




RESEARCH ARTICLE

Post-fire peatland recovery by peat moss inoculation depends on water table depth

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Funding information

Natural Environment Research Council, Grant/Award Number: NE/L002531/1 and NE/SE11943/1

Handling Editor: Miriam Muñoz-Rojas

Abstract

1. Peatland restoration is essential to preserve biodiversity and carbon stored in peat soils. Common restoration techniques such as rewetting do not always result in the full recovery of peatland taxonomic and functional properties, threatening the resilience of restored peatlands and their carbon stores.
2. Here, we study the use of peat moss inoculation in stimulating the short-term taxonomic and functional recovery of a wildfire-impacted peatland using mesocosms at high and low water table depth, representing ideal and adverse hydrological conditions respectively.
3. Inoculation in conjunction with high water tables accelerated the recovery of the vascular plant and prokaryote communities. Importantly, *Sphagnum*—the keystone genus in these peatlands—only established in inoculated mesocosms. Together, this resulted in an increased CO₂ uptake by approximately 17 g m⁻² day⁻¹ and reduced overall nutrient content in the peat pore water.
4. *Synthesis and applications.* Our results indicate that inoculation can be used to accelerate the establishment of peatland-specific species. In addition, they suggest the potential to combine peat moss inoculation and hydrological restoration to accelerate the uptake of carbon back into the system post-fire. This offers a basis for future work exploring the long-term use of inoculation to return disturbed peatlands to their pre-degraded state, and a wider application of soil inoculation as a mechanism for functional recovery.

KEYWORDS

carbon uptake, functional restoration, microbial inoculation, post-fire recovery, rewetting, *Sphagnum*, wildfire

1 | INTRODUCTION

Peatlands are key global carbon stores, holding up to at least 500 Gt of carbon in their soils (Yu, 2012). Peatland carbon storage is driven largely by high water table depths that provide anaerobic conditions

which hamper decomposition. Consequently carbon-rich peat can build up in the form of slowly accumulated, partially decomposed, plant material (Clymo, 1984; Ingram, 1982; Page & Baird, 2016). Recent centuries have however reported widespread degradation of peatlands including drainage and nutrient enrichment (Swindles

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et al., 2019; Tanneberger, Appulo, et al., 2021). In Europe, for example, a recent estimate suggests that almost half of all peatlands excluding European Russia are degraded, driven largely by drainage for agriculture and peat extraction (Tanneberger, Moen, et al., 2021). Importantly, peatland degradation results in the loss of key ecosystem functions, including the release of large quantities of carbon into the atmosphere (Larmola et al., 2013; Leifeld et al., 2019), switching these ecosystems from carbon-sinks to sources. The effect of drainage is exacerbated by the fact that drainage increases peatland vulnerability to wildfire (Turetsky et al., 2015). Under natural hydrological conditions, peatland wildfires are rare and largely superficial, removing surface vegetation but having minimal impact on all but the surface peat (Granath et al., 2016). Under drained conditions however, peatland wildfires can smoulder deep into the peat soil, stimulating the release of previously locked up carbon (Granath et al., 2016; Rein & Huang, 2021; Turetsky et al., 2015). Alongside this, they can result in the complete loss of aboveground vegetation (Maltby et al., 1990), cause shifts in belowground microbial composition (Andersen et al., 2013) and change peat soil hydraulic properties (Holden et al., 2014). Importantly, wildfire can accelerate shifts towards shrub-dominated plant communities, increasing the risk of further wildfires and result in peatlands becoming a net-source of carbon (Kettridge et al., 2015; Nelson et al., 2021). As such, peatland conservation and restoration is therefore essential to ensure peatlands remain carbon stores and help to mitigate the current rise in global atmospheric carbon (Leifeld & Menichetti, 2018).

Peatland restoration commonly involves rewetting—the raising of previously lowered water tables, which can be an effective approach in returning peatlands to their original state as carbon sequestering ecosystems and to restore peatland-specific biodiversity (Günther et al., 2020; Schwieger et al., 2021). However, recently it has been shown that after hydrological restoration, the recovery of peatland plant communities and functional properties lag behind their undisturbed counterparts; even decades after restoration measures (Kreyling et al., 2021). Considering ongoing increases in atmospheric carbon and rising global temperatures, a rapid return of typical peatland vegetation is crucial to minimise the loss of previously locked-up carbon (Nugent et al., 2019). The restoration of peatland vegetation and subsequent ecohydrological processes can also enhance the resistance and resilience of restored peatlands and minimise carbon loss to future extreme climatic events (Blieck-Langdeau et al., 2022; Loisel & Gallego-Sala, 2022). Consequently, additional restoration action may be necessary along with rewetting to push restored peatlands towards pre-disturbed states and ensure the long-term stability of restored peatlands (Granath et al., 2016).

Alongside rewetting, additional peatland restoration action commonly aims to achieve two aspects: the re-introduction of lost vegetation and the re-establishment of desirable abiotic conditions (Rocheffort et al., 2003). For example, techniques such as litter spreading and moss layer transfer can provide desirable propagules to peatlands, which can stimulate vegetation recovery (Quinty & Rocheffort, 2003; Rocheffort et al., 2016). Alternatively, top-soil removal and liming can be used to control nutrient availability and pH,

producing abiotic conditions that can benefit the re-establishment of desirable vegetation (Huth et al., 2022; Quinty & Rocheffort, 2003). A relatively neglected aspect of peatland recovery is the restoration of microbial communities, which has become increasingly recognised as a powerful tool in the restoration of terrestrial ecosystems (Coban et al., 2022; Harris, 2009). Soil microbial communities can promote or inhibit the performance of plant species, controlling overall compositions and consequent directions in vegetation succession (Bauer et al., 2015; van der Putten et al., 2013) as well as ecosystem functions (Bardgett & van der Putten, 2014). Ecosystem degradation can alter the soil microbiome, which hampers the natural recovery of systems back to their pre-disturbance state (Harris, 2009). While many peatland restoration techniques are likely to alter the microbial community alongside their main restoration aims (Putkinen et al., 2018), the focus has often been on the aboveground, not belowground, recovery (but see for example Bobuřská et al., 2020; Emsens et al., 2020). Yet, focusing action on restoring peatland soil microbiomes, either alone or in conjunction with the aboveground community, could help steer succession towards desired taxonomic compositions (Wubs et al., 2016) and restore lost or degraded functions (Coban et al., 2022).

Soil inoculation—the addition of a small amount of soil or living matter from an intact target ecosystem—is one method used to restore degraded microbial communities (Wubs et al., 2016). Soil inoculation can provide a disturbed ecosystem with an intact microbial community, accelerating the course of recovery and steering it towards a target aboveground plant community (Wubs et al., 2016). In addition, inoculation can also provide propagules that help plant species to overcome dispersal filters and delayed arrival times which can provide advantages to early colonisers (Weidlich et al., 2017). However, despite a number of promising studies on the use of soil inoculation, evidence is often focused on i) grasslands and heathlands and ii) taxonomic, rather than functional recovery (Emsens et al., 2022; Middleton & Bever, 2012; Neuenkamp et al., 2019; Wubs et al., 2016). Consequently, questions remain as to the wider effectiveness of soil inoculation across a range of terrestrial systems, and in recovering key functions lost through ecosystem degradation.

In this study, we assess the use of inoculation in enhancing the post-fire recovery of peatland plant and microbial communities. We test this method using peat from a recently burned bog, the Deurnsche Peel, in the Netherlands. Due to the key role of *Sphagnum* in shaping peatland ecosystems and the strong links between *Sphagnum*, microbial biota and peatland functioning (van Breemen, 1995), we tested the use of blended *Sphagnum* as an inoculate. We hypothesise that the addition of *Sphagnum* inoculate will provide (i) a new microbial community, (ii) vascular plant propagules and (iii) a source of peat moss that together can steer the taxonomic and functional recovery of a peatland following a wildfire. As rewetting is a commonly used peatland restoration technique (Kreyling et al., 2021), we trial the use of peat moss inoculate at two water table depths: high (5 cm below surface level) and low (25 cm below surface level). In doing so, our work will provide insights into the use of *Sphagnum* inoculate as a tool for peatland restoration, and in the general restoration of lost or diminished ecosystem functions.

2 | MATERIALS AND METHODS

2.1 | Study site and experimental design

The Deurnsche Peel is a raised bog-remnant located in the Netherlands (51°24'59.3"N 5°52'37.2"E), which is part of a larger peatland complex—*De Verheven Peel*—which covers an area of roughly 6000 ha. The mean annual temperature is 9.7°C and the mean annual precipitation is 773 mm year⁻¹ (Fick & Hijmans, 2017). The water table in the sites varies with the irregular microtopography resulting in average water table depths ranging from 30 to 70 cm below surface with seasonal fluctuations (Knotters et al., 2008). In April 2020, the Deurnsche Peel suffered a wildfire that burned for over 2 months and affected c. 800 ha. The fire was mainly superficial but left large areas of peatland void of vegetation. Pre-fire vegetation was dominated by *Molinia caerulea* and *Sphagnum cuspidatum* and *S. fallax*, with sparse cover of *Betula pubescens*, *Calluna vulgaris* and *Erica tetralix* (Bakker, 2018). In November 2020, 5 months after the fire, the fire-affected area was heavily dominated by *Molinia caerulea* and was accompanied by young *Betula pubescens* and *Populus nigra*. Areas where the peat smouldered for a longer time remained barren.

In November 2020 (i.e. 7 months after the fire), 20 intact soil cores (mesocosms; 40 cm diameter, 30 cm deep) were collected from barren locations in the post-fire peatland (Figure 1a). Core extraction was performed as to align with the intended experimental design. As such, we have chosen five locations that were ≥25 m apart. Within each location, four cores were taken and placed in tight-fitting PVC

buckets with small holes in the bottom. These cores were collected in close proximity to maximise the similarity in soil edaphics and fire exposure between the four cores per location (i.e. replicates). At the same time as the mesocosm collection, *Sphagnum* moss—mainly *Sphagnum fallax* and *S. cuspidatum*—was collected at an unburned location at the same site. Permission to sample the Deurnsche Peel was provided by the Dutch State Forestry Service (Staatsbosbeheer).

The mesocosms (i.e. buckets with burned peat soil) were transported to Radboud University (Nijmegen) where they were stored in the experimental garden for 11 days to acclimatise. The mesocosms were then brought into the experimental glasshouse for a further 12 day-acclimation period. The average temperature in the glasshouse was 20°C, with slightly higher (20.3°C–21.9°C) during the day than during the night (19.4°C–19.7°C), comparable with Dutch summer-time temperatures. Humidity in the glasshouse varied between 18% and 85% with an average of c. 50%. Light levels were supplemented to resemble growing season light levels, with average radiation approximately 250 μmol m⁻² s⁻¹. To control the water table in the mesocosm, they were placed in larger PVC buckets (50 cm diameter) that drained at the mesocosm-specific water table (see below). To prepare the inoculate for each mesocosm, 650 g of the fresh peat moss collected from the unburned area of the Deurnsche Peel was mixed with 0.9 L of demineralised water to produce 0.09 L of inoculate per mesocosm ($n = 10$). The inoculate was homogenised using an immersion blender, to produce a slurry with small (c. 0.5 cm) dia-spores of peat moss.

In the experimental glasshouse, all mesocosms were placed in a full-factorial randomised block design, keeping the 5 × 4 collection

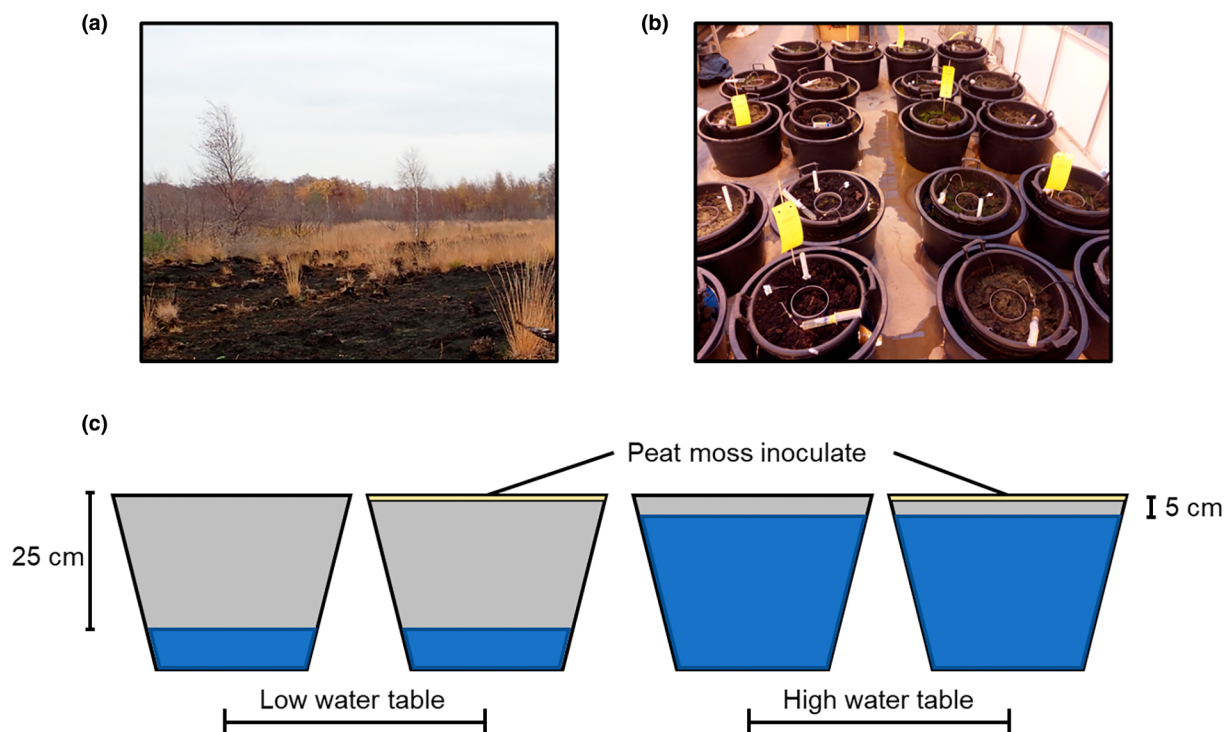


FIGURE 1 Study site and experimental set-up. (a) Site of mesocosm collection (Credit: Ralph Temmink). (b) Mesocosm set-up in experimental greenhouse (Credit: Isa Martin). (c) An outline of each experimental treatment.

set-up (5 locations, 4 mesocosms per location). In each block, all mesocosms were randomly assigned an inoculation and water table treatment. The homogenised inoculate was spread over the surface of half of the mesocosms ($n = 10$), while the other half were left non-inoculated to serve as controls. Simultaneously, half of the inoculum and control mesocosm treatments received a water table treatment: high (5 cm below surface level) and low (25 cm below surface level). This resulted in four treatments: (1) inoculation, high water table; (2) inoculation, low water table; (3) control, high water table and (4) control, low water table (Figure 1b,c). To maintain the required water tables and simulate rainfall, mesocosms were watered twice a week using collected rainwater. Water was added as rainfall using a garden-hose with a nozzle. All mesocosms were watered for 30 s on the lowest jet intensity, which equalled c. 4 mm of rain. This amount is in line with the average of 1 mm of rain per day which is normal in the Netherlands. Following a 120-day period, we terminated the experiment in April 2021.

2.2 | Plant (functional) and microbial community composition estimations

In each mesocosm, vascular plant and bryophyte covers (%)—at species level if possible—were estimated 4 months post-inoculation. Total vascular plant cover, due to community structure, can exceed 100%, while maximum bryophyte cover, which is based on the surface cover, could not exceed 100%. To determine aboveground biomass (g m^{-2}) at the end of the experiment, the aboveground vascular plants were harvested and oven dried for 7 days at 70°C.

We compiled trait data for five plant traits: seed mass (mg), specific leaf area (SLA; $\text{mm}^2 \text{mg}^{-1}$), leaf dry matter content (LDMC; mg g^{-1}); plant height (m) and Ellenberg moisture value (EMV). Traits selected were core plant traits (Díaz et al., 2016) and/or have previously been shown to be selected for within recolonising peatland vascular plant communities (Shepherd et al., 2021). Trait values for each species were extracted from LEDA (Kleyer et al., 2008) except EMV which was taken from Ecoflora (Fitter & Peat, 1994). If species-level data were unavailable, genus-level means were used.

To assess the composition of the prokaryote communities and their trajectory of recovery in the mesocosms, we extracted peat samples (2.5 cm diameter; 5 cm deep) at three time points (10, 35 and 112 days) in the post-inoculation period. We sampled the top 5 cm of the peat due to it representing the point in which the recovering plant and microbial communities have the closest interactions (Lamit et al., 2021) and, as we added the inoculate to the peat surface, it allowed us to follow the initial changes in the microbial community. From each sample, DNA was extracted from a 0.25 g subsample using the QIAGEN DNeasy powersoil pro kit following standard manual specifications. Samples were then packaged with dry ice and shipped overnight to Novogene Co., Ltd (Cambridge, UK; <https://en.novogene.com>) for DNA amplification and sequencing. Extracted DNA was sequenced using the 515F/806R primers that target the V4 regions of the 16S rRNA gene. Amplicons were

then sequenced on Illumina paired-end platform, generating 250 base pair reads. Detailed sequencing information is provided in the Supplementary Methods. Prokaryote sequences were quality checked and amplicon sequence variants (ASVs) assembled through the DADA2 pipeline (Callahan et al., 2016) before further analysis. The SILVA database (<https://www.arb-silva.de>) was used as a reference to match ASVs to their taxonomic identities.

2.3 | Greenhouse gas measurements and peat soil edaphics

Carbon dioxide (CO_2) and methane (CH_4) fluxes at the mesocosm level were measured using a plexiglass transparent PVC chamber (20 cm diameter, 40 cm high) equipped with a fan and connected to an LI-COR LI-7810 $\text{CH}_4/\text{CO}_2/\text{H}_2\text{O}$ Trace Gas Analyser (LI-COR Biosciences). The CO_2 flux represents net ecosystem exchange (NEE), defined as the difference between the assimilation of carbon through photosynthesis and the release of carbon through respiration at the mesocosm level. The chamber had a rubber seal on the bottom and a venting hole on the top which remained open to avoid pressure issues when the chamber was placed on the PVC collars that were pre-inserted in all mesocosms to a depth of 5 cm. The venting hole was then closed prior to the gas flux measurement to ensure a closed chamber system.

The measurements began 6 weeks post-inoculation, when the vegetation started to emerge. Measurements were taken twice a week for the first 5 weeks, before reducing to once a week for the remaining 7 weeks of the experiment. All flux measurements were carried out around midday local time, ensuring optimal conditions for plant photosynthesis. Each measurement lasted 2 min by which we avoided excessive heat and humidity causing condensation inside the chamber. During measurements, CO_2 and CH_4 measurements were monitored and in the case of an ebullition event measurements were discarded and repeated. CO_2 and CH_4 fluxes ($\text{mg m}^2 \text{day}^{-1}$) were then calculated as a linear change in concentration (ppm) following (Zhao et al., 2017), using the equation:

$$\text{Flux} = (P/R \cdot T) \cdot dG/dt \cdot (V/A) \cdot M \cdot 10^{-3} \cdot 3600 \cdot 24.$$

P represents the average daily air pressure (kPa), R represents the universal gas constant ($\text{latm K}^{-1} \text{mol}^{-1}$), T represents the average daily air temperature (K), dG/dt represents the slope of the flux measurement (ppm s^{-1}), V represents the chamber volume (l), A represents the chamber base area (m^2) and M represents the gas molar mass ($\text{CO}_2 = 16.04246$; $\text{CH}_4 = 44.0095$). The average daily air pressure and temperatures were recorded from a nearby meteorological station (<https://www.knmi.nl/nederland-nu/klimatologie/daggegevens>). Gas temperature was monitored by the LI-COR analyser. CO_2 fluxes were then converted to $\text{g m}^2 \text{day}^{-1}$. The flux calculation was implemented using the R package FLUXCALR (Zhao, 2019). Flux R^2 values increased over the study as vegetation was established increasing from relatively low values (CO_2 : 0.55 ± 0.07 ; CH_4 : 0.45 ± 0.07 ; mean \pm SE) to

well-fitting flux measurements ($\text{CO}_2 = 0.86 \pm 0.04$; $\text{CH}_4 = 0.89 \pm 0.04$). This is in line with ambient gas exchange having poor fitting 'linear' relationships before increasing in fit as ecosystem processes recovered. We did not account for soil temperature in our calculations as this is likely to change as vegetation recolonises (Brown et al., 2015) and therefore is linked to post-fire recovery. We excluded CH_4 fluxes that were exceptionally low or high ($< -5 \text{ mg m}^{-2} \text{ day}^{-1}$ & $> 5 \text{ mg m}^{-2} \text{ day}^{-1}$) to reduce the impact of erroneous measurements and outliers on our models. In total, we retained 311 CO_2 and 304 CH_4 flux measurements retained for further analysis. In this study, positive CO_2 and CH_4 exchange values represent a net CO_2 and CH_4 uptake respectively by the mesocosms, following ecosystem sign convention.

Pore water samples were collected in the first 10 cm below the peat surface using Rhizon soil moisture samplers (type MOM, pore size 0.2 μm , Eijkelkamp, Giesbeek, NL). Samples were taken from the mid-point between the outer mesocosm wall and the PVC collar, 7-, 32-, 64- and 98-days post-inoculation and stored in collection syringes before being transported to the laboratory. Following pore water extraction, pH was measured using a titrator (Metrohm 877 Titrino plus). All samples were analysed spectrophotometrically for NO_3^- -N, NH_4^+ -N and PO_4^{3-} -P and Cl^- concentrations using an AutoAnalyser 3 (Bran+Luebbe GmbH). Na^+ and K^+ were measured using a Sherwood 420 flame-photometer.

The peat soil C to N ratio was assessed at the end of the experiment from 10 cm deep peat soil cores (2.5 cm diameter) taken at the centre of each mesocosm. Each core was dried for at least 48 h at 70°C, ground and then subsampled (0.25–0.35 mg per sample). Carbon and nitrogen content was then measured in a CHNO element analyser (EA NA1500 – EA 1110 device, Carlo Erba/Thermo Fisher Scientific).

2.4 | Statistical analyses

The effects of soil inoculation and water table depth on community compositions of the vascular plants, bryophytes and prokaryotes were examined using non-metric multidimensional scaling (NMDS). To test the impact of the experimental treatments on each community composition, we performed a permutational multivariate analysis of variance (PERMANOVA, permutations = 999). Plant species abundance matrices were standardised before inclusions using Hellinger transformations, with species appearing in less than 25% of all mesocosms removed before analysis. Inoculation and water table depth were included as interacting factors for each plant PERMANOVA. For prokaryote composition, time was included as an additional interacting variable and mesocosm permutations were consequently constrained by mesocosm identity to account for repeat measurements. To further examine the effect of inoculation on the prokaryote community, we used linear mixed effect models (LMMs) to determine changes in the relative proportions of the 10 most abundant prokaryote ASVs. In each LMM, we considered individual phylum abundances as functions of inoculation (yes/no), water table depth (high/low) and time

(days) since inoculation and their interactions. Mesocosm identity was included as a random intercept to account for repeat measurements. The best performing model for each phylum was then determined following a selection process outlined in Appendix S1 in Supporting Information.

To examine the functional composition of the aboveground plant community, we performed principal component analysis (PCA) using trait community-weighted means as explanatory variables. To examine the effect of inoculation and water table depth on *Sphagnum* cover, we performed bootstrapped two-sample Kolmogorov–Smirnov (KS) tests ($n_{\text{boot}} = 1000$). We performed this test only on mesocosms where inoculation had occurred, as no *Sphagnum* was observed in uninoculated plots (Appendix S2).

To assess the effect of the inoculation and water table depth on functional recovery over time, we performed LMMs on the effect of treatments on CO_2 fluxes (NEE), CH_4 fluxes and pore water biogeochemical composition, following the same structure as in the prokaryote phylum abundance models. Pore water biogeochemical composition was determined using the first axis of a PCA constructed using the concentrations of NO_3^- , NH_4^+ , PO_4^{3-} , Cl^- , K^+ and Na^+ and pH as the response variable. Model performance was assessed following the protocol in Appendix S1. Finally, measures of ecosystem functions—taken at the end of the experiment (aboveground biomass, peat C to N ratio)—were examined using two-way ANOVA, with inoculation and water table depth as interacting variables. Assumptions of ANOVA (e.g. normality of residuals, homogeneity of variance) were examined visually, with homogeneity of variance examined additionally using Levene's test for homogeneity. CN ratio was consequently log-transformed to ensure adherence to these assumptions.

We considered $p < 0.05$ to indicate a significant effect of an experimental treatment. All statistical analyses were conducted in R v. 4.1.2 (R Core Team, 2022). A list of all packages and references used in the analyses is provided in Appendix S1.

3 | RESULTS

3.1 | Aboveground community composition

Inoculation caused a shift in the overall composition in both the vascular plant and bryophyte communities (Figure 2a,c; Appendix S3). Under natural, non-inoculated, conditions the aboveground vegetation became dominated by *Molinea caerulea* ($17.9 \pm 5.8\%$; average \pm SE) and *Bryum* spp. ($39 \pm 10.0\%$; Appendix S2). Inoculation resulted in the vegetation being dominated by *Juncus bulbosus* ($43.5 \pm 7.6\%$), *Sphagnum* spp. ($21.6 \pm 8.3\%$) and *Hypnum cupressiforme* ($15.3 \pm 7.0\%$; Appendix S2). Functionally, inoculation led to a vascular plant community that possessed lower leaf dry matter content, plant height and seed mass, and higher EMVs compared with uninoculated communities (Figure 2b; Appendix S4). *Sphagnum* was only found in inoculated plots (Figure 2d). Despite its establishment in double the amount of mesocosms when the

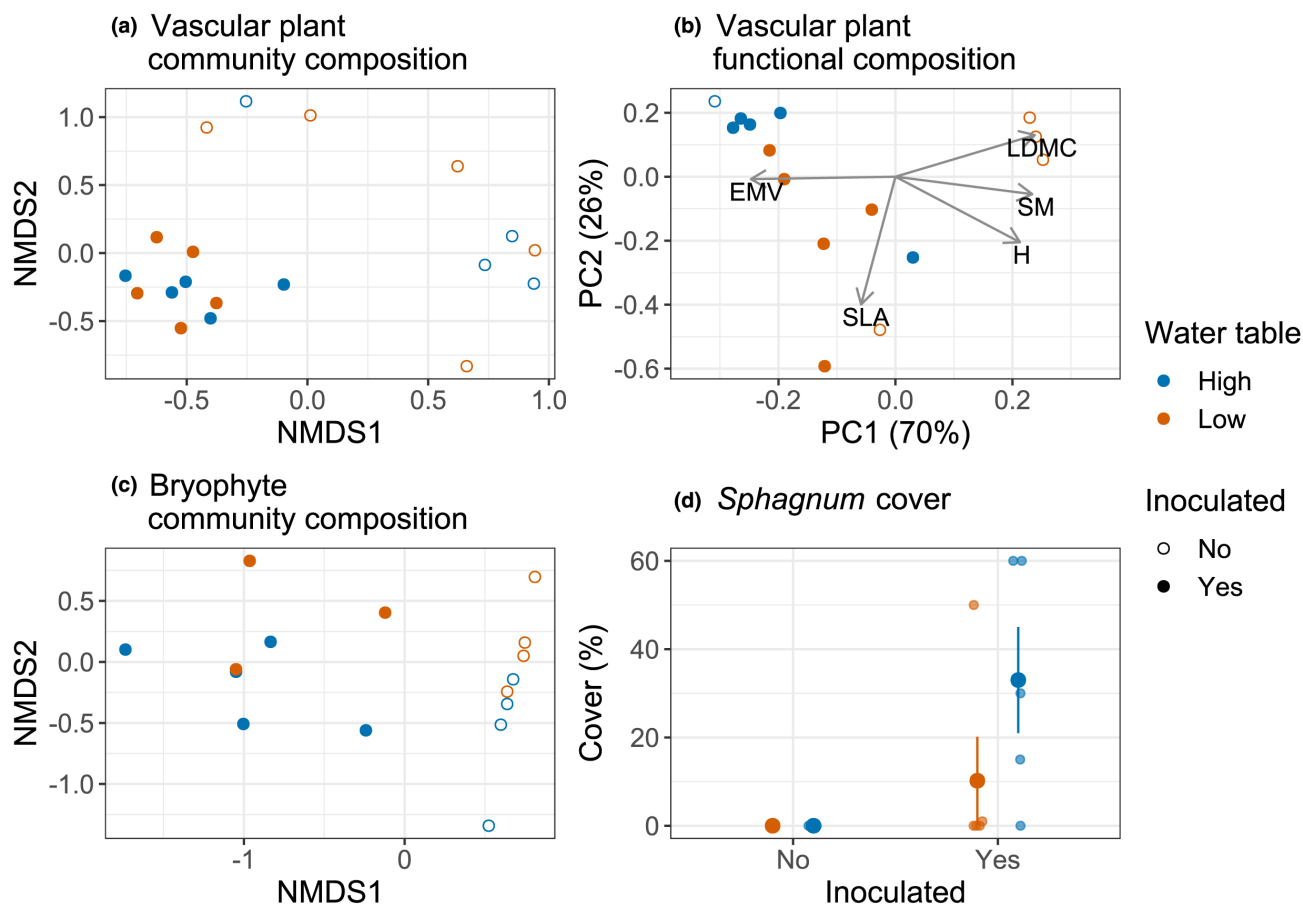


FIGURE 2 Effect of inoculation and water table depth on peatland aboveground taxonomic and functional composition. (a) Vascular plant communities (non-metric multidimensional scaling; $stress = 0.14$); (b) Functional composition of recovered vascular plant communities (principal component analysis); (c) Bryophyte community composition (non-metric multidimensional scaling; $stress = 0.05$); (d) *Sphagnum* cover. EMV, Ellenberg moisture value; LDMC, leaf dry matter content; H, plant height; SLA, specific leaf area; SM, seed mass. Plots with high water table and uninoculated were functionally identical so appear layered in b. Smaller circles in d represent individual plot values. Error bars in d represent \pm SE.

water table was raised (80% in high water table depths, 40% in low water table depths), we did not find evidence that wetter conditions increased overall *Sphagnum* cover (Two-sample bootstrapped Kolmogorov-Smirnov test, $D = 0.6$, $p = 0.24$). Neither did the water table result in an overall shift in the bryophyte composition (Figure 2c; Appendix S3) or vascular plant community (Figure 2a; Appendix S3). However, we did observe *Sphagnum* species differences across water table depths, with *S. cuspidatum* in greater abundance in higher water tables (KS test, $D = 0.8$, $p = 0.04$, Appendix S2), whereas *S. fallax* was unaffected by the water table depth (KS test, $D = 0.2$, $p = 0.793$, Appendix S2). Overall, the use of inoculation was the strongest driver of aboveground community composition (Figure 2, Appendix S3).

3.2 | Prokaryote composition

Time (days) since inoculation was the strongest driver of prokaryote composition throughout the course of the recovery (Figure 3a-c; Appendix S3). Additionally, both inoculation

and water table depth drove changes in the overall composition (Figure 3a-c; Appendix S3), with an interaction observed between the two experimental treatments (Appendix S3). There was also an interaction observed between water table depth and days since inoculation (Figure 3a-c; Appendix S3). At the phylum level, the communities were dominated by Actinobacteria, Acidobacteria and Proteobacteria, constituting up to 50% of the entire prokaryote community (Figure 2d-g). Time (days) since inoculation appeared a significant predictor in 9 out of the 10 most abundant prokaryote phyla best-performing models (all except for WPS-2; Appendix S4). The effects were more variable with certain phyla responding to the treatments, and others showing minimal effect, with inoculation present in four of the 10 top phylum models, but only demonstrating a significant effect in one (Cyanobacteria, estimate = -0.023 , $p = 0.007$; Appendix S5). Water table depth was present in four of the 10 top models but only showed a significant effect in two (Cyanobacteria, estimate = -0.019 , $p = 0.039$; Verrucomicrobia, estimate = -0.020 , $p = 0.001$, Appendix S5). Interactions between water table depth and inoculation were included within three of the top models (Bacteroidetes,

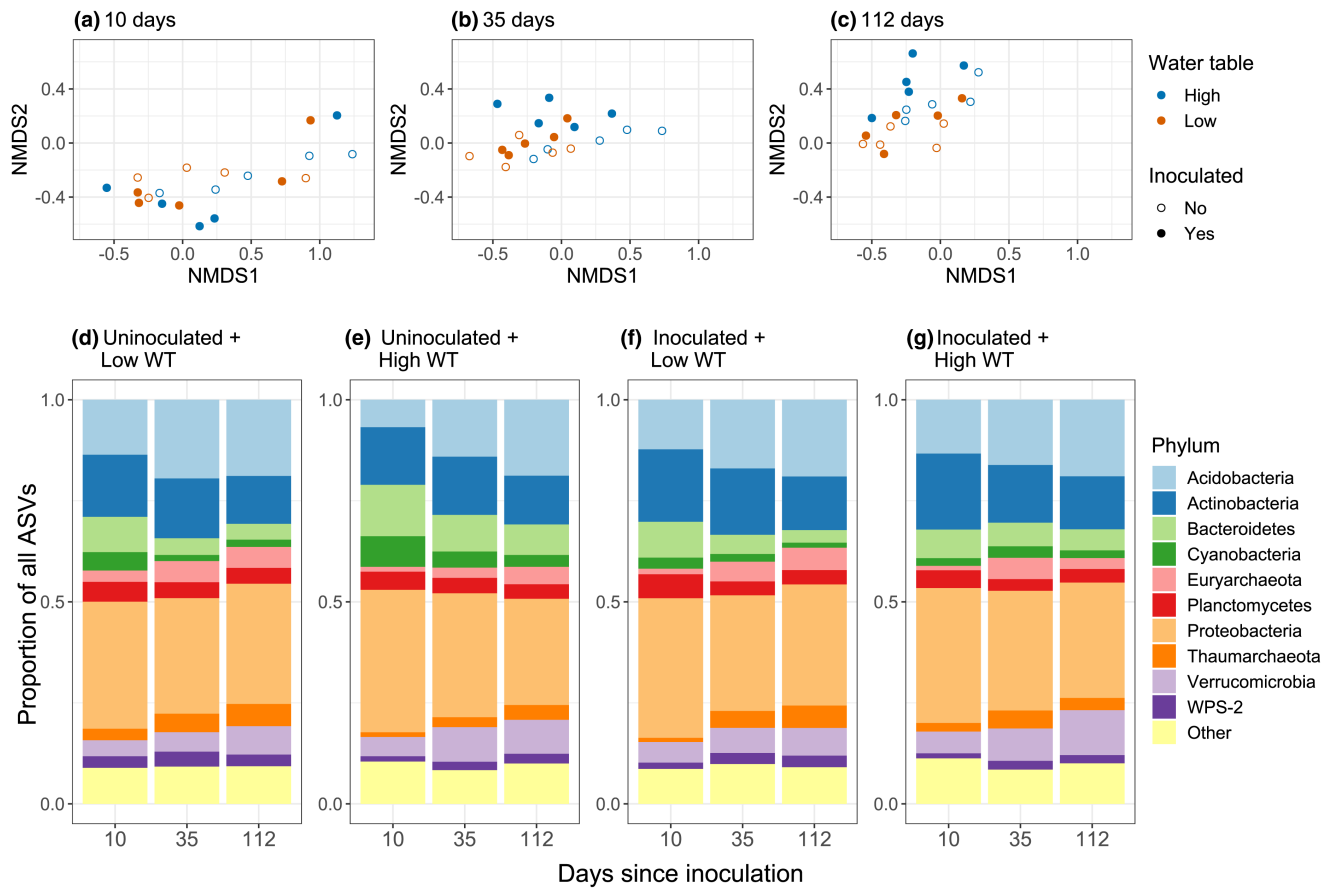


FIGURE 3 Effect of inoculation and water table depth on the belowground prokaryote composition during the initial wildfire recovery. (a–c) non-metric multidimensional scaling (NMDS) of the initial post-fire community across three different time points throughout the initial recovery ($stress = 0.18$). Each panel is representative of one time point but is part of the same NMDS, split to aid interpretability. (d–g) total proportion of amplicon sequence variants of the top 10 most observed phyla across each of the four experimental treatments at three separate time points. The ‘Other’ group refers to all phyla not contained within the top 10 most abundant.

Cyanobacteria, Verrucomicrobia), but the effects of these interactions were not statistically significant.

3.3 | Ecosystem functions

We observed an interaction between inoculation and water table depth on NEE, highlighting that inoculation resulted in increased CO_2 uptake over time when water tables are high (Figure 4a; Appendix S6). This led to an average CO_2 uptake of $\sim 19 \text{ gm}^{-2} \text{ day}^{-1}$ 120 days post-inoculation under a high water table, compared with just $\sim 2.2 \text{ gm}^{-2} \text{ day}^{-1}$ when water tables were lowered (Figure 4a). However, methane production was driven by water table depth and time since inoculation (Figure 4b; Appendix S6), with higher water tables generally resulting in a net release of CH_4 (day 120 average: $-0.83 \text{ mgm}^{-2} \text{ day}^{-1}$) compared with lower water tables which resulted in a net uptake of CH_4 (day 120 average: $0.81 \text{ mgm}^{-2} \text{ day}^{-1}$). Inoculation did result in changes in pore water composition over the course of the initial mesocosm recovery by increasing the PC1 score of inoculated plots, with an interaction between inoculation and days since inoculation (Figure 4c; Appendix S6). The pore water PC1 itself explained $\sim 54\%$ of the total variation with a higher PC1

correlating with the reduction in concentration of PO_4^- , K^+ , and Cl^- (Appendix S7). Inoculation also led to higher C:N ratios in the peat soil (ANOVA; $F_{1,19} = 4.6$ $p = 0.047$; Figure 4d), corresponding with reductions in peat nitrogen content (Appendix S8). Finally, higher water tables reduced aboveground biomass (ANOVA; $F_{1,19} = 22.2$, $p < 0.001$; Figure 4e).

4 | DISCUSSION

Inoculation has become increasingly recognised as a potential tool for ecosystem restoration (Wubs et al., 2016). Yet, previous studies have largely focused on a select few systems including grasslands and heathlands and only on taxonomic recovery (Emsens et al., 2022; Wubs et al., 2016). Our results show that *Sphagnum* inoculation can alter the initial community composition of vascular plants, bryophytes and the prokaryote community (Figures 2 and 3), leading to differences in the functioning of the recovered peat (Figure 4). This included reductions in pore water nutrient concentrations and increasing C:N ratios of the peat. Notably, inoculation and raising water table depth interacted to control both aboveground (*Sphagnum* establishment) and belowground (prokaryote)

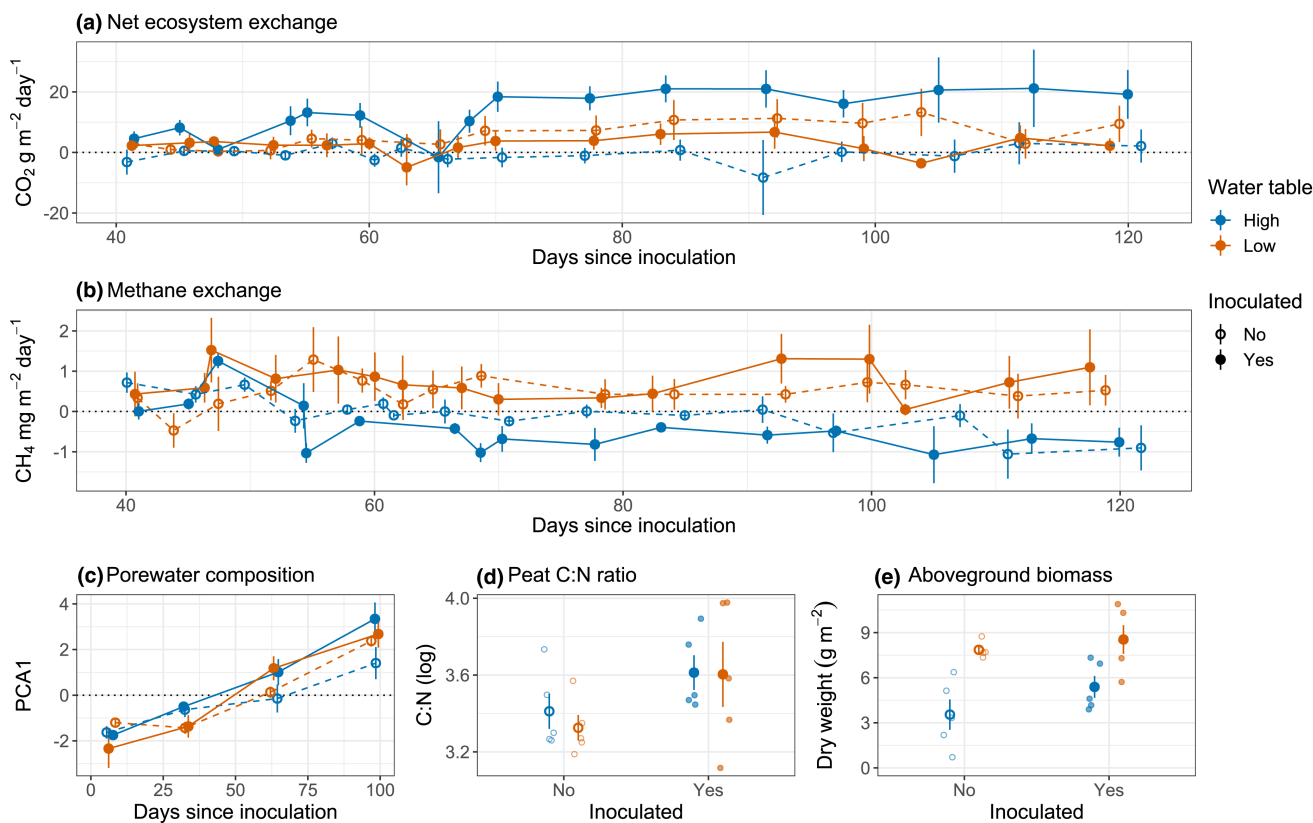


FIGURE 4 Effect of inoculation and water table depth on ecosystem functioning during the initial post-fire recovery. Change over time (days) since inoculation of (a) net ecosystem exchange, (b) methane exchange and (c) pore water composition. 18 weeks post-inoculation (d) peat C:N ratio and (e) aboveground harvested dried biomass (g m^{-2}). Larger circles represent treatment means; intervals represent \pm SE. Smaller circles in d and e, represent individual plot values. Data are jittered to aid interpretation. Pore water PCA1 explained 54% of pore water variation (Appendix S7). a-b are transformed such that a positive value represents a net uptake of CO₂ and CH₄, respectively.

compositions, and the initial carbon dynamics by increasing the amount of CO₂ taken up. Therefore, we argue that inoculation could be a useful tool alongside hydrological restoration to enhance the recovery trajectory of degraded peatlands. Moreover, inoculation aids in the initial taxonomic and functional recovery of a previously untested ecosystem type (i.e. peatlands) and may, thus, be suitable to trial in other ecosystems such as fresh and saltwater wetlands.

4.1 | Initial taxonomic and functional recovery

Inoculation had a strong effect on the aboveground community composition, altering both the taxonomic and functional composition of vascular plants and bryophytes (Figure 2). This included the presence of early colonising vascular plants that indicate moist conditions such as *Juncus bulbosus*, and *Sphagnum* moss, which were both absent without the use of inoculation. The establishment of *J. bulbosus* could be key to further encouraging the re-establishment of *Sphagnum* mosses and more typical peatland vascular plant species as the ecosystem recovers (Farrell & Doyle, 2003). Interestingly, we found no effect of raising the water table on the vascular plant community. This is despite the use of inoculation producing a vascular plant community that preferred wetter conditions (Figure 2b). Providing a greater functional breadth of vascular plant

colonists could, however, allow abiotic factors such as water table depth to increasingly shape the community as recovery continues with a greater pool of species to 'filter' from (Belyea & Lancaster, 1999). This suggests an initial overriding effect of dispersal limitation on initial vascular plant composition post-fire (Shepherd et al., 2021). *Sphagnum* establishment success was doubled when water tables were raised (Figure 2d), which suggests a potential interaction between inoculation and water table depth in re-establishing lost peat moss communities. This agrees with previous work, which shows that raising water table depths can increase *Sphagnum* recolonisation (Ferland & Rochefort, 1997; Robroek et al., 2009). However, it is important to note that the effects of water table on *Sphagnum* recolonisation were driven largely by *S. cuspidatum*, which prefers wetter conditions (Andrus et al., 1983) and only established in our mesocosms at high water table depths. *Sphagnum* establishment can vary depending on individual species microhabitat preferences (Robroek et al., 2009) and our results suggest that *Sphagnum* establishment may therefore depend on both inoculation and the species chosen for use in the inoculate. Regardless, inoculation showed clear changes to the taxonomic and functional composition of the initial post-fire aboveground community.

Inoculation did drive a change in the prokaryote composition, but the effect was less pronounced than in the aboveground community (Figure 3). The driver of these changes remains unclear and could be due to the direct effect of adding a new prokaryote community through

inoculation or as an indirect consequence of differences in establishing vegetation that promotes the presence of certain phylum (e.g. increased vegetation cover; Elliott et al., 2015). However, evidence for phylum level effects from inoculation was limited (Appendix S5). The lack of interaction between time and inoculation suggests this could be driven by the direct addition of a new microbial community. Yet, when focusing on single time points, we did not find strong evidence of an initial change in community composition following inoculation (Appendix S9). Consequently, the mechanism behind altered prokaryote communities upon *Sphagnum* inoculation remains unclear. Along with this, water table depth also altered the composition (Figure 3) and interacted with time, suggesting the response of the prokaryote community was in part driven by its adjustment to the new hydrological conditions. However, the strongest driver of prokaryote composition was time, suggesting the initial direction of belowground recovery is largely dictated by the process of post-fire recovery. This is perhaps unsurprising given the mesocosms were collected from a barren site and the process of re-vegetation is likely to lead to changes in microclimate (Brown et al., 2015) that may drive prokaryote recovery. If the experiment was continued longer, we may expect to see stronger effects of plant community composition on the microbial community than observed during the 4 months of recovery. Over the length of this study, however, specific abiotic and biotic controls resulted in more subtle changes in prokaryote community structures.

Inoculation led to changes in the overall functioning of the mesocosms, reducing the concentration of nutrients (e.g. PO_4^-) in the pore water composition (correlated to increasing PCA axis) and increasing the C:N ratio through reductions in peat nitrogen concentration (Figure 4, Appendix S8). Together, along with raising water table depths, it led to an increase in the uptake of CO_2 (NEE) across the course of the recovery. The drivers of these changes in function are likely to be the shift in composition in aboveground and belowground communities that together drive peatland functions (Robroek et al., 2015; Wang et al., 2021). The effect of inoculation on NEE was, however, reversed when the water table was lowered, which could be the result of increased ecosystem respiration driven by the addition of a functional microbial community alongside the highly aerobic soil conditions that shifts the mesocosms towards a neutral carbon balance. However, the exact mechanism behind these functional changes is largely beyond the scope of this study due to the lack of data on other important drivers of peatland function such as fungi communities (Juan-Ovejero et al., 2020). It does demonstrate that through steering the aboveground and belowground compositions, inoculation can result in changes to ecosystem functions during initial peatland recovery.

4.2 | Implications for peatland restoration

Rewetting is not always successful in returning degraded peatlands to their pre-disturbance state (Gaffney et al., 2020; Granath et al., 2016; Kreyling et al., 2021). This could be due to several limiting variables, including propagule limitations, and altered microbial communities (Emsens et al., 2020; Shepherd et al., 2021). Consequently, additional restoration

action may be required. Additional peatland restoration techniques that are often introduced along with rewetting include removing the top layer of the surface peat, seeding target species and moss layer transfer (Chimner et al., 2017; Huth et al., 2022; Quilty & Rochefort, 2003). This can be with the aim of returning degraded peatlands to their pre-disturbed state, or for use in paludiculture (e.g. *Sphagnum* farming, Temmink et al., 2017). *Sphagnum* inoculation is one potential restoration method that could also be used to enhance the restoration of peatlands by introducing new microbial communities and propagules that can steer peatland recovery back towards pre-disturbance conditions. Our results indeed show that the initial recovery can be directed by the introduction of *Sphagnum* inoculate, resulting in changes to the taxonomic composition and functioning of the recovered community. Raising water tables also showed a significant role in determining the initial recovery, interacting with *Sphagnum* inoculation, and suggesting that rewetting and inoculation in combination could be used to steer peatland recovery. Gas flux measurements were within comparable ranges of those observed in other studies focused on moss layer transfer (Lazcano et al., 2018) and rewetting (Dinsmore et al., 2009); however, wider comparisons of carbon budgets are not possible given the short duration of the study. Notably, our results show that *Sphagnum* inoculation can result in the successful re-colonisation of *Sphagnum* onto wildfire-damaged peat, which is an important component of peatland restoration (Huth et al., 2022; Rochefort, 2000). The provision of both propagules and microbes within the peat moss inoculate makes determining the driver of these changes difficult within this experimental setup, and therefore the exact mechanism governing post-fire recovery remains uncertain. For now, this study provides evidence for an initial role in *Sphagnum* inoculation in steering the initial taxonomic and functional recovery of degraded peatlands.

Future work should now look to increase our mechanistic and applied understanding of peat moss inoculation in controlling peatland recovery. A number of follow-up questions that could be addressed include: how long do the effects of *Sphagnum* inoculation on taxonomic and functions last in peatlands? What mechanism (microbial or propagule addition) drives recovery post-inoculation? Does inoculation increase taxonomic and functional similarities between restored and baseline (undisturbed) sites? Do the effects of inoculation vary across peatland gradients (e.g. fen-to-bog transitions)? Does inoculate origin (e.g. species, environmental conditions) drive target species establishment? What is the optimal ratio of moss harvested to area of peatland restored? Answering each of these questions will help inform on the feasibility and limitations of this technique and result in a greater understanding of the potential role of peat moss inoculation in peatland restoration.

4.3 | Soil inoculation as a general tool for ecosystem restoration

Soil inoculation has been shown as a powerful tool to steer ecosystem recovery towards target community compositions (e.g. Wubs et al., 2016). However, much of our understanding in the use of soil inoculation has come from studies focused on a select few systems (e.g. grasslands and heathlands) and on taxonomic recovery. Key

carbon-storing ecosystems such as wetlands have received little, if any, attention. Restoration is however increasingly focused on restoring the functional properties of ecosystems (Kollmann et al., 2016). Our study provides evidence that *Sphagnum* inoculation can lead to changes in the direction of recovery of peatlands in the short term and that this can impact the functioning of the system. Consequently, our work sets the basis for future work to explore the use of inoculation to steer the functional recovery of degraded ecosystems.

The success of restoration action is often limited by numerous constraints, such as post-disturbance abiotic conditions and dispersal limitations (Pywell et al., 2006). Consequently, despite repeated success in steering ecosystem recovery, soil inoculation may not always be an effective restoration tool (Emsens et al., 2022). Understanding when and where soil inoculation is effective is key to the techniques widespread use in restoration projects. Our results suggest that hydrological conditions could mediate the use of peat moss inoculation in peatlands. This is unsurprising given the key role of water table depth in determining peatland composition and function (Waddington et al., 2015). In grasslands, soil pH has been observed to mediate the effectiveness of soil inoculation (Emsens et al., 2022). However, inoculation has also been shown to override abiotic conditions (Radujković et al., 2020). Consequently, the relationship between soil inoculation and factors that may mediate its effectiveness remains unclear. Expanding research into soil inoculation across a wider range of ecosystems, such as peatlands, could provide broader insight into the use of the technique. In turn, this may offer greater opportunities for generalities to be drawn and consequently help to establish soil inoculation as a general tool for ecosystem restoration.

AUTHOR CONTRIBUTIONS

Harry E. R. Shepherd and Bjorn J. M. Robroek conceived the idea for the manuscript. Isa Martin, Andreea Marin, Peter M. J. M. Cuijssen, Ralph J. M. Temmink & Bjorn J. M. Robroek collected the mesocosms. Isa Martin, Andreea Marin and Peter M. J. M. Cuijssen carried out the experiment and data collection, with key guidance from Harry E. R. Shepherd and Bjorn J. M. Robroek. Harry E. R. Shepherd led the analysis and wrote the first draft of the manuscript, with input from Isa Martin, Ralph J. M. Temmink and Bjorn J. M. Robroek. All authors contributed to subsequent revisions.

ACKNOWLEDGEMENTS

We thank the Dutch State Forestry Service (Staatsbosbeheer), and notably Rick Verrijt, for permission to sample in the Deurnsche Peel. We are indebted to Sebastian Krosse, Paul van der Ven, Germa Verheggen and Roy Peters for their help with chemical analyses, and Koos Janssen for mesocosm maintenance. We thank three anonymous reviewers for their comments that helped improve the manuscript. We thank Anna Stanworth for help with the graphical abstract, constructed by Biorender.com.

CONFLICT OF INTEREST

The authors declare they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and R scripts used in this study are available at the University of Southampton repository: <https://doi.org/10.5258/SOTON/D2276> (Shepherd et al., 2023).

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SUPPORTING INFORMATION

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

How to cite this article: Shepherd, H. E. R., Martin, I., Marin, A., Cruijnsen, P. M. J. M., Temmink, R. J. M., & Robroek, B. J. M. (2023). Post-fire peatland recovery by peat moss inoculation depends on water table depth. *Journal of Applied Ecology*, 60, 673–684. <https://doi.org/10.1111/1365-2664.14360>