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RESEARCH ARTICLE

Ericoid shrub encroachment shifts aboveground–belowground linkages in three peatlands across Europe and Western Siberia

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Abstract

In northern peatlands, reduction of *Sphagnum* dominance in favour of vascular vegetation is likely to influence biogeochemical processes. Such vegetation changes occur as the water table lowers and temperatures rise. To test which of these factors has a significant influence on peatland vegetation, we conducted a 3-year manipulative field experiment in Linje mire (northern Poland). We manipulated the peatland water table level (wet, intermediate and dry; on average the depth of the water table was 17.4, 21.2 and 25.3 cm respectively), and we used open-top chambers (OTCs) to create warmer conditions (on average increase of 1.2°C in OTC plots compared to control plots). Peat drying through water table lowering at this local scale had a larger effect than OTC warming treatment *per see* on *Sphagnum* mosses and vascular plants. In particular, ericoid shrubs increased with a lower water table level, while *Sphagnum* decreased. Microclimatic measurements at the plot scale indicated that both water-level and temperature, represented by heating degree days (HDDs), can have significant

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effects on the vegetation. In a large-scale complementary vegetation gradient survey replicated in three peatlands positioned along a transitional oceanic–continental and temperate–boreal (subarctic) gradient (France–Poland–Western Siberia), an increase in ericoid shrubs was marked by an increase in phenols in peat pore water, resulting from higher phenol concentrations in vascular plant biomass. Our results suggest a shift in functioning from a mineral-N-driven to a fungi-mediated organic-N nutrient acquisition with shrub encroachment. Both ericoid shrub encroachment and higher mean annual temperature in the three sites triggered greater vascular plant biomass and consequently the dominance of decomposers (especially fungi), which led to a feeding community dominated by nematodes. This contributed to lower enzymatic multifunctionality. Our findings illustrate mechanisms by which plants influence ecosystem responses to climate change, through their effect on microbial trophic interactions.

KEYWORDS
dissolved organic C, enzyme, microorganism, open-top chamber warming, phenolic compound, *Sphagnum* moss, vascular plant, water table

1 | INTRODUCTION

Peatlands contain large amounts of organic matter (Limpens et al., 2008), primarily as peat moss litter (Hajek et al., 2011; Kroken et al., 1996; Painter, 1991), making them global sinks of atmospheric carbon (C). Despite their small land cover (~3% of the Earth's land surface), peatlands are estimated to contain ~1000 Pg C (Nichols & Peteet, 2019, 2021). Hydrological conditions that favour soil waterlogging, combined with the dominance of decay-resistant *Sphagnum* mosses, hamper microbial litter decomposition so that a net accumulation of organic matter occurs. In northern peatlands, *Sphagnum* mosses are therefore fundamental 'engineers' (Van Breemen, 1995) of this C sequestration and are critical to the stability and resilience of these ecosystems (Turetsky et al., 2012). Although *Sphagnum* mosses typically dominate the plant community in northern peatlands, competition for space and nutrients with vascular plants, whose litter is more decomposable (Hobbie, 1996; Limpens et al., 2008), determines the net accumulation of peat. Thus, changes in the plant community composition of peatlands, especially reduced *Sphagnum* dominance in favour of vascular vegetation, are likely to significantly influence C storage (Bragazza et al., 2013, 2016; Dieleman et al., 2015; Jassey et al., 2018).

There are a growing number of observations about the increase in shrub cover in tundra ecosystems at both high latitudes and high altitudes. These changes have been attributed to climate warming, with potentially both positive and negative feedbacks on ecosystem processes and properties (Myers-Smith et al., 2011). In peatland ecosystems in particular, climate warming has been shown to promote the growth of vascular plants, especially ericaceous shrubs (Breeuwer et al., 2009; Buttler et al., 2015; Dieleman et al., 2015; Jassey et al., 2013). In these ecosystems, the water table is a key factor for soil capillarity and soil moisture in the rooting zone, and its level is closely related to the local climate (Słowińska et al., 2010), meaning that the effects of warmer and drier conditions are intertwined. Air warming affects soil water content, which can decrease concomitantly. Thus, shrub encroachment can be seen as a result of the combined effect of warmer and drier conditions.

Shrub encroachment over *Sphagnum* mosses is expected to modify aboveground–belowground interactions because specific changes occur in litter chemistry and/or root exudates (Crow & Wieder, 2005; Meier & Bowman, 2008; Ofiti et al., 2022; Robroek et al., 2016). For instance, increased shrub cover, and therefore more root exudates, can stimulate belowground microbial activity (Malhotraa et al., 2020) through an increased labile C content (dissolved organic C, DOC) and/or reduce the inhibitory effect on microorganisms of phenolic compounds exuded by *Sphagnum* mosses (Fenner & Freeman, 2011; Hamard et al., 2019). However, increased shrub cover can also increase the phenol content in litter and peat pore water, with cascading effects on peat biogeochemical processes, such as increased CO_2 respiration and reduced release of nitrogen (N) from decomposing litter (Bragazza et al., 2013; Dieleman, Branfireun, et al., 2016).

Besides the direct effects of vascular plant encroachment on biogeochemical processes, climate changes can influence the survival of *Sphagnum* mosses (Bragazza, 2008; Eppinga et al., 2009; Fenner & Freeman, 2011), microbial communities (Barreto et al., 2021, 2023; Jassey et al., 2013; Jassey, Chiapusio, et al., 2011; Jassey, Gilbert, et al., 2011) and plant–microbial interactions (Jassey et al., 2018), indirectly reinforcing possible changes in biogeochemical processes. For example, *Sphagnum* mosses tend to produce more secondary metabolites under warmer conditions (Sytiuk et al., 2023), especially during summer, which in turn can negatively influence microbial community structure and functions (Sytiuk et al., 2021). On the contrary, drier and warmer conditions can strongly modify fungal community composition and functioning (Asemaninejad et al., 2018; Jassey et al., 2018), which can potentially positively influence ericaceous shrubs by facilitating the symbiotic acquisition of dissolved organic N (DON; Bragazza et al., 2013). Climate change can thus have contrasting effects on microbial communities, making predictions difficult. Hence, investigations of the effects of vascular plant encroachment and warming on the linkages between plants, microbial communities and biogeochemical processes are needed, as is a deeper understanding of the impact of shrubs on the response of peatland C cycling to climate change.

In the present study, our goals were twofold. First, we aimed to better understand what drives shrub encroachment in peatlands (warming, drier conditions or both). Second, we aimed to explore the effect of ericoid shrub encroachment on peatland biogeochemistry, the interactions between vegetation and microbial communities, and possible changes in trophic relationships. We addressed these objectives by combining results after 3 years in a manipulative warming and water-level manipulation experiment in a Polish peatland (Linje mire; Lamentowicz et al., 2016) with a survey of a natural vegetation gradient in three peatlands located along a transitional oceanic–continental and temperate–boreal (subarctic) gradient. Using this unique combination of field experiment and survey, we were able to tease apart the effects of shrub encroachment and climate change on plant–soil feedbacks in biogeochemical cycling. At the local site scale, we hypothesized that (i) peat drying would have a larger effect than warming in causing the shift from *Sphagnum*-dominated to vascular plant-dominated communities with encroachment of ericaceous shrubs; (ii) the increase in ericaceous shrubs would translate to an increase in phenols, DOC and total dissolved N (TN) in peat pore water as a result of the high phenol content in vascular plant biomass; and (iii) the encroachment of ericaceous shrubs would promote fungi over bacteria, resulting in (iv) a cascade effect on soil enzymatic activities. At a large survey scale, we predicted that (v) plant–soil interactions would be modulated by mean annual temperature, with stronger cascading effects from vegetation to soil biogeochemical processes occurring in warmer sites.

2 | MATERIALS AND METHODS

2.1 | Field sites

We investigated three peatlands across a longitudinal gradient: Forbonnet in north-eastern France, Linje in northern Poland and Mukhrino in Western Siberia (Russia) (Supporting Information S1). We selected these three peatlands for several reasons: first, the sites have been monitored for several years in the context of warming and drying (open-top chamber (OTC) experiments; see project references in acknowledgements); second, they show some similarities in terms of species and microhabitats, with a high abundance of *Andromeda polifolia* and some other ericaceous shrubs (from no to high cover); third, the moss carpet is dominated by *Sphagnum* of the Cuspidata section, either *Sphagnum fallax* or *Sphagnum balticum*, which have an equivalent ecology. Overall, these sites are positioned along a transitional oceanic–continental and temperate–boreal (subarctic) gradient and at different altitudes, enabling investigation of a set of biogeochemical processes along a natural temperature gradient (see Supporting Information S1). Vascular plant species names are given according to Tutin et al. (1964–1980), and moss species names according to Corley et al. (1981).

The Forbonnet peatland is situated near the village of Frasne in the Jura Mountains of north-eastern France (46°49′35″ N, 6°10′20″ E; Supporting Information S1). The peatland site studied here covers a surface of 111 ha within a complex of three peatlands covering 300 ha and lying at 840 m a.s.l, surrounded by *Picea abies* forest patches and pastures. The peatland was listed among the EU Natura 2000 protected areas in 2002. Peat deposits reach down to 9 m depth in some places (Gauthier et al., 2019). The climate is predominantly oceanic, with humid winds from the Atlantic (westerlies) and continental anticyclones. The mean annual air temperature is ca. 6.5°C, and the annual precipitation is about 1600 mm (average 2009–2013 data from the weather station installed on site). Cold winters (mean temperature in January ca. −1.4°C) and mild summers (mean temperature in July ca. 14.6°C) characterize the climate. The study site corresponds to an undisturbed, ombrotrophic *Sphagnum*-dominated peatland encompassing a narrow transition zone from a wetter, slightly minerotrophic area (mean water table depth 16.3 cm) to a drier ombrotrophic area (mean water table depth 18.3 cm). The relatively flat wetter area is characterized by a moss cover dominated by *Sphagnum fallax* and *Sphagnum flexuosum*. Vascular plant species have low abundance in this area; the most common species are *Eriophorum vaginatum* and *Andromeda polifolia*, followed by *Scheuchzeria palustris*, *Drosera rotundifolia* and *Vaccinium oxycoccus*. The drier area is characterized by patterns of hummocks, dominated by *Sphagnum magellanicum*, *V. oxycoccus*, *E. vaginatum* and *Calluna vulgaris*, and lawns, with *Sphagnum fallax*, *Carex rostrata* and *A. polifolia* (Buttler et al., 2015). Encroachment by the tree species *Pinus rotundata* has occurred in this drier microhabitat.

Linje mire is located in northern Poland, near the city of Bydgoszcz (53°11′13″ N, 18°18′34″ E; Supporting Information S1). The mire covers a surface of 6 ha within a nature reserve of 12.7 ha (Słowińska et al., 2010) and is located at 91 m a.s.l. Since 2008, the peatland has been listed among the EU Natura 2000 protected areas. Biogenic deposits reach 11.9 m depth in the southern part of the mire (Kloss & Żurek, 2005). The mire lies in the contact zone between oceanic and continental air masses, and thus experiences transitional climate conditions. The mean annual air temperature in the area is 8.2°C and the total annual precipitation is about 530 mm (average 1951–2015 data from a station maintained by the Institute of Meteorology and Water Management, located about 25 km from the mire; Słowińska et al., 2010, 2022; Lamentowicz et al., 2016). Linje mire is surrounded by a mixed forest dominated by *Pinus sylvestris*, *Betula pendula*, *Quercus robur* and *Picea abies*. It is classified as poor fen, while ombrotrophic vegetation is present in the centre of the mire (Kucharski & Kloss, 2005). The water table depth in the study site is 15–30 cm. The moss layer is dominated by *Sphagnum* *fallax*, while the herbaceous layer is characterized by the graminoids *E. vaginatum* and *Carex rostrata*, together with the ericoids *V. oxycoccus* and *A. polifolia* (Jassey et al., 2018). *Betula nana* is also present. Linje mire and other mires in the area were drained in the past, but the peatland has been under protection since 1901 (Boińska & Boiński, 2004; Lamentowicz et al., 2016).

Mukhrino mire is located on the eastern bank of the Irtysh river, near the confluence with the Ob river in the middle taiga zone of Western Siberia, about 20 km south-east from the city of Khanty-Mansiysk. The peatland covers a surface of 65 km^2 and is located at 38 m a.s.l. (60°53′35″ N, 68°40′57″ E; Supporting Information S1). The study site lies in the UNESCO Mukhrino Field Station area (Elger et al., 2012), which covers about 1 km^2. Peat depth is 3.3 m on average and reaches about 5 m in some areas (Bleuten et al., 2020). The site is situated in the boreal climate zone, which corresponds to the subarctic climate zone of Western Europe. The data recorded over the period 2010–2019 at a weather station installed on site indicate an average mean annual air temperature of −1.0°C, with a mean monthly temperature of the warmest month (July) of 17.4°C and of the coldest month (January) of −21.5°C (Dyukarev et al., 2021). Mean annual precipitation is 553 mm (Kremenetski et al., 2003). Mukhrino mire is surrounded by mixed taiga forests dominated by *Pinus sibirica*, *Abies sibirica*, *Picea obovata*, *Populus tremula* and *Betula pubescens*. The mire is typical of the vast ombrotrophic raised *Sphagnum* bogs area in the middle of the West Siberian Plain (Ivanov & Novikov, 1976; Terentieva et al., 2016). The study site encompasses an open, flat, wet area dominated by *Sphagnum balticum* and a ridge–hollow complex. Vascular plants, such as *A. polifolia*, *Carex limosa*, *Scheuchzeria palustris* and *V. oxycoccus*, occur with high frequency in wet areas. The ridge–hollow complex combines a hummocky pine–dwarf-shrub–*Sphagnum* community dominated by *Sphagnum fuscum*, with a few *Pinus sylvestris* trees and abundant dwarf shrubs (*Ledum palustre*, *Chamaedaphne calyculata*) with *Andromeda polifolia*–*Eriophorum vaginatum* hollows dominated by *Sphagnum balticum*. The hydrology is dependent on microtopography and changes seasonally. During the summer, groundwater is about 0–10 cm below the moss surface in the wet *Sphagnum* lawn area, 5–20 cm in the *Andromeda polifolia*–*Eriophorum vaginatum* hollows, and 30–50 cm on ridges with *Sphagnum fuscum* hummocks (Dyukarev et al., 2021). Permafrost is absent from the site (Bleuten & Filippov, 2008; Filippov & Lapshina, 2008).

2.2 | Warming and water-level manipulation field experiment

To disentangle the effects of air temperature and water table depth on ericoid shrub encroachment, we manipulated both of these variables in a controlled field experiment in Linje mire (see Lamentowicz et al., 2016 for a complete description of the experimental design). We set up the experiment in May 2012 and did the measures in 2013 and 2014. We used open-top chambers (OTCs) to experimentally increase air and soil temperatures (OTC vs. ambient temperature). OTCs were constructed according to the ITEX protocol (Shaver et al., 2000); they consisted of transparent polycarbonate hexagonal chambers (50 cm high, 1.7 m top-width, 2.4 m base-width), which were placed 10 cm above the peat surface to allow air circulation. OTCs have been shown to be an effective tool to manipulate temperature at the scale of small plots in remote areas (Hollister et al., 2022). OTC treatment was combined with a hydrological manipulation modifying the peatland microtopography, to create microhabitats such as hollows and hummocks. We selected 1 m^2 plots within the bog with homogeneous plant species assemblage and comparable water table depths. Using 18 plots, three water table manipulations were randomly assigned to plots and combined with warming (OTC), yielding six treatments in triplicates—wet treatment with and without OTC, dry treatment with and without OTC, and intermediate control plots with and without OTC. In these plots, we cut four peat blocks of 50 × 50 × 30 cm on the 1 m^2 surface. For the wet treatment, we excavated further 10 cm of peat and replaced the peat blocks in a 10 cm lower position. For the dry treatment, we added the excavated peat from the wet treatment, so that the peat blocks were placed in a 10 cm higher position. In the intermediate control plots, the four peat blocks were cut and replaced immediately in their original positions. We used six additional plots were OTC and control plots were set without cutting the peat.

Each plot was equipped with air temperature and humidity sensors placed in radiation shields above the vegetation canopy (HOBO U23 pro v2 with an external data logger, Onset Computer Corporation, Bourne, MA, USA). We measured air temperature and humidity at a height of 30 cm to capture the microclimate at the plot scale. We used the temperature to calculate the heating degree days (HDDs) in years 2013 and 2014, given as the total number of degrees that day's average temperature was below 18°C. Less negative values of HDD indicate warmer conditions. In the centre of each plot, we inserted a piezometer pipe down to 100 cm depth for manual readings of water table depth. Additionally, we calculated the water table level for weekly intervals using automatic diver loggers (Onset HOBO U20-001-Ox) installed in the vicinity; we used these data to recalculate (and verify) the daily water table depth values from the piezometers.

We surveyed the vegetation following the protocol of Buttler et al. (2015), which involved field point-intercept frequency measurements with a pin at 400 points using a frame of 40 × 40 cm. We completed these surveys at peak biomass, 1 (2013) and 2 (2014) years after the beginning of the experiment. We then calculated the relative frequency (used as a percentage cover estimation) of each of the 12 species in the plots, by dividing the number of presence observations of each species by 400.

2.3 | Large-scale shrub encroachment survey

2.3.1 | Sampling design and vegetation survey

We established plots in each of the three peatland sites (Forbonnet, Linje and Mukhrino) at peak biomass in August 2014 and we did the measurements only once during that period. Specifically, we set up three plots of 50×50cm in each of four shrub classes (except in Mukhrino where three additional plots were set up in total; in Linje, these plots were separate from the experimental plots, but taken in the vicinity), using the number of *Andromeda polifolia* individuals per square metre as a reference: 0 (no cover), ~150 (low cover), ~600 (intermediate cover) and ~1200 (high cover). This resulted in a total of 39 plots across the three sites (Supporting Information S2 shows the results from the final protocol using picture analysis in all three sites). *Andromeda polifolia* was selected because (i) it is sensitive to climate change (Buttler et al., 2015; Jassey et al., 2013), (ii) it was abundant in the three peatlands and (iii) it was the most convenient plant to survey and represent the gradient of ericoid shrubs (see below).

To clearly define the four shrub classes, we first performed a preliminary field assessment of the cover and aboveground biomass of the main vascular plant species in Siberia (Mukhrino peatland) by recording the number of individuals of *A. polifolia*, *E. vaginatum*, *D. rotundifolia*, *Scheuchzeria palustris*, *V. oxycoccus* and *C. limosa* in each of the 15 plots at that site. We conducted this counting on a frame of 50×50cm placed on the soil, which was, for ease, subdivided into four cells of 25×25cm. *Andromeda polifolia* biomass correlated very well with its number of shoots ($R^2=.96$, $p<.001$, ANOVA) and the classes were best separated with boundaries set at 0, 1–150, 151–600 and 601–1200 individuals per square metre. Thus, the final sampling protocol in all three sites was based on the abundance of *A. polifolia* using these four classes.

To accurately classify the plots in all three sites, we took four high-resolution photos in each plot, one for each subplot of 25×25cm, and analysed plant cover according to Buttler et al. (2015). We performed the image analysis on a computer screen by overlaying the four images with a grid of 100 points (Gimp, version 2.8.16; see Jassey et al., 2018 for details). We identified the species overlaying the grid intersects at 200% digital magnification. After that, we merged the four grids into a single 400-point-grid image for each plot. This method compares well with the point-intercept method (Buttler et al., 2015, Appendix S1) and is less time-consuming in the field. Because we could not reliably distinguish *Sphagnum fallax* from *Sphagnum balticum* in the image analysis, we pooled these two species. Altogether, we recorded the frequencies of 13 species and calculated their relative frequencies (used as a percentage cover estimation) by dividing the number of presence observations of each species under the grid intersects by 400.

2.3.2 | Vascular plant biomass and phenol content

We cut the aboveground biomass of vascular plants within each plot at ground level and removed the vascular plant litter to leave only the moss carpet. We sorted the species into the following categories: *A. polifolia*, *V. oxycoccus*, other ligneous species, herbaceous species (e.g., other dominant species, such as *Scheuchzeria palustris* and *E. vaginatum*) and litter. We then dried the plant material in each category at 60°C until a constant dry mass was reached and weighed it, expressing the values as grams of dry matter per square metre (g DM m^{-2}). Finally, we calculated total vascular plant biomass and the ratio of total vascular plant biomass to vascular plant litter.

We quantified the total water-soluble phenol content of vascular plants and litter as a potential environmental driver of microbial communities (Jassey et al., 2014; Jassey, Chiapusio, et al., 2011). To do so, we ground 0.05g of dried plant material in a mortar, mixed the sample with 10mL distilled water, bubbled it with N, agitated it on a reciprocal shaker (150rpm) for 3h and finally filtered it (Jassey, Chiapusio, et al., 2011). We then quantified water-soluble phenols using the Folin–Ciocalteau reagent, expressing values in mg equivalent gallic acid (A760) per gram of dry matter (mg g^{-1} DM).

2.3.3 | Microbial biomass and predator: Prey mass ratio

In each plot, we extracted nine bunches of living *Sphagnum* mosses from the moss carpet according to a regular grid. We then sampled two to three *Sphagnum* shoots from each of the nine pre-sampled bunches and cut the top 3cm (including the capitula) from the shoots. We pooled these subsamples to keep one sample for each plot. We immediately fixed the samples in 20mL of glutaraldehyde (2% final concentration) and kept them in darkness at 4°C until microscopic analyses. We extracted microorganisms from the *Sphagnum* samples according to Jassey, Gilbert, et al. (2011) and counted them using inverted microscopy (fungal hyphae, cyanobacteria and microeukaryotes) or a flux cytometer (bacteria) (see Reczuga et al., 2018 for details). We determined the abundance and the size of microalgae, cyanobacteria, ciliates, flagellates, testate amoebae, rotifers and nematodes, and we identified them to the species level, when possible, using a 3-mL subsample and an inverted microscope (400×, LEICA DM IL; Utermöhl method). For fungi, we recorded in the same subsample the number and length of hyphae, as well as spores. For bacterial counts, we stained a 1-mL subsample with SYBR Green (1% final concentration) and incubated it in the dark for 15min. We then ran the subsamples in a cytometer (Guava® easyCyte) at a speed of 2μLs^{-1} and a count rate not exceeding 1000 events s^{-1}. We used epifluorescence microscopy to determine the size of bacteria: we stained the 1-mL subsamples with DAPI (4,6-diamino-2-phenylindole; 3μgmL^{-1} final concentration), incubated them in the dark for 15min, filtered them on 0.2μm black membrane filters, and examined them using fluorescence microscopy at 1000× magnification. We determined bacteria sizes manually under a microscope, following the protocol of Jassey, Gilbert, et al. (2011). We then converted the abundance of bacteria, microalgae, cyanobacteria and consumer species into biovolume ($μm^3$), calculated based on geometrical shapes using dimensions measured under the microscope (length or diameter; width; height). We converted the biovolumes to biomass (μgCg^{-1} DM) using the conversion factors given in Gilbert et al. (1998).

Using the biomass data of each microbial group, we calculated the predator: prey mass ratio (PPMR), as detailed in Reczuga et al. (2018). We used log-transformed biomass data of prey (bacteria, fungi, cyanobacteria and microalgae) and predators (ciliates, testate amoebae, rotifers and nematodes) to calculate PPMR. Although PPMR has a low taxonomic resolution, it allows comparisons across gradients (Reczuga et al., 2018) and is an important parameter capturing the complex patterns of feeding links between microbial species in a more simplified way than a food web.

2.3.4 | Peat sampling and peat enzymatic analyses

In each plot, we cut out one peat monolith of 10 cm length, 10 cm width and 20 cm depth using a knife. We discarded the upper 4 cm, comprising the moss carpet, and sampled the layer 4–9 cm from the rhizosphere. We removed roots and other living vascular plant material manually, and we stored the final sample at 4°C.

We used a catabolic response profile approach to quantify the activities of four hydrolytic enzymes. We used subsamples of 10 g from the fresh peat sampled from each plot, and we assessed relative enzyme activities under saturating substrate conditions and stable temperature (25°C). Following the methods in Jassey et al. (2016), we quantified the enzymes in microplates. Briefly, we used substrates labelled with the fluorophores 7-amino-4-methylcoumarin (MUC) or methylumbelliferone (MUB) to quantify the relative activity of enzymes responsible for the hydrolysis of one peptide (leucine-alanine-7-amido-MUC, leucine aminopeptidase), one carbohydrate (4-MUB-ß-glucopyranoside, ß-glucosidase), one N-acetyl-glucosaminidase (4- MUF-N-acetyl-b-D-glucosaminide, chitinase or acetyl-glucosidase) and one phosphate ester (4-MUB-phosphate, acid phosphatase; all substrates supplied by Sigma-Aldrich, Merck & Cie, Buchs, Switzerland). We extracted the enzymes following the protocol of Jassey et al. (2016) and analysed them in microplates. For each sample, we included four pseudo-replicate wells in a 96-well microplate. Assay wells received 38 μL of extract and 250 μL of enzyme substrate. For each sample, we included four pseudo-replicate wells containing 38 μL of boiled extract (3 h at 90°C) as a control. We then incubated the microplates at 25°C for 3 h. We monitored fluorescence spectrophotometrically with an excitation wavelength of 365 nm and emission detection at 450 nm (SynergyMX microplate reader, Agilent Technologies). We converted all measurements to nanomoles per gram of dry peat per minute (nmol g^{-1} DM min^{-1}).

2.3.5 | Peat pore water chemistry

We collected 50 mL of peat pore water from each plot by draining the water from the peat core taken at 4–9 cm depth. We analysed the samples immediately for pH and conductivity (μs cm^{-1}) in the field, and then filtered them with a 0.45 μm glass filter in a refrigerator. We measured total dissolved nitrogen (TN) and dissolved organic carbon (DOC) concentrations in the laboratory with a total C and N analyser (SHIMADZU SSM-5000A, Shimadzu Corp.). We analysed ammonium (NH_4^+), nitrite (NO_2^-), nitrate (NO_3^-) and phosphate (PO_4^{3-}) concentrations colourimetrically using a continuous flow analyser (FLOWSYS, Systea Analytical Technologies). We applied the ultraviolet visible (UV–VIS) technique to characterize the properties of DOC, measuring absorbance at 200–700 nm. We assessed humification parameters with the absorbance ratios set at 254 and 365 nm (E2:E3) and at 465 and 665 nm (E4:E6). The E4:E6 ratio has been widely used to study the humic acid fractions (Aranda et al., 2011). We determined total phenolics as described above. We estimated the dissolved organic N (DON) by subtracting NO_3^- and NH_4^+ (= dissolved inorganic N, DIN) from TN, and then calculated the DON:DIN ratio.

2.4 | Statistical analyses

2.4.1 | Warming and water-level manipulation experiment

To assess the effect of warming and water table level on peatland vegetation composition, we first performed a nonmetric multidimensional scaling (NMDS) analysis for a specific interpretation of vegetation community structure in the different warming and water table level treatments. We Hellinger-transformed the vegetation frequency data beforehand (Borcard et al., 2011) and performed NMDS using the *vegan* package (version 2.6-4) in R (R Core Team, 2022, version 4.2.2). Second, we used a multivariate distance matrix regression in R (MDMR package, version 0.5.1) analysis with 1000 permutations to test the effect of year (2013, 2014), warming treatment (OTC vs. ambient temperature) and water-level treatment (wet, intermediate or dry) on vegetation composition. Finally, we pooled all shrub frequencies (*A. polifolia*, *Betula nana*, *B. pubescens*, *Vaccinium oxycoccus* and *V. uliginosum*) to test for the response of shrub cover to warming and water table level. We used linear mixed-effects (LME) models in R (*nlme* package, version 3.1-161) with year, warming and water-level treatment as fixed effects and plot nested within year as random effects on the intercept to correct for the inflation of residual degrees of freedom that would have occurred if we had used repeated measurements as true replicates (Pinheiro et al., 2016). We checked model assumptions, including residual normality, using histograms of the residuals, Shapiro–Wilk tests and QQ plots.

2.4.2 | Shrub encroachment survey

We analysed peat pore water chemistry, peat enzymatic activities, microorganisms in *Sphagnum* mosses, phenols in plant material, and the total biomass and frequency of vascular plant species for the effects of shrub cover class (no, low, intermediate and high cover of *A. polifolia*) and site (Forbonnet, Linje and Mukhrino). We first performed LME models, followed by ANOVAs with type III sums of squares to account for the unbalanced design (*car* R package, version 3.1-1), to test the effect of shrub cover on the different variables measured in the large-scale survey. The models included cover class (i.e. the four classes of *A. polifolia* cover) and site (Forbonnet, Linje and Muckhrino) as fixed effects and plot as a random effect on the intercept. For each model, we checked the residual normality assumption using a histogram of the residuals, Shapiro–Wilk tests and QQ plots. When model assumptions were not fulfilled, we used a permutation test, implemented with the 'PermTest' function in R (pgirmess package, version 2.0.0). We first checked if the interaction term in the model was significant. If not, we simplified the model by dropping the interaction term. When the interaction between site and cover class was significant, interpretation of the main factors site and cover class would not be meaningful. Therefore, in this situation we tested the factor cover class within site. Finally, we ran multiple comparison tests (Tukey post-hoc tests) using the 'glht' function in the *multcomp* R package (version 1.4-20). The multiple comparison tests for cover class within site are not presented because there were too many pairwise comparisons for a meaningful interpretation. Instead, we applied the multiple comparison tests within each site.

Second, we ran a multiple factor analysis (MFA) for a specific interpretation of the general patterns observed between cover classes and sites. We described the entire dataset with six subtables containing variables of plant frequencies, the biomass of vascular plants including litter, peat pore water chemistry, peat enzymatic activities, phenols in vascular plants and litter, and microbial communities in *Sphagnum* mosses. We log-transformed and standardized the variables. We then layered a hierarchical clustering (ward method) of MFA site scores on a factorial map of the plots. In a second step, we ran a redundancy analysis (RDA) of the sampled plots described by the same biogeochemical response variables, using the 'rda' function in R (*vegan* package, version 2.6-4). For this analysis, we included as explanatory variables the coordinates of the samples on the first three axes of a principal component analysis (PCA) ordination applied to the vegetation matrix (species frequencies and biomass). To remove the effect of climate in the three sites, we used a matrix of covariables, containing the mean annual values of monthly average temperature, monthly maximum temperature, monthly precipitation sum and monthly average vapour pressure, extracted from the WorldClim database (https://www.worldclim.org/data/index.html). We also used RDA to analyse the dependence of microbial communities on the three selected vegetation explanatory variables, that is, biomass of *A. polifolia* and frequencies of *E. vaginatum* and of *Sphagnum fallax* plus *Sphagnum balticum*, after removing, as before, the effect of climate in the three sites.

We analysed complex interactions between mean annual temperature and abundance of *A. polifolia*, and the response of total vascular plant biomass, phenols in vascular plants, enzymatic multifunctionality, biomass of decomposers and predator:prey mass ratio across the three sites using structural equation modelling (SEM; Grace et al., 2014). We used a path analysis approach, a particular case of SEM involving only quantified variables. We calculated enzymatic multifunctionality (Menz) as described in Jassey et al. (2018). Specifically, we used sites scores from the PCA as a proxy for Menz, an averaging method that attempts to summarize multiple enzyme activities, where high values of Menz mean high values of many, but not necessarily all, of the enzyme activities included (Maestre et al., 2012). Based on current knowledge of shrub encroachment, we built an a priori model of hypothesized causal relationships among all the measured variables that we subjected to SEM. We fitted the paths of the SEM as previously described for the LME models, using the *piecewiseSEM* R package (version 2.3.0; Lefcheck, 2016). We selected this approach because it made it possible to use the Shipley's test of d-separation to assess whether direct or indirect paths were missing from the a priori model. We evaluated the adequacy of the model via several tests, including a non-significant Fisher's C statistic ($p > .05$), and a low Akaike information criterion (AIC; Grace et al., 2010).

3 | RESULTS

3.1 | Effect of experimental warming and water-level manipulation on abiotic conditions

On average, air temperature was 1.2°C higher in OTC plots compared to plots without OTC (marginally significant). Increase in mean daily maximum air temperature was 1.1 to 1.8°C (Samson et al., 2018). The mean water depth in the dry treatment was 25.3 cm (lower than in wet treatment, $p < .001$, ANOVA), in the intermediate treatment it was 21.2 cm (lower than in the wet treatment, $p < .001$, ANOVA), and in the wet treatment it was 17.4 cm. Interaction between warming and water table manipulation was not significant.

3.2 | Vegetation response to experimental warming and water-level manipulation

In the field experiment at Linje mire, the NMDS analysis showed that vegetation differed significantly among the wet, intermediate and dry water-level treatments, in both 2013 and 2014 ($R^2 = .17$, $p < .01$; Figure 1a,b). By contrast, OTC warming did not significantly impact the vegetation ($R^2 = .03$, $p = .59$; Figure 1a,b). The NMDS analysis further indicated a difference in vegetation between 2013 and 2014 ($R^2 = .16$, $p < .01$; Figure 1a,b).

Annual variability in the vegetation composition was driven by shifts in annual temperature and precipitation. On average, the water table depth was 28 cm in 2014 and 15 cm in 2013, indicating drier conditions in 2014. In addition to being drier, 2014 was also warmer than 2013, with fewer HDDs in 2014 (−277) than in 2013 (−319). Shifts in vegetation composition were driven by a decrease in *Sphagnum* cover (−77% after 2 years, $p < .001$, LME model) and by an increase in vascular plant cover (graminoids and ericoids; +47%, $p < .001$, LME model). In particular, the total frequency of shrubs increased by 28% in 2013 and 23% in 2014 with the drop in water-level ($p < .001$, LME model; Figure 1c). The RDA ordination plot shows that the frequencies of shrubs, such as *V. oxycoccus*, *B. nana* and *A. polifolia*, correlate negatively with a higher water table and positively with

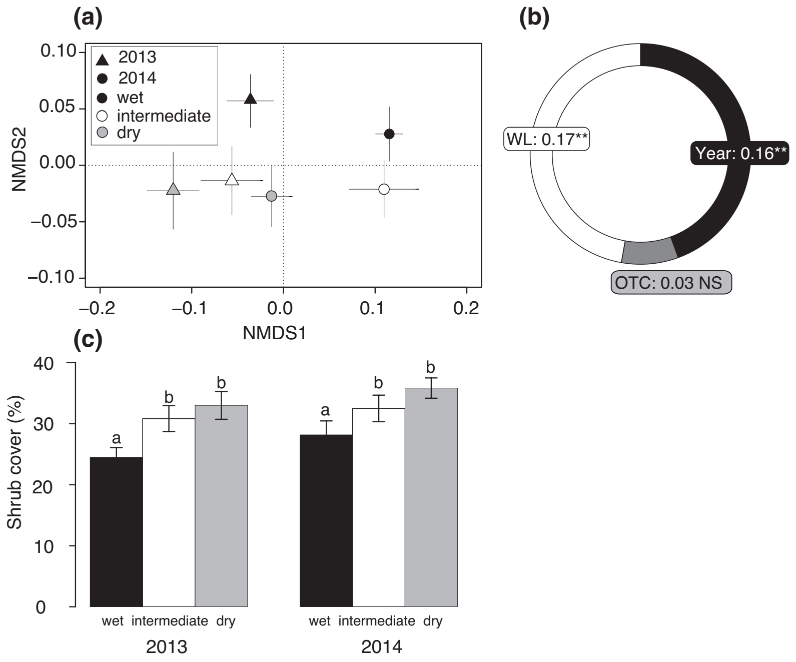

FIGURE 1 Relationship between vegetation (species frequencies) in the plots of the manipulative field experiment in Linje mire, Poland and water table level (dry, intermediate or wet), warming treatment (warming with open-top chambers [OTCs] vs. ambient temperature) and sampling year (2013 or 2014) ($N=24$). Scatter plot of nonmetric multidimensional scaling (NMDS) analysis (a), R^2 and its significance for water-level treatment (WL), warming treatment (OTC), and sampling year in MDMR analysis, with NS, not significant ($p\geq.1$); '*' $.05\leq p<.1$; *$.01\leq p<.05$; **$.001\leq p<.01$; ***$p<.001$ (b), and shrub cover in the different treatments and years (c). Different letters indicate significant differences according to multiple comparison Tukey post-hoc tests. In (a) and (c), warming treatments are pooled for the sake of clarity and since this treatment was not significant.

warmer conditions (HDD^{-1}) (Supporting Information S3), as does the frequency of *Eriophorum vaginatum*, while other species have a central position along the main gradient of axis 1 and therefore had a weaker response to the treatments.

3.3 | Response of vegetation and peat pore water chemistry to shrub encroachment across sites

Total plant biomass and phenol concentration in plant biomass varied among the three sites, but both showed a consistent increase with increasing shrub encroachment, by +82% and+60% respectively (Table 1, Figure 2). Linje had the highest phenol content in total biomass, while in Mukhrino the litter was richer in phenols under no or low cover of *A. polifolia* (Supporting Information S4). Peat pore water chemistry generally showed a significant site effect (Table 1). Linje had the highest values for DOC, phenols, conductivity, NO_3^-, PO_4^{3-} and DON:DIN (Figure 3; Supporting Information S5). In contrast, Mukhrino had the highest values for NH_4^+ and TN and the lowest for NO_3^- (Figure 3; Supporting Information S5). The effect of shrub encroachment was significant only for DOC, phenols, conductivity, NO_2^- and NO_3^-, and marginally significant for pH (Table 1). Overall, pore water chemistry showed the lowest values under no cover of *A. polifolia* and higher values when *A. polifolia* cover increased, although differences between low, intermediate and high cover did not show a clear and significant trend (Figure 3). Extinction rates E2:E3 and E4:E6 responded significantly to site and shrub cover class, but they showed different responses among the sites (Table 1). Linje had higher E2:E3 ratios under no cover of *A. polifolia* (Supporting Information S6). E4:E6 showed the opposite trend, increasing with increasing *A. polifolia* cover. Such patterns were not detected in the two other sites.

3.4 | Response of microbial community composition, PPMR and enzyme activity to shrub encroachment across sites

Microbial community composition differed widely among the sites (Figure 4a; site, $p<.001$; $R^2=.40$). Forbonnet was characterized by a greater biomass of microalgae and nematodes compared with the other sites, while Linje was characterized by a greater biomass of cyanobacteria compared with Forbonnet and Mukhrino (Table 1, Figure 5; Supporting Information S7 and S8). Furthermore, Mukhrino was characterized by a greater biomass of bacteria (Table 1; Supporting Information S7). Shrub cover class was significant within each site (Figure 4a; site × cover class, $p=.002$), especially in Forbonnet and Linje where microbial communities without *A. polifolia* cover differed considerably from communities with *A. polifolia* cover. More specifically, fungi, testate amoebae, nematodes and microalgae were particularly sensitive to shrub cover (Table 1, Figure 5; Supporting Information S7), although their respective

TABLE 1 Peat pore water chemistry, peat enzymatic activities, microorganisms in *Sphagnum* mosses, phenols in plant material and total biomass and frequency of ericaceous shrubs according to *Andromeda polifolia* cover class and site.

		***Andromeda polifolia* cover class**			
Parameter	**Unit**	**High ($N = 9$)**	**Intermediate ($N = 12$)**	**Low ($N = 9$)**	**No ($N = 9$)**
Pore water chemistry					
Dissolved organic C (DOC)	mg L^{-1}	132.0 ± 22.1 b	149.9 ± 19.3 b	138.6 ± 23.0 b	88.0 ± 14.0 a
Dissolved total N (TN)	mg L^{-1}	3.5 ± 0.8 a	5.3 ± 1.2 a	4.0 ± 0.5 a	2.3 ± 0.5 a
Phenols	mg L^{-1}	25.9 ± 2.9 ab	28.3 ± 3.3 b	26.7 ± 3.8 ab	19.3 ± 1.9 a
Extinction ratio E2.E3		3.9 ± 0.2	4.1 ± 0.2	4.0 ± 0.3	4.7 ± 0.2
Extinction ratio E4.E6		3.3 ± 0.3	3.3 ± 0.3	3.4 ± 0.4	2.4 ± 0.1
pH		4.9 ± 0.3 a	4.8 ± 0.2 a	4.6 ± 0.3 a	5.1 ± 0.2 a
Conductivity	μs cm^{-1}	60.3 ± 3.0 ab	62.3 ± 2.2 b	63.4 ± 3.6 b	55.7 ± 3.4 a
Nitrite (NO_2^-)	mg L^{-1}	0.04 ± 0.01 ab	0.05 ± 0.01 b	0.06 ± 0.02 ab	0.02 ± 0.00 a
Nitrate (NO_3^-)	mg L^{-1}	0.09 ± 0.02 ab	0.12 ± 0.02 b	0.11 ± 0.03 ab	0.07 ± 0.01 a
Ammonium (NH_4^+)	mg L^{-1}	0.91 ± 0.57 a	1.28 ± 0.45 a	0.55 ± 0.26 a	0.30 ± 0.15 a
Phosphate (PO_4^{3-})	mg L^{-1}	0.13 ± 0.08 a	0.23 ± 0.16 a	0.17 ± 0.09 a	0.10 ± 0.09 a
DON:DIN ratio		8.35 ± 2.78 a	6.87 ± 2.02 a	10.52 ± 2.62 a	10.19 ± 3.54 a
Enzymatic activities in peat					
Acid phosphatase	nmol min^{-1} g^{-1} DM[†]	3.30 ± 0.95	1.02 ± 0.14	2.39 ± 0.72	1.43 ± 0.17
Acetyl-glucosidase	nmol min^{-1} g^{-1} DM	0.10 ± 0.03 a	0.10 ± 0.02 a	0.17 ± 0.03 a	0.18 ± 0.06 a
β-glucosidase	nmol min^{-1} g^{-1} DM	0.15 ± 0.03	0.13 ± 0.02	0.14 ± 0.02	0.30 ± 0.08
Leucine aminopeptidase	nmol min^{-1} g^{-1} DM	5.37 ± 1.02 a	3.97 ± 0.49 a	4.94 ± 0.45 a	13.50 ± 3.68 b
Enzymatic multifunctionality		−0.21 ± 0.14 a	−0.35 ± 0.1 a	−0.24 ± 0.1 a	0.92 ± 0.46 b
Microorganisms in Sphagnum mosses					
Microalgae	μg C g^{-1} DM	126 ± 50	75 ± 33	57 ± 18	49 ± 20
Cyanobacteria	μg C g^{-1} DM	86 ± 28 a	52 ± 23 a	98 ± 44 a	245 ± 174 a
Flagellates	μg C g^{-1} DM	2 ± 1	7 ± 5	10 ± 6	16 ± 7
Testate amoebae	μg C g^{-1} DM	461 ± 77	382 ± 59	315 ± 65	379 ± 108
Ciliates	μg C g^{-1} DM	22 ± 17	5 ± 3	7 ± 3	9 ± 5
Rotifers	μg C g^{-1} DM	65 ± 16	64 ± 15	73 ± 28	85 ± 19
Fungi	μg C g^{-1} DM	195 ± 41	251 ± 54	294 ± 81	63 ± 24
Nematodes	μg C g^{-1} DM	18 ± 3 ab	18 ± 8 ab	34 ± 15 b	7 ± 3 a
Bacteria	μg C g^{-1} DM	37 ± 8 b	36 ± 6 ab	28 ± 10 a	58 ± 10 b
Phenols in plant material					
Andromeda polifolia	mg g^{-1} DM	16.3 ± 0.5 b	16.7 ± 0.5 b	16.7 ± 0.9 b	0.0 ± 0.0 a
Vaccinium oxycoccus	mg g^{-1} DM	15.3 ± 0.2	13.7 ± 1.3	15.5 ± 0.1	6.8 ± 2.7
Other vascular plants	mg g^{-1} DM	10.3 ± 0.8 a	10.5 ± 0.6 a	10.9 ± 0.6 a	10.3 ± 0.7 a
Total biomass	mg g^{-1} DM	42 ± 1.2 b	40.9 ± 1.6 b	43.1 ± 1.2 b	17.1 ± 3.4 a
Litter	mg g^{-1} DM	4.6 ± 0.3	4.3 ± 0.4	4.9 ± 0.8	6.1 ± 0.7
Ericaceous shrubs[‡]					
Biomass	g m^{-2} DM	158.3 ± 29.8 ab	102.7 ± 15.4 b	115.3 ± 46.5 ab	27.3 ± 10.1 a
Total frequency	%	28 ± 4 b	17 ± 2 b	18 ± 6 a	7 ± 3 a
Total biomass of vascular plants	g m^{-2} DM	211 ± 47 c	182 ± 35 b	286 ± 68 b	55 ± 17 a

Note: Values are means ± SE. Different letters indicate significant differences between cover classes and sites, where b > a (Tukey post-hoc tests). Significance levels are indicated for the full (with interaction) and reduced (without interaction) models. The statistical significance of cover class, site, site × cover class interaction and cover class within site is indicated with: NS, not significant ($p \geq .1$); '*' $.05 \leq p < .1$; * $.01 \leq p < .05$; ** $.001 \leq p < .01$; *** $p < .001$. Sites are Forbonnet in France (F), Linje in Poland (L) and Mukhrino in Siberia (M).

[†] Peat dry mass.

[‡] Includes *Andromeda polifolia*, *Vaccinium oxycoccus*, *Ledum palustre and Betula nana*.

Site			Full model			Reduced model	
F (*N* = 12)	L (*N* = 12)	M (*N* = 15)	Site × cover class	Cover class	Site	Site	Cover class within site
78.2 ± 3.9 a	199.1 ± 17.7 b	113.2 ± 10.0 a	NS	***	***		
2.2 ± 0.2 a	3.8 ± 0.3 ab	5.2 ± 1.0 b	NS	NS	*		
19.7 ± 0.9 a	35.7 ± 3.1 b	21.4 ± 1.6 a	NS	*	***		
4.1 ± 0.1 ab	3.7 ± 0.3 a	4.5 ± 0.2 b	***	(NS)	(**)	**	***
2.5 ± 0.1 a	3.8 ± 0.4 b	3 ± 0.1 a	***	(NS)	(***)	**	**
5.0 ± 0.2 b	4.1 ± 0.1 a	5.3 ± 0.1 b	NS		***		
54.7 ± 2.7 a	70.3 ± 0.7 b	57.4 ± 1.8 a	NS	*	***		
0.04 ± 0.00 a	0.07 ± 0.01 b	0.02 ± 0.00 a	NS	*	***		
0.11 ± 0.01 b	0.15 ± 0.02 b	0.05 ± 0.01 a	NS	*	***		
0.30 ± 0.07 a	0.18 ± 0.12 a	1.70 ± 0.43 b	NS	NS	*		
0.01 ± 0.01 a	0.51 ± 0.15 a	0.00 ± 0.00 a	NS	NS	NS		
5.78 ± 1.16 a	15.72 ± 2.03 b	5.73 ± 2.22 a	NS	NS	**		
2.64 ± 0.46	1.35 ± 0.55	1.90 ± 0.53	*	(.)	(.)	(.)	*
0.13 ± 0.02 a	0.24 ± 0.04 b	0.05 ± 0.01 a	NS	NS	***		
0.21 ± 0.02	0.24 ± 0.06	0.09 ± 0.01	*	(NS)	(NS)	NS	*
7.49 ± 1.72 a	8.58 ± 2.90 a	4.60 ± 0.39 a	NS	*	NS		
0.38 ± 0.21 b	0.1 ± 0.37 ab	−0.39 ± 0.06 a	NS	*	**		
185 ± 39 b	25 ± 5 a	31 ± 4 a	*	(**)	(***)	**	*
49 ± 10 a	307 ± 123 b	15 ± 3 a	NS	NS	***		
3 ± 2	15 ± 7	8 ± 4	NS	NS	NS		
376 ± 85	342 ± 78	424 ± 40	***	(***)	(NS)	NS	***
21 ± 13	2 ± 1	9 ± 3	NS	NS	NS		
83 ± 12	102 ± 25	36 ± 3	NS	NS	NS		
236 ± 69	197 ± 55	185 ± 36	*	(*)	(NS)	NS	*
41 ± 12 b	5 ± 1 a	13 ± 2 a	NS		***		
45 ± 6 b	12 ± 5 a	57 ± 5 b	(.)	(***)	(***)	***	***
11.0 ± 1.9 a	13.5 ± 2.4 b	13.6 ± 1.8 b	NS	***	***		
12.8 ± 1.7	15.6 ± 0.1	10.8 ± 1.7	*	(*)	(NS)	NS	**
10.2 ± 0.4 b	12.8 ± 0.2 c	8.9 ± 0.4 a	NS	NS	***		
34 ± 3.7 a	41.9 ± 2.5 b	33.2 ± 3.4 a	NS	***	***		
3.4 ± 0.4	4.5 ± 0.1	6.5 ± 0.5	***	(**)	(NS)	NS	***
67.1 ± 12.0 a	194.9 ± 32.6 b	53.1 ± 11.0 a	***	(***)	(***)	***	***
11 ± 2 a	31 ± 4 b	11 ± 2 a	***	(***)	(***)	***	***
207 ± 45 a	304 ± 44 b	68 ± 12 a	***	(***)	(***)	***	***

responses to increasing *A. polifolia* cover differed among sites. For example, testate amoebae responded negatively to shrub cover in Forbonnet and positively in Linje and Mukhrino ($p<.001$, ANOVA, Supporting Information S7), while nematodes and fungi responded positively in each site ($p=.01$, ANOVA; Figure 5 and Supporting Information S7). Overall, these specific changes resulted in shifts in the PPMR ratio (Figure 4b), which was driven mostly by a shift in the total biomass of predators (Figure 4c). In particular, the biomass of predators decreased with increasing shrub cover in Forbonnet ($p<.01$, ANOVA, Figure 4c), while it increased in Linje and Mukhrino ($p<.01$, ANOVA, Figure 4c).

As for microbial community composition, enzyme multifunctionality differed widely among sites and shrub cover classes (site × shrub cover class, $p<.01$, ANOVA, Figure 5b). Enzyme multifunctionality was highest in Forbonnet, intermediate in Linje and lowest in Mukhrino (Table 1, Figure 5b). Among the *A. polifolia* cover classes, enzyme multifunctionality decreased by 70% between no cover and the low, intermediate and high cover classes ($p<.01$, ANOVA, Figure 5b). This pattern was driven by an apparent decrease in leucine aminopeptidase with increasing cover of *A. polifolia* (Figure 5a), and also in β-glucosidase at the Linje site (Supporting Information S9). A similar trend, albeit not significant, appeared for acetyl-glucosidase. Acid phosphatase had the highest values in Mukhrino under a high cover of *A. polifolia*.

3.5 | Linkages between climate, shrub encroachment and aboveground and belowground components

Figure 6 shows the change in microbial communities along the gradient of changing vegetation, in particular with respect to the species that were significant in the RDA. *Sphagnum* mosses are correlated with bacteria, ciliates, rotifers and flagellates, while on the opposite side of the ordination nematodes and fungi are correlated with *A. polifolia* and *E. vaginatum*. The global multivariate approach with the MFA using all biogeochemical variables is given in Supporting Information S10. As seen in the sample's factorial map, the three sites do not overlap and have some distinct characteristics, despite following a similar overall gradient. This might be related to the different climate conditions and minerotrophic statuses in the three sites and their potential influence on some biogeochemical properties. To remove the climate effect and clarify the relationship between the gradient of ericaceous shrubs and the biochemical pattern, we ran an RDA by removing, as covariables, the climate properties in the three sites. Furthermore, we simplified the vegetation gradient by using the coordinates of samples on the first three axes of a PCA ordination applied to the vegetation matrix. Most of the dataset's variability lies along axis 1 in the resulting scatter plot (Figure 7). Here, the right side of axis 1, which represents the vascular plant side, in particular the ericoid shrub component, is correlated with high fungi biomass, as opposed to bacteria biomass, with high values of DOC, TN, E4:E6, phenolics in peat pore water and phenol concentration in vascular plant biomass. On the left side of axis 1, where *Sphagnum* mosses are dominant, the enzymatic activities of leucine aminopeptidase and β-glucosidase are highest, the E2:E3 ratio is higher, and the biomasses of bacteria, ciliates and rotifers are also higher. A higher phenol concentration in litter is also characteristic of this side of the gradient.

The SEM model shows the dual effect of warming and shrub encroachment on the linkages between *A. polifolia* cover, vascular plant biomass and microbial properties (Figure 8). First, it confirms that an increase in the frequency of *A. polifolia* mirrored the increase in vascular plant biomass ($r\partial=0.61$) and consequently phenols in vascular plant biomass ($r\partial=0.97$). The SEM model also shows that total vascular plant biomass increased with increasing air temperature ($r\partial=0.59$). Increased plant biomass ($r\partial=-0.86$) and phenols ($r\partial=-0.35$) in plant biomass directly and negatively impacted enzymatic multifunctionality. These shifts also indirectly influenced enzymatic multifunctionality through changes in microbial communities. Increased total plant biomass promoted decomposer biomass ($r\partial=0.79$), which in turn negatively fed back on PPMR ($r\partial=-0.53$). Shifts in PPMR further triggered shifts in enzymatic multifunctionality ($r\partial=-0.25$). Finally, the SEM results also highlight a direct effect of warming on decomposers ($r\partial=-0.6$), PPMR ($r\partial=-0.35$) and enzyme multifunctionality ($r\partial=1.08$).

4 | DISCUSSION

The direction and magnitude of responses of peatland vegetation to climate changes are indicators of a shift in ecosystem functioning (Dise, 2009). Peatland functioning, in particular the accumulation of peat, strongly depends on the physiological status and photosynthetic activity of plants, which are tightly related to soil and water physico-chemical properties, as well as on the proportions of plant functional groups (Kuiper et al., 2014; Mao et al., 2018). Our aims were to explore whether warmer and/or drier conditions drive vascular plant encroachment in peatlands and to test the consequences of vascular plant encroachment for peatland plant–soil interactions across climatic gradients. In line with our first hypothesis, our manipulative field experiment in Linje mire showed that drier conditions were the main driver of vascular plant encroachment in the peatland. Temperature increase through OTCs (i.e. OTC treatment and measured HDD) caused only marginal shifts in vegetation composition, which contradicts previous findings (Buttler et al., 2015; Lyons et al., 2020). Such discrepancies among findings can be explained by the intensity of the OTC effect (Hollister et al., 2022), which was slightly lower in our study compared with other studies (Delarue et al., 2015; Jassey et al., 2013). This difference could have resulted from the use of sun shields with the temperature sensors and the sensor placement at 30 cm height in our study, in contrast to the use of unprotected thermocouples in other experiments, where temperature reacts faster to changes in the amount of radiation. However, the shrub encroachment survey replicated in three peatlands spread along a climatic gradient revealed the dual effect of a warmer climate

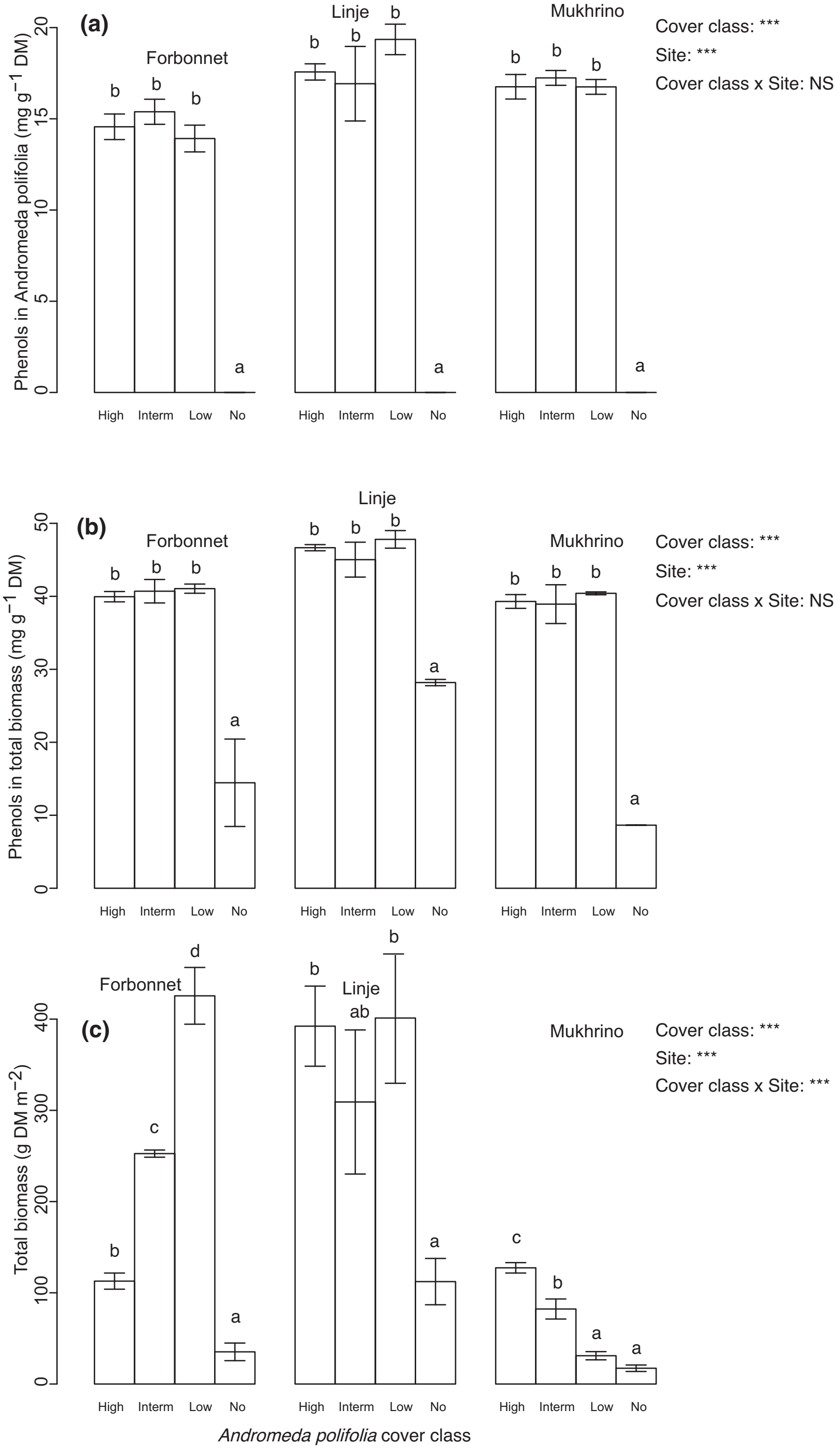

FIGURE 2 Phenol concentrations in *Andromeda polifolia* leaves (a) and in total biomass (b), and total biomass of vascular plants (c) in the four different cover classes of the ericaceous shrub *A. polifolia* in each of the three sites (Forbonnet in France, Linje in Poland and Mukhrino in Siberia). Phenol concentrations are expressed in milligrams per gram of plant dry matter (DM). Each bar represents the mean value ± SE. The statistical significance of cover class, site and their interaction is indicated with: NS, not significant ($p \geq .1$); '*' $.05 \leq p < .1$; *$.01 \leq p < .05$; **$.001 \leq p < .01$; ***$p < .001$. Different letters indicate significant differences in pairwise comparisons (Tukey post-hoc tests) (see Table 1 for complete results of tests).

and shrub encroachment on peatland plant–soil interactions, and hence peatland functioning. These findings confirm that the combination of altered temperature and water regime in manipulative field experiments provides a more truthful perspective than changes in only one climatic variable (Antala et al., 2022). Our study also demonstrates that both a vegetation shift and warming have the capacity to affect rates of belowground processes involved in the peatland carbon cycle. This validates the suggestion by Dieleman, Lindo, et al. (2016), who worked with monoliths, that contributions from the aboveground system are needed to fully understand changes in DOC quality and subsequent ecosystem dynamics.

We found in our experiment that climate change, and especially drier conditions, favours most peatland shrubs, which are becoming more abundant. This finding was previously described in

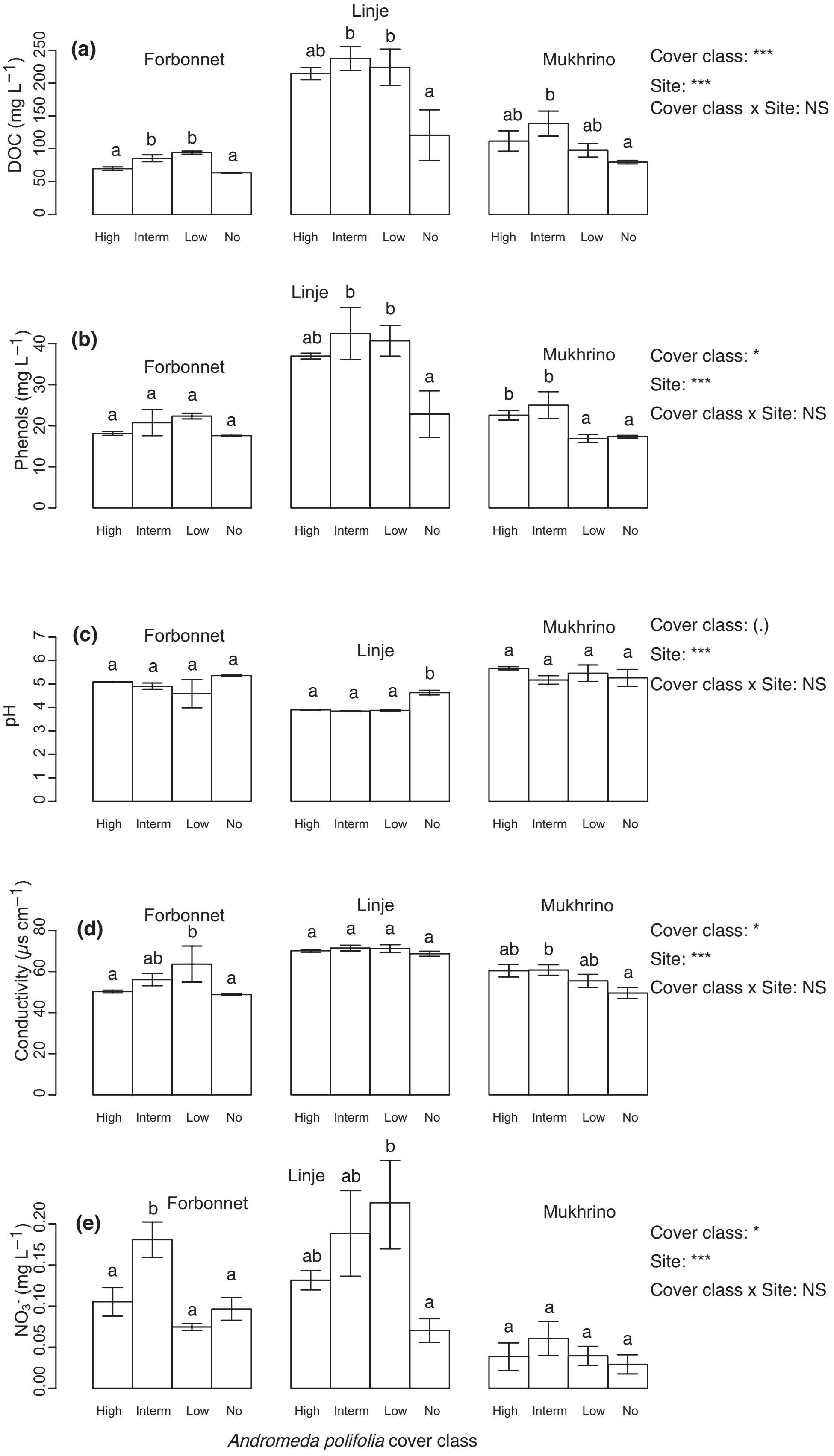
(a)
DOC (mg L−1)
0 50 100 150 200 250
Forbonnet
a b b a
Linje
ab b b a
Mukhrino
ab b ab a
Cover class: ***
Site: ***
Cover class x Site: NS
High Interm Low No
(b)
Phenols (mg L−1)
0 10 20 30 40
Forbonnet
a a a a
Linje
ab b b a
Mukhrino
b b a a
Cover class: *
Site: ***
Cover class x Site: NS
(c)
pH
0 1 2 3 4 5 6 7
Forbonnet
a a a a
Linje
a a a b
Mukhrino
a a a a
Cover class: (.)
Site: ***
Cover class x Site: NS
(d)
Conductivity (μs cm−1)
0 20 40 60 80
Forbonnet
a ab b a
Linje
a a a a
Mukhrino
ab b ab a
Cover class: *
Site: ***
Cover class x Site: NS
(e)
NO3- (mg L−1)
0.00 0.05 0.10 0.15 0.20
Forbonnet
a b a a
Linje
ab ab b a
Mukhrino
a a a a
Cover class: *
Site: ***
Cover class x Site: NS
High Interm Low No
Andromeda polifolia cover class

FIGURE 3 Dissolved organic carbon DOC (a), phenols (b), pH (c), conductivity (d) and nitrate (NO_3^-; e) in peat pore water in the four different cover classes of the ericaceous shrub *Andromeda polifolia* in each of the three sites (Forbonnet in France, Linje in Poland and Mukhrino in Siberia). Each bar represents the mean value ± SE. The statistical significance of cover class, site, and their interaction is indicated with: NS, not significant ($p \geq .1$); '*' $.05 \leq p < .1$; *$.01 \leq p < .05$; **$.001 \leq p < .01$; ***$p < .001$. Different letters indicate significant differences in pairwise comparisons (Tukey post-hoc tests) (see Table 1 for complete results of tests). Nitrite (NO_2^-) is not displayed; it follows the same pattern as nitrate.

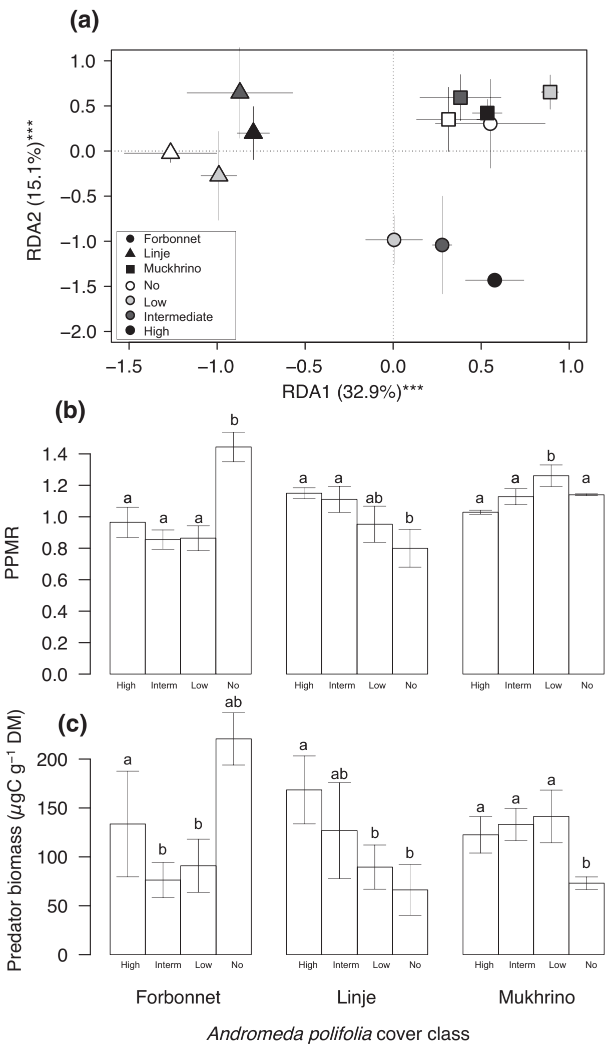

FIGURE 4 Microbial communities in the three peatland sites (Forbonnet in France, Linje in Poland and Mukhrino in Siberia) sampled along a gradient of increasing cover of the ericaceous shrub *Andromeda polifolia* (no, low, intermediate and high). Ordination plot of redundancy analysis (RDA; a), predator:prey mass ratio (PPMR; b), and predator biomass, expressed per gram of dry matter (DM) of peat (c). In (b) and (c), each bar represents the mean value ± SE, and different letters indicate significant differences in pairwise comparisons (Tukey post-hoc tests). Significance of axes is given with: NS, not significant ($p \geq .1$); '*' $.05 \leq p < 0.1$; *$.01 \leq p < .05$; **$.001 \leq p < .01$; ***$p < .001$.

other climate change experiments (Breeuwer et al., 2009; Buttler et al., 2015; Gunnarsson et al., 2002). In particular, Breeuwer et al. (2009) showed in their mesocosm experiment that an increased occurrence of periods with low water table depth shifts the peatland vegetation from graminoid to ericoid vascular plant cover, resembling the change from hollow to lawn or hummock vegetation. Drought is perhaps the greatest abiotic stress limiting plant growth and development, also in peatlands (Dise, 2009). This phenomenon can happen even in peatlands commonly believed to be wet, particularly at the soil surface where there is an important functional layer known as acrotelm (Ingram, 1982). Shrubs use different strategies to cope with drier conditions and drought: (i) they possess leaf traits adapted to a low water table, such as a thick layer of waxes, stomata only on the abaxial side or revolute margins; and (ii) they are associated with ericoid fungi, which help with nutrient acquisition and water supply (Cullings, 1996). Fungi are particularly tolerant to drought and are able to compensate for unfavourable soil moisture conditions, as long as water is still available in other zones of the mycelial network (Guhr et al., 2015). This mechanism operates after water-level drawdown, which explains, in our study, the increase in fungi biomass with shrub encroachment. Alternatively, changes in plant phenology are also part of the mechanism of vegetation shifts in response to climate change (Parmesan & Yohe, 2003; Visser & Both, 2005). Such changes can involve shifts in the flowering of *A. polifolia* (Aerts et al., 2004) or in the seasonal growth rates of leaves and roots of *E. vaginatum* (Sullivan & Welker, 2005). In the context of climate change, shifts in plant phenology and species composition, or even the loss of certain plant functional types (PFTs), are expected to alter nutrient availability, energy budget, trace gas fluxes and carbon storage in response to environmental stress (Dieleman et al., 2015; Kuiper et al., 2014; Ward et al., 2009; Weltzin et al., 2003).

Using a natural gradient of increasing cover of ericoid shrubs across France, Poland and Western Siberia, we further demonstrate that the increase in ericaceous shrubs modifies soil biogeochemistry and plant–soil interactions and that this cascading effect is supported by warmer conditions, which agrees with our fifth hypothesis. The SEM model confirmed the influence of *A. polifolia* cover and its effect on the various compartments of above and below components, finally leading to lower enzymatic multifunctionality. The SEM model demonstrated not only that the effect of shrub encroachment is greater in warmer sites (e.g. large total vascular plant biomass and biomass of ericaceous shrubs in Linje, which has the highest mean temperature; Figure 2 and Supporting Information S2), but also that this cascades down to the dominance of decomposers (especially fungi), which ultimately contributes to lower enzymatic multifunctionality. The increase in ericoid shrubs was marked by an increase in phenols in peat pore water, verifying our second hypothesis. This is the consequence of higher phenol concentrations in vascular plant biomass and

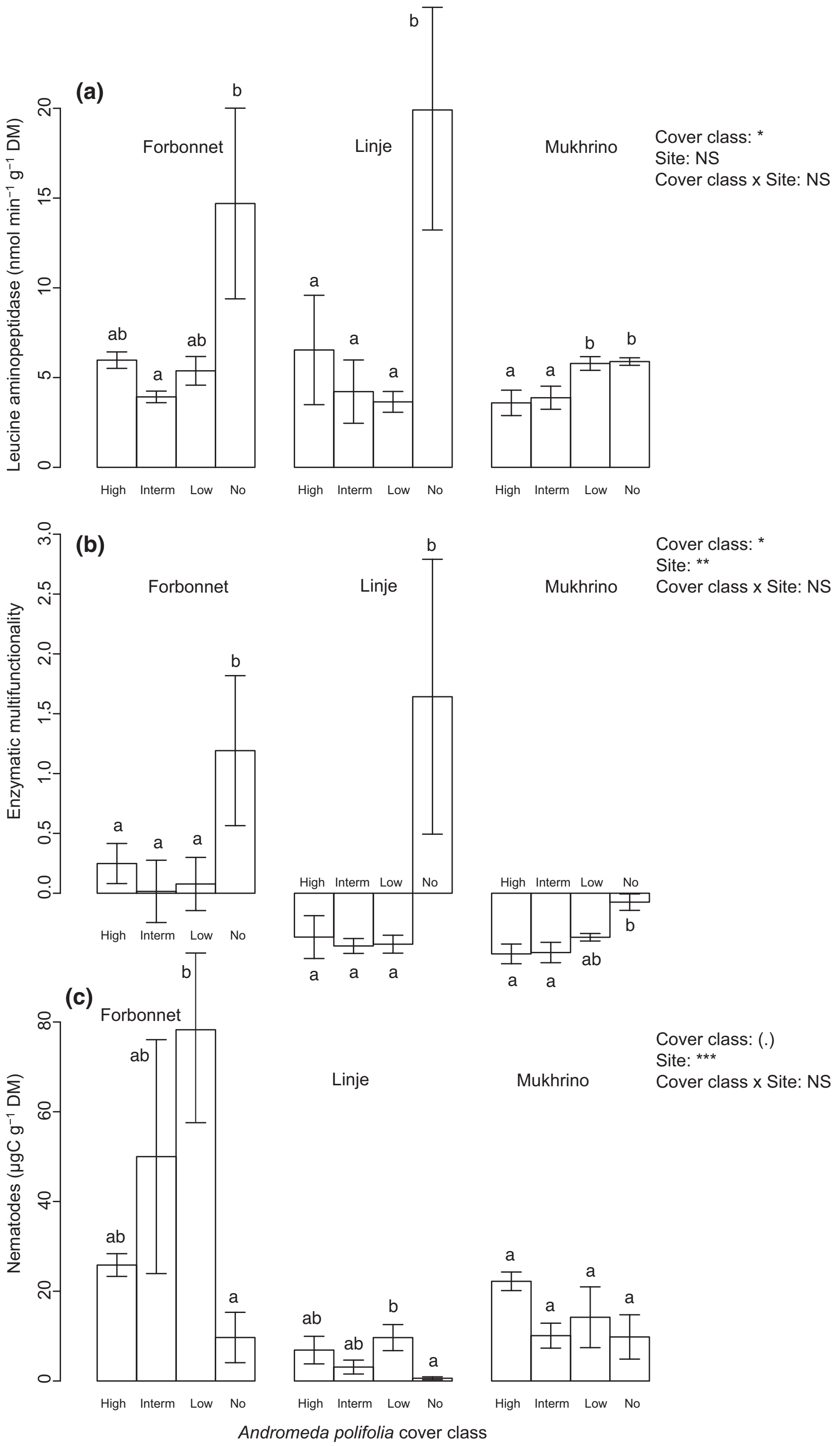

FIGURE 5 Leucine aminopeptidase enzyme activity in peat (a), enzymatic multifunctionality (b), and nematode biomass per gram of dry matter (DM) of peat (c) in the different cover classes of the ericaceous shrub *Andromeda polifolia* in each of the three sites (Forbonnet in France, Linje in Poland and Mukhrino in Siberia). Each bar represents the mean value ± SE. The statistical significance of cover class, site, and their interaction is indicated with: NS, not significant ($p \geq 0.1$); '*' $.05 \leq p < .1$; $*.01 \leq p < .05$; $**.001 \leq p < .01$; $***p < .001$. Different letters indicate significant differences in pairwise comparisons (Tukey post-hoc tests) (see Table 1 for complete results of tests).

translated to higher concentrations of DOC and, to some extent, TN in the pore water.

Phenols are critical compounds related to peat properties (Naumova et al., 2013; Wang et al., 2015). Vascular plants produce easily leachable polyphenols or exude polyphenolic compounds by roots, which then persist in pore water (Dieleman, Branfireun, et al., 2016; Dorrepaal et al., 2005). In particular, shrubs produce long-chain phenols with high resistance to breakdown (McClymont et al., 2011). This suggests that shrub expansion modifies peat chemistry by introducing more recalcitrant compounds and by reducing N availability (Bragazza et al., 2013; Dieleman et al., 2015; Frey et al., 2013), thus hindering peat from decomposition (Wang et al., 2015). Our results corroborate such a hypothesis. We found that the increase in polyphenols in plant biomass was negatively

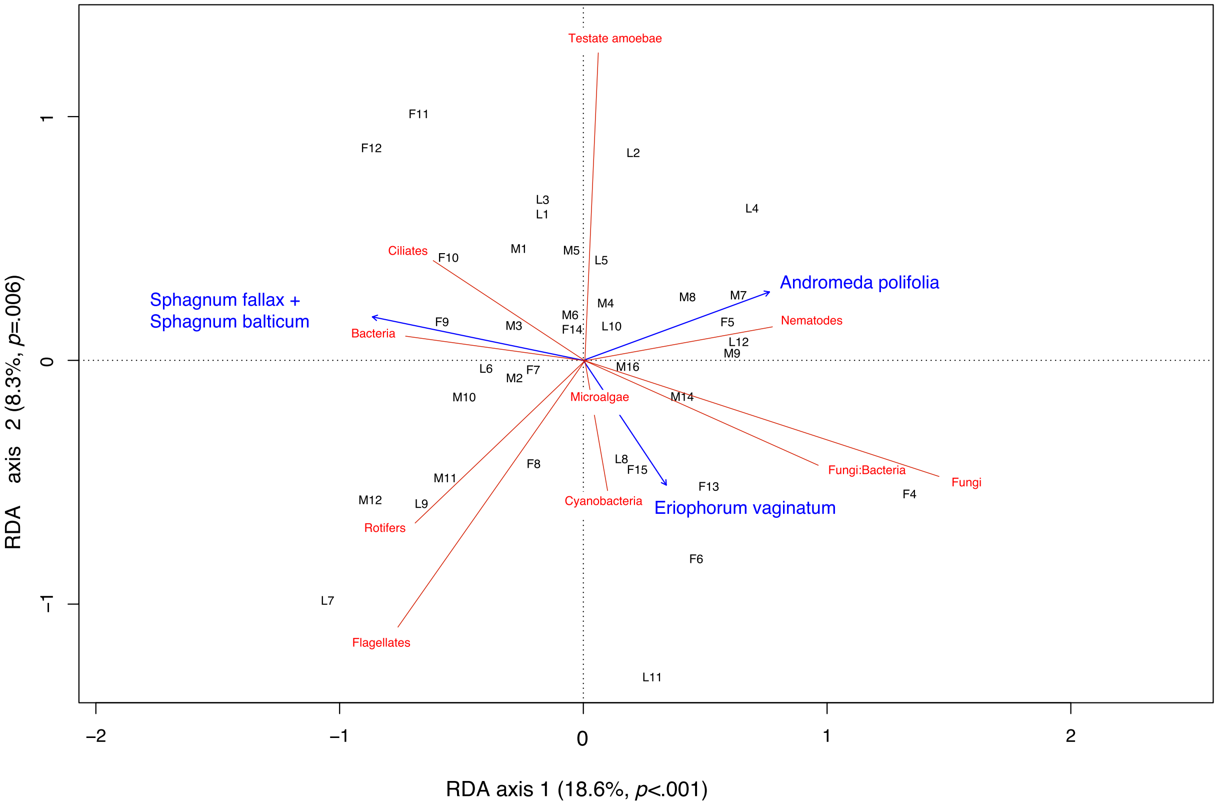

FIGURE 6 Redundancy analysis (RDA) of plots ($N = 39$) in the three peatland sites sampled along a gradient of increasing cover of the ericaceous shrub *Andromeda polifolia*, described by their microbial communities and their relationships with the significant vegetation variables. To remove the effect of climate in the three sites, a matrix of covariables was used, containing the mean annual values of monthly average temperature, monthly maximum temperature, monthly precipitation sum and monthly average vapor pressure. Climate covariables removed 28.7% of variability of the response matrix and the explanatory variables explained 21.6%, while 49.7% remained unexplained. The overall model was significant ($p < .001$), with first RDA axis ($p < .001$) representing 18.6% of the variance and the second RDA axis ($p = .006$) 8.3%. Explanatory variables are the frequencies of *Eriophorum vaginatum* ($p = .007$) and of *Sphagnum fallax* plus *Sphagnum balticum* ($p = .001$), and the biomass of *A. polifolia* (marginally significant, $p = .054$. Plot numbers are indicated for Forbonnet (F), Linje (L) and Mukhrino (M).

correlated with enzyme multifunctionality, verifying our fourth hypothesis. Specifically, leucine aminopeptidase, and to some extent also N-acetyl-glucosidase, decreased with increasing shrub encroachment, while β-glucosidase decreased only in one of the sites (Linje). *Sphagnum* phenols can drastically decrease the population of microbes and their activity through antimicrobial effects (Hamard et al., 2019). Hence, our findings suggest that the phenols produced and released by shrubs also have antimicrobial effects, reducing the capacity of microbial communities to seek N and C.

Besides increasing the amount of phenolic compounds in the system, shrub encroachment led to additional changes in peat dissolved organic matter (DOM). A significant relationship between the DON:DIN ratio and both the frequency and biomass of ericaceous shrubs was found in the Linje site (Figure 9), which had the highest values for these variables (Supporting Information S2 and S5). This suggests a shift in functioning from a mineral-N-driven to an organic-N-driven ecosystem with increasing ericoid shrub encroachment and thus an increasing dependency on fungi-mediated nutrient acquisition (Bragazza et al., 2013), as observed with the increase in fungi biomass. The E4:E6 ratio is inversely related to the degree of condensation and aromaticity of the humic substances and their degree of humification (Senesi et al., 2003). We observed that the peat pore water had a higher E4:E6 ratio with increasing ericoid shrub encroachment, particularly in Linje, the warmest site, reflecting a higher proportion of aliphatic compounds, which are easily decomposable, in the humic substances of newly formed peat.

Shrub-related changes in peat DOM cascaded down to the microbial communities and related functions. We found a greater biomass of fungi than bacteria when there were more ericoid shrubs and vascular plants, in line with our third hypothesis. Fungal communities are highly microhabitat specific (Chronáková et al., 2019), and therefore the change in peatland vegetation, in particular from moss to ericoid shrub patches, engenders a shift from more bacterial to more fungal communities. This corroborates previous findings in other systems (Li et al., 2017; Yannarell et al., 2014) and suggests potential consequences for soil processes and plant–microbe interactions. In particular, the growth of fungi and the release of easily degradable compounds both have the potential to feed back positively to ericaceous shrubs by facilitating the symbiotic acquisition of dissolved organic N (Bragazza et al., 2013; Cullings, 1996). Indeed, fungi-enriched plant communities possess more C-degrading enzymes, which can speed up peat degradation

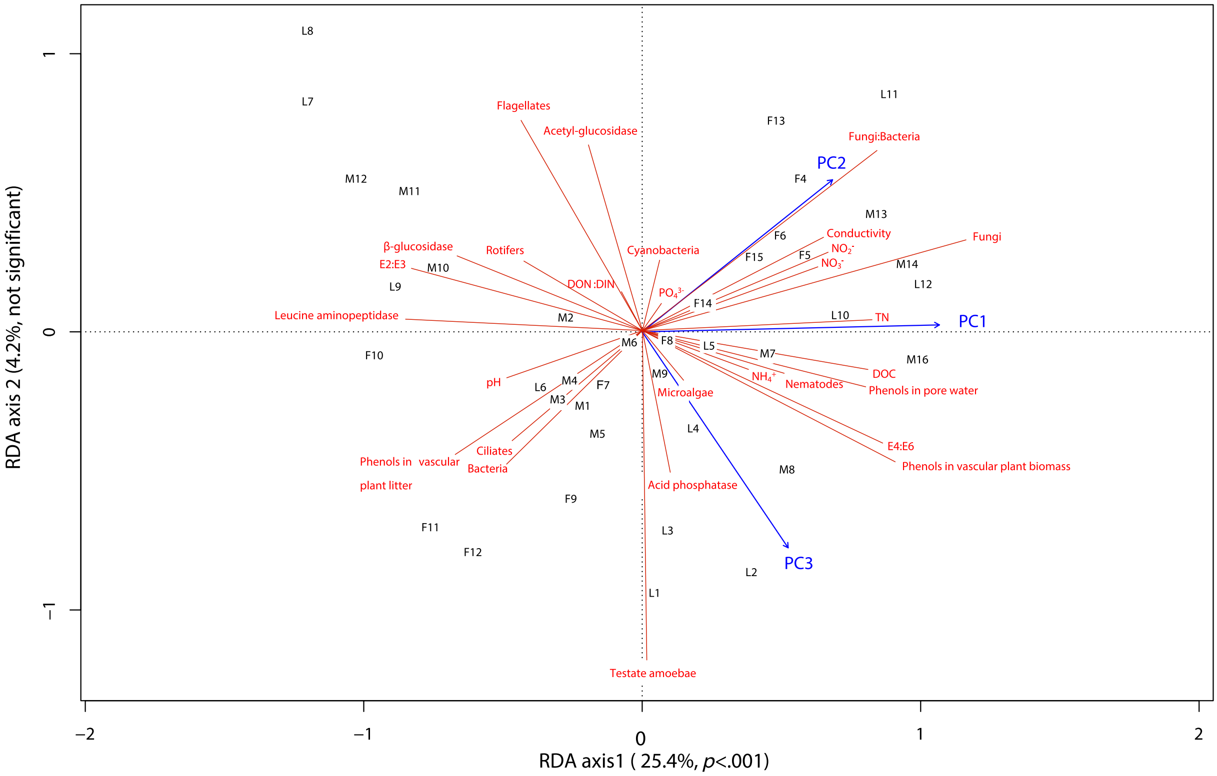

FIGURE 7 Redundancy analysis (RDA) of plots ($N=39$) in the three peatland sites sampled along a gradient of increasing cover of the ericaceous shrub *Andromeda polifolia*, described by all biogeochemical response variables and relationships with the vegetation community. Explanatory variables PC1 ($p=.001$), PC2 ($p=.088$) and PC3 ($p=.089$) represent the first three axes of a principal component analysis (PCA) ordination using the vegetation matrix. To remove the effect of climate in the three sites, a matrix of covariables was used, containing the mean annual values of monthly average temperature, monthly maximum temperature, monthly precipitation sum and monthly average vapor pressure. Climate covariables removed 32.9% of variability of the response matrix and the explanatory variables explained 21.7%, while 45.4% remained unexplained. The overall model was significant ($p<.001$), with the first RDA axis ($p<.001$) representing 25.4% of the variance and the second RDA axis (not significant) only 4.2%. Plot numbers are indicated for Forbonnet (F), Linje (L) and Mukhrino (M). E2:E3 is the absorbance ratio in pore water at 254 and 365 nm; E4:E6 is the absorbance ratio in pore water at 465 and 665 nm; DON:DIN is the ratio dissolved organic N to dissolved inorganic N; DOC: dissolved organic carbon; TN: dissolved N.

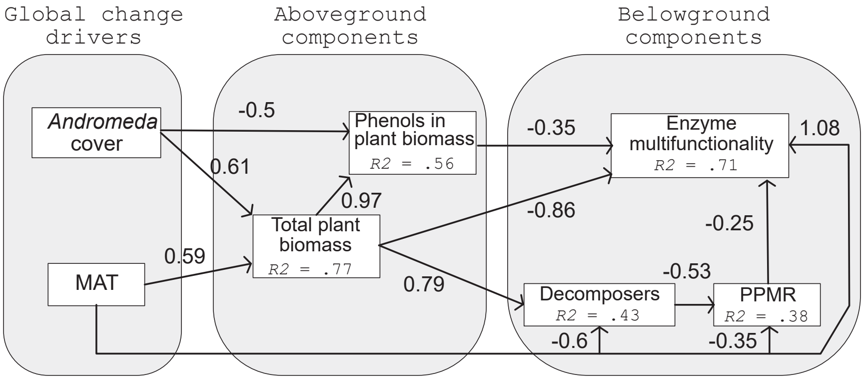

FIGURE 8 Minimal adequate structural equation model for the effects of global change drivers, such as mean annual temperature (MAT) in the three sites and abundance of *Andromeda polifolia*, on total vascular plant biomass and phenols in plant biomass in the aboveground component, and enzyme multifunctionality, biomass of decomposers and predator:prey mass ratio (PPMR) in the belowground component. Arrows show significant relationships (pathways) between variables. Square multiple correlations (R^2 values) for the predicted/dependent factor are given in the box of the dependent variables. SEM global goodness-of-fit are Fisher's C = 23.48, p = .101, df = 16 and AIC = 67.5.

(Bragazza et al., 2015), yet our study showed opposite results with decreased enzyme activity. This decrease was linked to the increase in antimicrobial compounds (see above) but also to a shift in the structure of the microbial food web. Shrub encroachment shifted the microbial predators from a bacteria-feeding community, including organisms such as flagellates, ciliates and rotifers,

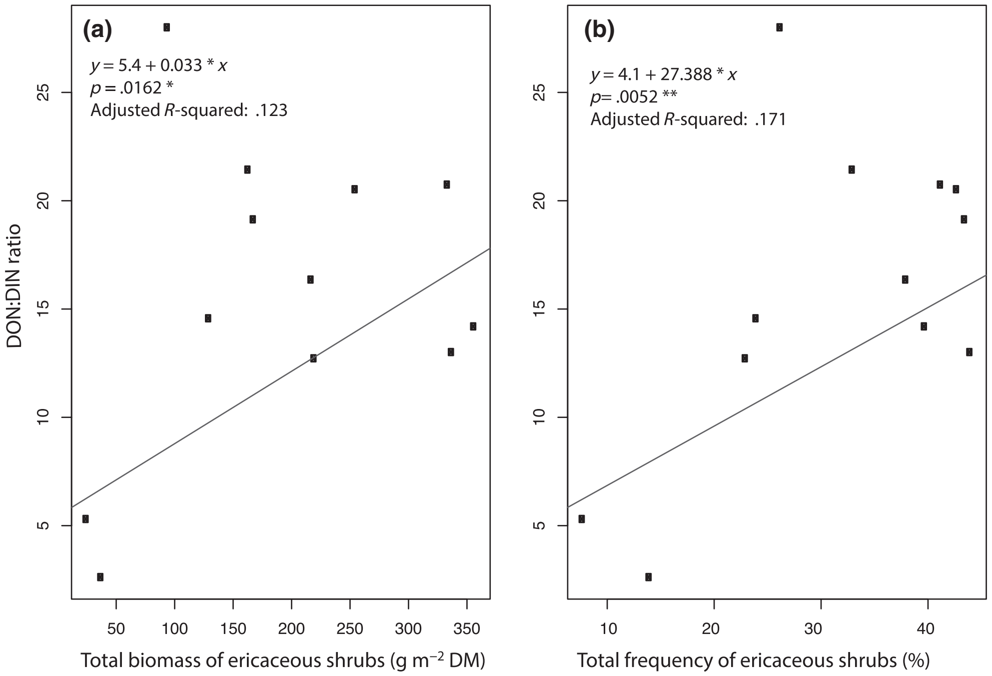

FIGURE 9 Relationship between the ratio of dissolved organic N to dissolved inorganic N (DON:DIN) in peat pore water and the total biomass (a) and the total frequency (b) of ericaceous species in Linje mire, Poland. The linear regression line, equation, significance and adjusted R^2 are indicated.

to a fungi-feeding community, dominated by nematodes and testate amoebae. Indeed, nematodes increased with increasing shrub cover in all three sites and testate amoeba in two sites (Linje and Mukhrino). Free-living testate amoebae and nematodes span several trophic levels (Potapov et al., 2022) and thus play a key role in structuring soil food webs (Jassey et al., 2013; Kamath et al., 2022). Although we do not have information on the prey testate amoebae and nematodes feed on in this study, we can reasonably speculate that they are mostly fungivores as this feeding habit is commonly found for testate amoebae (Gilbert et al., 1998) and nematodes (Wang et al., 2021). We acknowledge that additional macrofaunal investigations could be useful since their role is critical for C cycling (Józefowska et al., 2017). Changes in predator community structure modified the PPMR, which in turn negatively impacted enzyme multifunctionality, and hence cancelled out the potential positive effect of increasing fungal biomass on peat degradation. Surprisingly, in warmer sites, the above-described interactions can be the opposite, with a decrease in decomposers and an increase in enzymatic multifunctionality. However, in our study such a situation only happened under low or no cover of vascular plants when *Sphagnum* mosses remained dominant with an adequate water table level. Overall, these findings demonstrate the crucial role of trophic interactions among microorganisms in interpreting soil functions and ecosystem services.

The climate is currently shifting faster than in the last 20 million years, implying that the ongoing climate change is faster than existing peatlands have ever experienced (Tripati et al., 2009). When a change in vegetation occurs after environmental changes, it is a relatively rapid process, and a change in ecosystem functioning usually follows (Jassey et al., 2018; Loisel & Yu, 2013; Pellerin & Lavoie, 2003; Robroek et al., 2016). Our study underlines the importance of studying multiple trophic levels between plants and microbes for understanding the influence of climate change and its consequences on peatland functioning. We found that drier conditions were key in promoting shrub encroachment in peatlands, while the warming effect remained small. Shrub encroachment deeply modified peat DOM, with an increase in easily degradable compounds but also an increasing release of recalcitrant and antimicrobial compounds such as polyphenols, which ultimately modified microbial components. Increasing shrub cover functionally shifted microbial communities and their trophic interactions, diminishing their capacity to degrade peat through enzyme activities. These results suggest that shrub encroachment may play a major role in regulating overall biogeochemical cycles in peatlands and maintaining the C sink function of bogs under the future climate. However, the extent to which these trophic mechanisms will occur depends on the degree of resistance to shrub–moss coexistence under future climate conditions, and whether other factors associated with climate change, such as elevated CO_2 and N deposition, become dominant selective forces. We acknowledge that we measured these trophic mechanisms on only one date in the middle of the growing season. Future studies with a high temporal resolution are needed to test the generality of the plant–soil interactions detected here and their importance for peatland C sink function over time. Nevertheless, our results are in line with the most recent findings on the role of ericoid mycorrhizal fungi in peatland functioning (Shao et al., 2023), thus providing confidence in the mechanisms found here. In summary, our findings illustrate the capacity of peatland vegetation to modify the immediate effects of climate change on C cycling, and they reveal a further mechanism by which plants influence ecosystem responses to climate change, through their effect on microbial trophic interactions.

AUTHOR CONTRIBUTIONS

Alexandre Buttler conceived the experimental design. Alexandre Buttler, Vincent E.J. Jassey, Fatima Laggoun-Défarge, Sebastien Gogo, Marie-Laure Toussaint, Mariusz Lamentowicz, Bogdan H. Chojnicki, Michał Słowiński, Sandra Słowińska, Małgorzata Zielińska, Monika Reczuga, Jan Barabach, Katarzyna Marcisz, Łukasz Lamentowicz, Elena Lapshina, Daniel Gilbert, Kamila Harenda and Luca Bragazza completed the sampling in the different sites and experiments. Alexandre Buttler and Vincent E.J. Jassey ran the laboratory analyses. Alexandre Buttler, Rodolphe Schlaepfer and Vincent E.J. Jassey performed statistical analyses. Alexandre Buttler wrote the initial manuscript draft, in close consultation with Vincent E.J. Jassey, which was then improved by all co-authors.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest with this publication.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in repository figshare at doi: 10.6084/m9.figshare.23739117.

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SUPPORTING INFORMATION

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