capitula in three $2\times2\,cm$ squares per mesocosm) and capitulum diameter (CapDia, mm, an average of 10 randomly selected capitula). Height growth (Hgrow,

mm day^{-1}) was measured with the cranked wire method from all mesocosms at the end of the drought and at the end of the recovery period and converted to biomass growth using stem dry mass values (Laine, Korrensalo, et al., 2021). Traits that required destructive sampling were measured only at the end of the experiment. These traits were capitulum dry weight (CapMass, g, measured as the average oven-dry mass of several capitula) and capitulum N and C content (CapN and CapC, $g\,kg^{-1}$). From the measured traits, we further calculated the photosynthetic moss area (PhotoArea, $mm^2\,cm^{-2}$, as CapDen multiplied by CapDia) and photosynthetic biomass (PhotoMass, $g\,cm^{-2}$ as CapDen multiplied by CapMass) within each mesocosm. Change in moisture was quantified as the difference in average moisture content of cigarette filters between the drought and control mesocosms (MoistDry) of a given species, origin peatland type, and WT history. The relative moisture at the end of the recovery period (MoistRec) was similarly calculated as the difference between the control and drought-recovered mesocosms at the end of the recovery period.

During the experiment, the species changed structure, developing larger capitula with a lower density (Figure S5) irrespective of drought treatment or species, resulting in lower CapCount, CapDia, CapMass, PhotoArea and PhotoBio (Figure S5, Table S6). None of the measured traits were significantly impacted by the experimental drought treatment (Table S6).

2.5 | Data analysis

To investigate the impact that WT history (naturally deep or artificially deepened) had on the drought response and recovery of *Sphagnum* moss photosynthesis, we applied non-linear mixed-effects models. With the same model we tested if the moss origin peatland type (fen or bog) affected the response. Further on, we tested if the response was related to moss stand traits. To build models, we used the hyperbolic light response curve of photosynthesis (Smolander & Lappi, 1985):

$$A_{ijk} = R_{jk} + \frac{Pmax_{jk}\,PPFD_{ijk}}{\alpha_{jk} + PPFD_{ijk}} + e_{ijk} \qquad (1)$$

where A_{kji} is the observed net CO_2 exchange ($mg\,CO_2\,m^{-2}\,day^{-1}$) and the predictor $PPFD_{ijk}$ is the photosynthetic photon flux density ($\mu mol\,m^{-2}\,s^{-1}$) for measurement i in measurement round j on mesocosm k. The parameters to be estimated were the maximum rate of light-saturated net photosynthesis ($Pmax_{jk}$), the initial slope of the response curve indicating photosynthetic rate increase (α_{jk}) and dark respiration
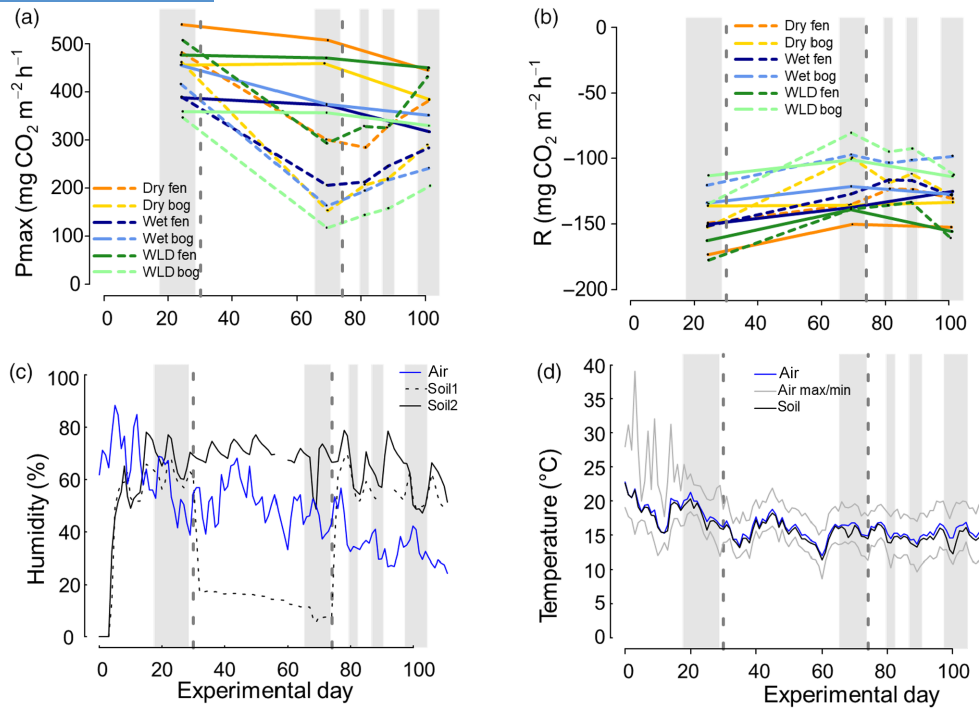
FIGURE 2 (a) Modelled maximum photosynthesis (P_{max}), (b) respiration (R) in all origin peatland type×water table (WT) history combinations, and (c and d) greenhouse environment over the course of the experiment. P_{max} (a) and R (b) values were estimated using the experimental design based non-linear mixed-effects model (Table SM1) for each mesocosm, then averaged. Each line represents the CO_2 flux values of two species (n=4 per species) at each measurement campaign. Mesocosms subjected to periodic drought (dashed line) were measured five times: pre-drought, peak drought, then weekly during a tree week recovery period. Control mesocosms without periodic drought (solid lines) were measured three times: pre-drought, peak drought and after 3 weeks of recovery. Each source subsite (origin peatland type×WT history combination) is represented by a different colour. Line type separates control from drought-treated mesocosms. (c) Air humidity was measured at the mesocosm level with two DHT22 sensors, the values of which were averaged. Soil moisture was measured using two Pino-tech Soilwatch 10 sensors, one in each of a drought-treated and control mesocosm. Soil moisture sensors were not calibrated for peat soil but describe the temporal variation. (d) Air temperatures were recorded at the mesocosm level with two DHT22 sensors, the values of which were averaged. Soil temperatures were measured using DS18B20 sensors in two mesocosms and the recorded values of these two sensors were also averaged. The chamber measurement campaigns (Table 2) are marked with grey shading, and the initiation and end of the drought period are marked with a grey dashed line.

(R_{jk}). The residual error (e_{ijk}) was normally distributed with mean zero and constant variance. Parameters $Pmax_{jk}$ and R_{jk} were written as linear functions of fixed predictors that characterized the effects of drought on photosynthesis and the recovery after the drought, while α_{jk} was assumed to be constant and any variation was accounted for in the random part of the model. The submodels for $Pmax_{jk}$ and R_{jk} were:

$$Pmax_{jk} = PmaxC_{jk} + PmaxDryEff_{jk} + PmaxRecEff_{jk}{}^* Recovery_{jk}{}^* RecovDate_{jk} \quad (2)$$

$$R_{jk} = RC_{jk} + RdryEff_{jk} + RRecEff_{jk}{}^* Recovery_{jk}{}^* RecovDate_{jk} \quad (3)$$

where $PmaxC_{jk}$ and RC_{jk} were the P_{max} and R in the mesocosms in control state, that is without drought treatment, $PmaxDryEff_{jk}$ and $RdryEff_{jk}$ were the impact of drought treatment on P_{max} and R, respectively, while $PmaxRecEff_{jk}$ and $RRecEff_{jk}$ were the daily recovery rate of P_{max} and R after the drought when WT had been returned to the pre-drought level. $RecovDate_{jk}$ indicates the number of days since the drought treatment had ended and $Recovery_{jk}$ is a dummy variable that was assigned a value of 1 in the mesocosms designated to the drought treatment in the measurement rounds after the WT

had been returned to the pre-drought level. The first six parameters ($PmaxC_{jk}$, RC_{jk}, $PmaxDryEff_{jk}$, $RdryEff_{jk}$, $PmaxRecEff_{jk}$, $RRecEff_{jk}$) were further written as linear functions of fixed predictors.

We fitted two types of such models: the first one with predictors based on the experimental design (Modelling supplement, Equations 1–6) and the second one with trait-related mechanisms (Modelling supplement, Equation 7–12). In both model fittings, $PmaxDryEff_{jk}$, and $RdryEff_{jk}$ had as a fixed predictor the treatment (a dummy variable of whether the mesocosm was designated to the drought or control treatment), and the impact of other fixed predictors were expressed as an interaction with this parameter. When focusing on the experimental design, we included origin peatland type, WT history, and their interaction as fixed predictors interacting with $PmaxDryEff_{jk}$, and $RdryEff_{jk}$. We aimed to quantify how mosses originating from different levels of exposure to permanently lowered WT and from different peatland types respond to and recover from experimental seasonal drought. When focussing on the mechanisms of drought impact and recovery, we took the traits of the mesocosm moss stand as potential fixed predictors interacting with $PmaxDryEff_{jk}$, and $RdryEff_{jk}$. We aimed to quantify which properties of the moss stand

significantly predict the response to drought and recovery after it. We added fixed predictors one by one and tested after each new addition whether the new model was significantly better than the previous simpler one using marginal ANOVA test and AIC values of the alternative models. The traits measured from the mesocosms as well as their abbreviations are described in the previous paragraph. The number of days since the beginning of the greenhouse experiment (experiment date) was an additional potential fixed predictor for parameters $PmaxC_{jk}$ and RC_{jk} to account for the potential change in the overall level of photosynthesis due to the greenhouse conditions. Species identity was originally listed as a potential fixed predictor but had to be excluded due to convergence problems, therefore species-specific differences were looked at outside the model.

Random effects included in the model were mesocosm identity and light level measurements repeated within a campaign to account for nested repeated measures. Mesocosm location in a row or block were excluded from the model as non-significant random effects. Residuals of both models were tested and met the assumptions of normality and equal variance.

To address relative changes in P_{max} we calculated the resistance (i.e. drought impact), recovery and resilience of mesocosm P_{max} using the definitions of Van Ruijven and Berendse (2010) as follows:

$$\text{Resistance} = \left[P_{max}(\text{pre}) - P_{max}\text{end} \right] / P_{max}(\text{pre}),$$

$$\text{Recovery} = \left[P_{max}(\text{rec}) - P_{max}\text{end} \right] / P_{max}(\text{end}),$$

$$\text{Resilience} = \left[P_{max}(\text{pre}) - P_{max}\text{rec} \right] / P_{max}(\text{pre}),$$

where $P_{max}(\text{pre})$ is the P_{max} measured prior to drought in campaign one, $P_{max}(\text{end})$ is the P_{max} at the end, that is maximum, of the drought measured in campaign two and $P_{max}(\text{rec})$ is the P_{max} after 3 weeks of recovery during campaign five.

To assess the impact that exposure to permanently lowered WT (deep or deepened WTs) and the species identity had on resistance, recovery and resilience parameters, we used linear mixed-effects models (R nlme package, lme function). These interactions were tested separately because species could not be fitted in the structure of the non-linear mixed-effects models. Similarly, the impact of species, WT history, measurement campaign and drought treatment on measured moss traits was evaluated using linear mixed-effects models. The random effect in these models was Mesocosm ID. Residuals were checked using the Kolmogorov–Smirnov test for normality and Levene's test for equal variance.

3 | RESULTS

3.1 | Impact of history with deep or deepened WT on moss drought response

Before the periodic drought, photosynthesis was impacted by WT history and was also affected by the origin peatland type (Table SM2). The photosynthesis of fen-originating mosses was
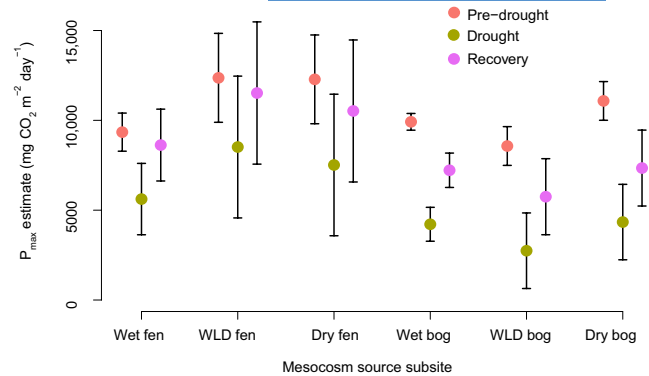

FIGURE 3 Maximal photosynthesis (Pmax) as impacted by the drought treatment, origin peatland type (fen or bog) and water table history (wet, WLD or naturally dry) based on the non-linear mixed-effects model (the experimental design model) of net carbon dioxide exchange. Values and standard errors were calculated from estimated effects found by the model. Each subsite (water table history * origin peatland type) contains 16 samples, half of which were exposed to periodic drought then rewetted. Pre-drought estimates were calculated using photosynthesis measured in all mesocosms ($n = 96$) prior to periodic drought being applied. Drought estimates are based on photosynthesis measurements conducted after 43 days of ecohydrological drought on half the mesocosms. Recovery estimates were calculated using measurements taken on drought-treated mesocosms after 3 weeks of rewetting. Species included in each subsite are listed in Table 1.

higher with a history of deep or deepened WT (naturally dry and WLD). In contrast, mosses with bog-origin had higher photosynthesis when they originated from the wet subsite or naturally dry subsite than mosses subjected to experimental WLD (Figures 2a and 3).

Long term exposure to deep water tables made photosynthesis of *Sphagnum* mosses more sensitive to drought (Figure 3, Table SM1). The mixed-effects model based on experimental design showed that drought decreased photosynthesis for all species and subsites (Figure 2a), and the extent depended on WT history. Photosynthesis dropped more in mesocosms from naturally dry sites than those from WLD and naturally wet areas (Figures 2a and 3). Respiration slightly decreased due to the drought, but the impact was not significant nor was it impacted by WT history (Figure 3, Table SM1).

After the drought period ended and WT was adjusted back to the original level, the P_{max} of all mosses gradually recovered at a constant rate of $143\,\text{mg}\,CO_2\,m^{-2}\,\text{day}^{-1}$ (Table SM1). The recovery of respiration was not as clear. The experimental model did not find respiration to recover significantly (Table SM1), however, respiration had a significant recovery rate of $10\,\text{mg}\,CO_2\,m^{-2}\,\text{day}^{-1}$ according to the trait model (Table SM3).

3.2 | Differences between fen- and bog-originating mosses in their response to periodic drought

The origin peatland type did not impact pre-drought (and general level of) photosynthesis of moss mesocosm (Table SM2), but there

was a significant interaction between the origin peatland type and WT history (Table SM2). Before drought, P_{max} was highest for the mosses originating from naturally dry conditions in the fen site (dry-fen) and lowest for the mosses originating from the WLD in the bog site (bog-WLD; Figure 3, Table SM1, Figure 2a). Respiration before drought was affected by origin peatland type (Table SM2) and was altogether higher for fen-originating mesocosms than for the bog-originating mesocosms.

The origin peatland type impacted drought sensitivity of the mosses (Figure 3, Table SM1); the drop in P_{max} due to drought was stronger for bog-originating species than fen-originating species (Figure 3, Table SM1). However, the impact of origin peatland type on P_{max} parameters is confounded as no species overlapped between the origin peatland types.

3.3 | Traits moderating the moss drought response

Only one moss trait clearly impacted the photosynthetic response to periodic drought, namely capitula mass, which had a significant positive impact on P_{max} during drought (Table SM3). Likewise, there was only one significant predictor of respiration response to drought; high

moisture at the end of the drought treatment (capability of retaining moisture MoistDry, Table SM3) decreased the impact of drought on respiration. Maximum photosynthesis prior to drought (and in general throughout the experiment) was significantly increased by high photosynthetic area and capitulum nitrogen content (PhotoArea and CapN, Table SM3). High capitula mass significantly increased respiration prior to drought (and in general) (CapMass, Table SM3). None of the measured traits affected the recovery of P_{max} based on the non-linear mixed-effects model (Table SM3). Yet, the analysis of the calculated P_{max} recovery and resilience parameters indicate that recovery was significantly lower in species with large capitula diameter (*Sphagnum divinum* vs *Sphagnum tenellum* Figure 4B, Figure S5).

Traits differed significantly between the *Sphagnum* species, with the largest differences occurring between the fen-originating and bog-originating species (Figure S6). The studied fen species were characterized by large capitula with high N content, while the bog species had small individuals with high capitulum density and high C:N ratio. *S. divinum* was the largest (CapMass, CapDia), while bog-originating *S. tenellum* was the smallest (Figure S5).

When the resistance, recovery or resilience of *Sphagnum* photosynthetic potential were separately addressed, they differed significantly between species (Table S5, Figure 4B,C). *S. divinum* stood
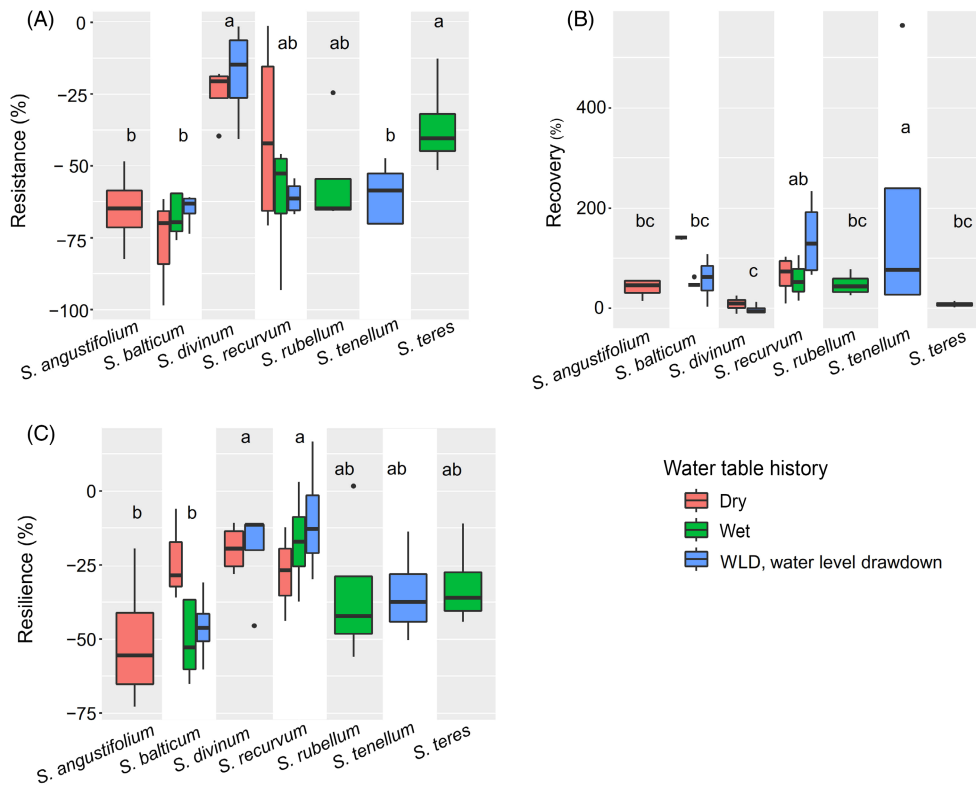

FIGURE 4 Resistance, recovery and resilience of photosynthesis by species. (A) Resistance measures the drop in maximum photosynthesis (P_{max}) from pre-drought to peak drought as a percent of pre-drought P_{max}. (B) Recovery is the percent increase of P_{max} from peak drought to the end of the recovery period. (C) Resilience is the drop in P_{max} from pre-drought to end of the recovery period as a percent of pre-drought P_{max}. Significant differences ($p < 0.05$) based on lme models (results in Table S5) between species are indicated with lettering (water table (WT) histories are averaged as differences were not significant). All mesocosms exposed to periodic drought were included ($n = 48$) with four replicates of each species × water table history. *Sphagnum recurvum* coll. includes species *Sphagnum fallax* and *Sphagnum flexuosum*.

out as the most resistant species and had the greatest capitula mass (Figure 4A, Table S6). Accordingly, capitula mass was a significant positive predictor of drought sensitivity (Table SM3). Recovery was highest for severely drought affected species *S. tenellum* and *Sphagnum recurvum* coll. originating from WLD subsites (Figure 4B). Resilience, which combines the impacts of resistance and recovery, was highest for the generalist species *S. divinum* and *S. recurvum* (Figure 4C).

Traits were also impacted by subsite. Photosynthetic area was highest in mesocosms originating from the dry fen (highest P_{max}) and lowest in WLD bog mesocosms (lowest P_{max}; Figure 5A). Capitulum nitrogen content was the highest in mesocosms from the dry and WLD fen and the lowest in the wet bog mesocosms (Figure 5B).

4 | DISCUSSION

In this study, we tested three alternative hypotheses on how mosses exposed to a consistently deep water table (over 17 years or more)

would respond to a periodic drought. The results gave no support to the first hypothesis that long-term exposure to a deeper water table makes *Sphagnum* mosses acclimate to a periodic drought. We found partial support for the second hypothesis as long-term stresses from WLD decreased *Sphagnum* photosynthesis prior to periodic drought in mesocosms originating from the bog, but not from the fen, suggesting that bog lawns are stressed by these deepened WTs. The third hypothesis was supported by the results: the history of naturally deep or deepened WT exacerbated the impact of periodic drought, regardless of the origin peatland type. The greatest drought-induced reduction in photosynthesis occurred in mosses originating from naturally dry subsites and least for wet subsites. Combining long-term drying and periodic drought stresses made mosses more vulnerable, less resistant, and less resilient. Increased drought vulnerability as a result of prolonged stress is contrary to patterns in vascular plants where plants become less vulnerable to drought with exposure to dry conditions—a capacity known as "drought memory" (Jacques et al., 2021). This contradiction between
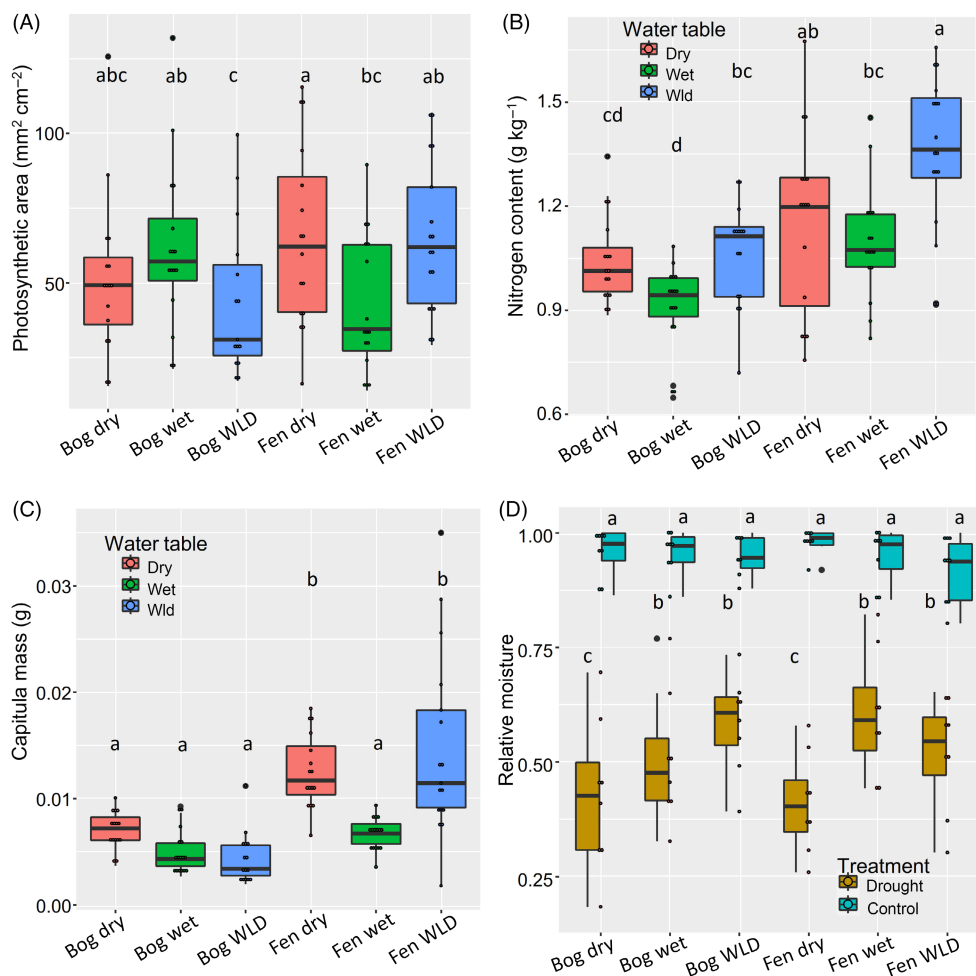

FIGURE 5 Differences between origin peatland types and water table histories in measured traits in the mesocosms (A) photosynthesizing area ($mm^2\,cm^{-2}$), (B) nitrogen content ($g\,kg^{-1}$), (C) mass of a capitulum (g) and (D) moisture of the moss stand at peak drought. Moisture is given as a relative value of each mesocosm to the wettest mesocosm that was given the value of 1. All mesocosms ($n=96$) were included, 16 from each subsite. Significant differences between groups ($p<0.05$) calculated using linear mixed-effects models are indicated using lettering (a–d).

Sphagnum mosses and vascular plants agrees well with their different mechanisms for resisting drought; while vascular plants have structures to control the loss of water (stomata, cuticle, pubescence, etc.) and roots, mosses lack both these structures.

4.1 | History with deep or deepened WT decreases drought resistance

Our finding that permanently deepened WTs make lawn mosses vulnerable could explain the species turnover found after long-term WLD in other studies (Kokkonen et al., 2019b; Miller et al., 2015; Strack et al., 2006; Weltzin et al., 2003). However, the impact of long-term exposure to deepened WTs on *Sphagnum* drought resistance has not been studied. Resistance appeared to be connected to mosses' ability to retain moisture more than to its ability to photosynthesize well at a low moisture content—a common trend found amongst *Sphagnum* studies (e.g. Robroek et al., 2009; Schipperges & Rydin, 1998; Titus & Wagner, 1984). This moisture can be retained as water stored outside of leaves in the moss carpet and structures, or within both photosynthetic and specialized hyaline cells (Bengtsson et al., 2020; Gerdol et al., 1996; Hájek & Vicherová, 2014).

All plants require water to photosynthesize, but mosses are especially sensitive to drought as they lack roots or a vascular system and rely on direct contact with a water source. *Sphagnum* photosynthesis has been directly linked to water content (Gong et al., 2020; Murray et al., 1989; Nijp et al., 2014; Robroek et al., 2009; Schipperges & Rydin, 1998) making photosynthetic resilience a direct indicator of moisture retention during drying. The phenomenon is connected to carpet and capitula traits (Bengtsson et al., 2020). Our trait measurements focussed on two main strategies that mosses have for avoiding desiccation: increased water retention within an individual's structures and formation of dense carpets, which increases capillary rise and decreases exposed surfaces (Bengtsson et al., 2020; Elumeeva et al., 2011; Laine et al., 2011; Laine, Korrensalo, et al., 2021; Lindholm, 1990; McCarter & Price, 2014; Nijp et al., 2014). However, we did not find evidence to support the assumption that long-term exposure to a consistently deep water table changes the moss carpet structure. Either the intraspecific trait plasticity was insufficient to find measurable differences, or the deepened WTs were insufficient to promote changes in moss carpet structure. There may be alternative explanations for the lack of such acclimatization such as moss traits being driven by other environmental drivers such as a sheltering canopy of vascular plants (Minkkinen et al., 1999; Rannik et al., 2013; Straková et al., 2012) or lawn mosses having adequate access to water even during dry periods due to their low microtopographic position. A sheltering canopy reduces the impact of hydrological drought in field conditions by decreasing solar radiation and increasing relative humidity (Straková et al., 2012). Mosses originating from a sheltered site may be more stressed by drought in greenhouse conditions than mosses originating from exposed habitats, adapted to higher winds and solar radiation and lower relative humidity.

In our study, the drought resistance of lawn Sphagna was significantly increased by one water-retaining moss trait, namely capitulum size. Large capitula can physically hold high volumes of extracellular water giving them a higher moisture holding capacity (Bengtsson et al., 2020; Hájek & Beckett, 2008; Jassey & Signarbieux, 2019; Laine, Korrensalo, et al., 2021; Sagot & Rochefort, 1996). In addition, large capitula have a lower surface to volume ratio, thus potentially lowering evaporation. Wide and convex leaves, which are common for large species of the subgenus *Sphagnum*, are also used to increase extracellular water storage capacity in capitula (Malcolm, 1996). Such mechanisms have been reported in *Sphagnum magellanicum* (including *S. divinum*) (Bengtsson et al., 2016, 2020; Jassey & Signarbieux, 2019), which indeed was the most drought-resistant species in our study. *S. divinum* included in our mesocosms had experienced deep periodic droughts in 2016 at origin subsites, meaning it may also be the most drought habituated species here; further studies of drought adaptations including physiological or metabolic processes could provide insights behind these differences.

4.2 | Species-level traits rather than WT history explains resilience to periodic drought

Building on the previously discussed resistance, drought resilience describes the ability of a species to recover after periodic drought (Van Ruijven & Berendse, 2010) and is often used as an indicator of a system's stability, that is if it is nearing a tipping point (Dakos et al., 2015; Scheffer et al., 2012). In this case, lawns transitioning to hummock vegetation would indicate a tipping point for these communities. We found that mesocosms with a higher moisture content at the end of the drought had better recovery. Following drought, metabolic recovery can be slow as in our study, and as earlier observed in lawn or hollow species (Nijp et al., 2014), while faster recovery has been observed in hummock species (Proctor & Tuba, 2002; Schipperges & Rydin, 1998). Generally, recovery after rewetting is faster and more complete when physiological drought impact is less (Nijp et al., 2014) owing to better moisture retention (Hájek & Beckett, 2008), suspended metabolism (Proctor & Tuba, 2002), increased albedo (Harris, 2008; Van Breeman, 1995; Van de Koot, 2022) or constitutive adaptations (Gerdol et al., 1996; Hájek & Vicherová, 2014).

Two species in this study stood out as the most resilient, both of which can occupy a range of habitat conditions (Laine et al., 2018). *S. divinum* was resilient primarily because of stable photosynthesis despite the drought, while S. *recurvum* coll., was both moderately resistant and recovered moderately well. The resistance and resilience of generalists is not a coincidence; resilient species should be able to continue to be productive and competitive across a range of conditions that would be unfit for a specialist species. We would expect communities dominated by these mosses—primarily fen lawns—to be stable when facing periodic drought, as resilient systems are unlikely to change their composition and function when perturbed (Scheffer et al., 2012).

Bryophytes can protect themselves by suspending metabolism when they dry; they are able to quickly shut down photosynthesis to prevent photosystem damage due to desiccation (Gerdol et al., 1996) and remain dormant until rewetting occurs (Proctor & Tuba, 2002). Our results show signs of such suspended metabolism for the lawn species *Sphagnum balticum* collected from the naturally dry bog. *S. balticum* from this habitat was the most vulnerable to desiccation, but also recovered better after rewetting than *S. balticum* from any other WT history.

4.3 | Potential consequences of climate change on peatland moss communities

The exact limit of how far drought can push the function of *Sphagnum* mosses before a tipping point is reached is unclear. Based on our results, it seems clear that long-term WT deepening does not increase the resilience of lawn Sphagna, particularly in bogs where it gradually moves them towards the edge of their ecological envelope. Periodic drought further pushes these mosses to their limits and beyond, which ultimately may result in species replacement.

In fens, the moss community can respond to deepened WT by the *Sphagnum* community shifting towards the dominance of large-sized species that can sustain water in their structures and support higher photosynthesis rates. However, even these mosses reacted to drought by clearly reducing photosynthesis and recovering slowly. Generally, structurally uniform systems are apt to undergo transitions quickly when a tipping point is reached (Scheffer et al., 2012) making fens susceptible due to a relatively homogenous microform distribution that is dominated by lawns. This is further exacerbated by good resource availability to support encroachment of competitive terrestrial (forest) species (Wright et al., 2004). Thus, in the face of repeated and extended drought periods the climate change may lead to rapid species turnover and a transition towards a community well-adjusted to dry conditions. Evidence from other studies suggests that fens are in fact quite vulnerable to sudden transitions (Kokkonen et al., 2019b; Laine et al., 2019; Miller et al., 2015; Strack et al., 2006).

Bogs, on the other hand, may have lawn mosses that are vulnerable to periodic droughts, but are overall more stable systems due to the internal flexibility of diverse microtopography that can adjust as a function of climate (Korrensalo et al., 2020) and promote resilience at the landscape scale (Nijp et al., 2019). If rainless periods become more frequent, lawns will be overtaken by hummock-forming *Sphagnum* species, with wicking and water-retaining carpet structures to avoid drought (Clymo, 1984; Robroek et al., 2007; Rydin, 1985; Rydin, Gunnarsson, et al., 2006).

Shifts in plant community composition will have consequences for the carbon balance both in fens and bogs as dry and wet microforms have been reported to have lower net CO_2 exchange than intermediate surfaces (Korrensalo et al., 2020; Riutta et al., 2007; Strack et al., 2006). However, the interactions between moss traits, microtopographical distribution, and vascular plants complicate our understanding of how these globally important ecosystems will continue to function in our changing climate. More research focusing on the length and severity of drought that pushes different *Sphagnum* species beyond the point of recovery is needed to help us to better understand the tipping point at which peatland ecosystems irreversibly change form and function. Such physiological insights are currently not implemented in peatland models but are key in understanding and predicting how climate change affects species competition, carbon sequestration and functioning of peatland ecosystems.

CONFLICT OF INTEREST STATEMENT

The authors declare no known conflicts of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14305.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad Digital Repository at https://doi.org/10.5061/dryad.02v6wwqb8 (Kokkonen et al., 2024) and in Pangaea Data Publisher at https://doi.org/10.1594/PANGAEA.904256 (Kokkonen et al., 2019a).

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SUPPORTING INFORMATION

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

Table S1. Mesocosm source site water table depth, distribution of microhabitats and vascular vegetation cover on each, based on a 2016 vegetation survey.

Table S2. Nutrient contents of the surface peat (to 10 cm depth) of the Lakkasuo mesocosm source sites in wet undrained fen (wet), water level drawdown (WLD) fen, wet undrained bog and WLD bog.

Table S3. pH and dilution ratios of water applied to mesocosms.

Table S4. Record of precipitation-free (<1 mm) days between the beginning of May to the end of September since 1986 at Hyytiälä Forestry Station (61°50′N, 24°18′E).

Table S5. Marginal ANOVA results of linear mixed effect models on impact of species and WT history on P_{max} resistance, recovery and resilience.

Table S6. Table of parameter estimates of the linear mixed-effects models of traits explained by the experimental factors: WT history, species, measurement campaign (Round) and drought treatment.

Figure S1. Greenhouse photosynthetically active radiation (PAR) over the duration of the experiment.

Figure S2. The construction of the photosynthesis chamber.

Figure S3. Maximum photosynthesis, P_{max}, by species over the measurement campaigns for (A) drought-treated ($n=48$) mesocosms and (B) control mesocosms ($n=48$).

Figure S4. (A) maximum photosynthesis (P_{max}) and (B) respiration (R) of different *Sphagnum* moss species over the course of the experiment.

Figure S5. Trait values of mesocosm mosses by species and campaign.

Figure S6. Principal component analysis of plant traits in relation to mesocosm origin peatland type (bog, fen), subsite WT history (naturally wet, naturally drier (dry) and water level drawdown (WLD)), moss species and experimental treatment (control and drought exposed).

Table SM1. Table of parameter estimates and random effects of the non-linear mixed-effects model based on the experimental design model of net CO_2 exchange, including the drought treatment, origin peatland type ("origin site") and water table history as fixed effects.

Table SM2. ANOVA results for significant effects of predictor variables included in the non-linear mixed-effects model based on the experimental design model of net CO_2 exchange, including the drought treatment, origin peatland type ("origin site") and water table history as fixed effects.

Table SM3. Table of parameter estimates and random effects of the nonlinear mixed-effects model based on the trait model of net CO_2 exchange, including drought treatment and functional traits as fixed effects.