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Host Species–Microbiome Interactions Contribute to *Sphagnum* Moss Growth Acclimation to Warming

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ABSTRACT

Sphagnum moss is the dominant plant genus in northern peatlands responsible for long-term carbon accumulation. *Sphagnum* hosts diverse microbial communities (microbiomes), and its phytobiome (plant host + constituent microbiome + environment) plays a key role in nutrient acquisition along with carbon cycling. Climate change can modify the *Sphagnum*-associated microbiome, resulting in enhanced host growth and thermal acclimation as previously shown in warming experiments. However, the extent of microbiome benefits to the host and the influence of host–microbe specificity on *Sphagnum* thermal acclimation remain unclear. Here, we extracted *Sphagnum* microbiomes from five donor species of four peatland warming experiments across a latitudinal gradient and applied those microbiomes to three germ-free *Sphagnum* species grown across a range of temperatures in the laboratory. Using this experimental system, we test if *Sphagnum*'s growth response to warming depends on the donor and/or recipient host species, and we determine how the microbiome's growth conditions in the field affect *Sphagnum* host growth across a range of temperatures in the laboratory. After 4 weeks, we found that the highest growth rate of recipient *Sphagnum* was observed in treatments of matched host–microbiome pairs, with rates approximately 50% and 250% higher in comparison to maximum growth rates of non-matched host–microbiome pairs and germ-free *Sphagnum*, respectively. We also found that the maximum growth rate of host–microbiome pairs was reached when treatment temperatures were close to the microbiome's native temperatures. Our study shows that *Sphagnum*'s growth acclimation to temperature is partially controlled by its constituent microbiome. Strong *Sphagnum* host–microbiome species specificity indicates the existence of underlying, unknown physiological mechanisms that may drive *Sphagnum*'s ability to acclimatize to elevated temperatures. Together with rapid acclimation of

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the microbiome to warming, these specific microbiome–plant associations have the potential to enhance peatland resilience in the face of climate change.

1 | Introduction

Pristine peatlands exert a cooling effect on global climate due to their long-term carbon (C) sequestration (Frolking, Roulet, and Fuglestvedt 2006) resulting in accumulation of deep peat deposits over millennia (e.g., Treat et al. 2019). The majority of C accumulation in northern peatlands is due to the dominant, peat-forming moss genus, *Sphagnum*, where net primary production (NPP) exceeds slow decomposition over time (Clymo and Hayward 1982; Turetsky et al. 2012). *Sphagnum* has adapted to waterlogged, nutrient poor, and highly acidic environmental (pH 3–5) conditions that characterize the majority of *Sphagnum*-dominated northern peatlands (Rydin and Jeglum 2013). Climate warming represents a unique challenge facing northern peatlands where predicted temperature increases are more pronounced than at more southern latitudes (IPCC 2022). Warming is predicted to perturb the long-term C sink of northern peatlands with some models predicting an increase while others predict a decrease in C storage (Gallego-Sala et al. 2018). *Sphagnum* mosses serve as ecosystem engineers in northern peatlands, regulating carbon and nutrient cycles. Given that northern peatlands store approximately one-third of global soil carbon (Gorham 1991; Yu et al. 2010), *Sphagnum* spp. are likely to play a key role in the response of the global carbon budget to climate change.

Warming experiments have been shown to cause a wide range of *Sphagnum* productivity and growth responses including increases (Dorrepaal et al. 2004; Robroek et al. 2007), no change (Weltzin et al. 2001; Walker et al. 2017), and decreases (Gunnarsson, Granberg, and Nilsson 2004; Bragazza et al. 2016; Norby et al. 2019, 2023). When warming coincided with decreasing water levels or with desiccation of *Sphagnum*, productivity declines were reported (Robroek et al. 2007; Bragazza et al. 2016). When subjected to whole-ecosystem warming at the Spruce and Peatland Responses Under Changing Environments (SPRUCE) experiment (Hanson et al. 2016), *Sphagnum* growth increased with moderate warming in the first treatment year but declined dramatically in the following year (Norby et al. 2019, 2023). The observed rapid decline in *Sphagnum* net primary productivity (NPP) was attributed to a combination of warming and desiccation or other indirect effects (e.g., competition with vascular plants for light or nutrients, Norby et al. 2019). The wide range of observed *Sphagnum* responses to warming highlights the need for improved mechanistic understanding of the drivers of *Sphagnum* productivity in response to climate drivers.

Sphagnum's growth and net photosynthetic rate have been demonstrated to follow a unimodal response to temperature. In short-term experiments, when moisture is not a limiting factor, *Sphagnum* plants reach maximum growth and photosynthetic rates at their temperature optima (Harley et al. 1989; Skre and Oechel 1981; Breeuwer et al. 2008), and similar findings have been reported for other bryophytes (Davey and Rothery 1997; Furness and Grime 1982; Kallio and Saarnio 1986). Temperature optima for *Sphagnum* growth and photosynthesis vary across studies and may depend on geographical location, season and local climate but also on the *Sphagnum* species (Skre and Oechel 1981; Harley et al. 1989; Asada, Warner, and Banner 2003; Haraguchi and Yamada 2011) and their associated microbiomes (Carrell et al. 2022). For example, temperature optima for photosynthesis in several *Sphagnum* species were found to be between 20°C and 25°C (Skre and Oechel 1981; Harley et al. 1989). In another greenhouse experiment, Breeuwer et al. (2008) found that *Sphagnum* growth reached its maximum at 17°C when exposed to temperatures between 11°C and 21°C over 6 months. However, much higher temperature optima were found in *Sphagnum* from temperate peatlands in Japan (Haraguchi and Yamada 2011). There, *S. palustre*, *S. fuscum*, and *S. papillosum* originating from a warm temperate region reached maximum photosynthetic rate at 35°C, while *S. fimbriatum* and *S. fallax* from cool-temperate peatlands had temperature optima at 30°C (Haraguchi and Yamada 2011). Similarly, the growth of *Sphagnum* spp. from northern sites in Sweden was more negatively affected by higher temperatures than southern *Sphagnum* spp. (Breeuwer et al. 2009). The environmental or physiological forcings driving temperature optima remain unclear. One possible explanation could be that thermal conditioning of the *Sphagnum*-associated microbiome contributes to the thermal response of *Sphagnum*'s growth and net photosynthetic rate.

Similar to observations in the human microbiome, growing evidence highlights that most, if not all, plants intimately interact with microbes (Partida-Martínez and Heil 2011) and that the associated microbial communities (microbiomes) represent an extension of the host phenotype that influences ecological interactions and evolutionary trajectories (Turner, James, and Poole 2013; Vandenkoornhuyse et al. 2015; Theis et al. 2016). This coevolution of diverse microbial communities and their plant hosts facilitates plant adaptation to local environments (Petipas, Geber, and Lau 2021) promoting their fitness and survival. For example, plant–microbe interactions have long been implicated in plant nutrient availability and status (e.g., Johnson et al. 2010). This is especially pronounced in peatlands, where nitrogen (N) limiting conditions have led to symbiotic interactions between *Sphagnum* plants and N_2-fixing bacteria (reviewed in Lindo, Nilsson, and Gundale 2013 and Kostka et al. 2016; Carrell et al. 2022). *Sphagnum*-associated N_2-fixing communities (diazotrophs), for example, transfer a considerable amount of N to the *Sphagnum*-host's biomass (Berg, Danielsson, and Svensson 2013), contributing 40%–96% of N input to pristine peatlands (Vile et al. 2014; Larmola et al. 2014; Salmon et al. 2021). In return, *Sphagnum*'s water-filled, dead hyaline cells may buffer the acidic bog environment providing shelter to diazotrophs and derive carbon-rich resources from neighboring photosynthetically active cells (Raghoebarsing et al. 2005; Carrell, Lawrence, et al. 2022). In addition to fixing N_2, many diazotrophs associated with *Sphagnum* also have unique and important C-cycling functions, showing a direct coupling of C and N cycles in the phytobiome (i.e., plant host + constituent microbiome + environment). For example, diazotrophs that are also obligate methanotrophs, provide a source of CO_2 to support *Sphagnum* photosynthesis (Raghoebarsing et al. 2005; Kip et al. 2010), thereby directly contributing to C fixation in peatlands. Coevolution is supported by the observation that *Sphagnum* contains a core microbiome of keystone bacterial taxa that plays an important role in host and ecosystem function.

The associated microbiome has been shown to facilitate plant responses to abiotic environmental stressors including drought (Lau and Lennon 2012; Marasco et al. 2012; Gehring et al. 2017), metal contamination (Meharg and Cairney 2000) and heat stress (Redman et al. 2011; Carrell et al. 2022). *Sphagnum* mosses host taxonomically diverse microbiomes (Opelt et al. 2007; Bragina et al. 2014; Kostka et al. 2016; Warren et al. 2017; Kolton et al. 2022) that are strongly driven by abiotic factors (Bragina et al. 2013; Petro et al. 2023). *Sphagnum* species growing in different abiotic environments therefore are often associated with highly site-specific bacterial community composition (Bragina, Berg, and Berg 2015). For example, Bragina, Berg, and Berg (2015) found that Alpha- and Gammaproteobacteria were the main bacterial groups in *S. magellanicum*, while Verrucomicrobia and Planctomycetes dominated in *S. fallax*. Additionally, environmental and climatic conditions were found to be key drivers in rewiring plant–bacterial interactions in peatlands, where new or different interactions between plants and microbes occurred (Robroek et al. 2021; Wieczynski, Moeller, and Gibert, 2023; Wieczynski, Yoshimura, et al. 2023). Climate warming is therefore expected to change *Sphagnum* microbiome structure and function (Carrell et al. 2019; Martí et al. 2019), associative bacterial biomass (Jassey et al. 2013), and potentially alter the link between the C and N cycle by decoupling key microbial processes such as methanotrophy and N_2 fixation (Petro et al. 2023). It has been shown that associated microbial communities respond to stresses, such as drought, more rapidly than plants, and host plant fitness is therefore improved through plant–microbe interactions (Lau and Lennon 2012). Recently, Carrell et al. (2022) found that when germ-free and temperature naive *Sphagnum* plants received a microbiome from *Sphagnum* growing at elevated temperatures, growth was nearly 60% greater under warming conditions relative to ambient temperature-conditioned microbiomes or no microbiome at all. These results indicate that the microbiome likely contributes to host thermal acclimation and response. However, it is still unclear to the extent which microbiomes benefit the plant host relative to inherent host genetic potential. Furthermore, it is unknown if there is host specificity on receiving microbial benefits to thermal acclimation and stress (Rodriguez et al. 2008).

In this study, we leverage global peatland warming experiments to provide a suite of donor microbiomes collected from multiple *Sphagnum* species and origin growth temperatures. We extract *Sphagnum* microbiomes from a wide range of peatlands from diverse climate zones (temperate, boreal, and subarctic zones) and inoculate those microbiomes into germ-free *Sphagnum* species grown across a range of temperatures in the laboratory matching field conditions. Using this microbiome transfer approach, we test (1) if *Sphagnum*'s ability to receive microbial benefits to warming (with regard to growth rates) depends on the species from which the microbiome was collected and transferred to and (2) determine how the microbiome's growth conditions in the field affect *Sphagnum* host growth across a range of temperatures in the laboratory.

We fit *Sphagnum* growth rates to experimental temperatures using a growth rate-temperature function (Figure 1). Then, we test if fitted maximum growth rates depend on the species from which the microbiome was collected and transferred to (Hypothesis 1). Finally, we test if fitted maximum growth rates are reached when temperature conditions in the laboratory are similar to temperatures that microbiomes were conditioned to in the field (Hypothesis 2).

2 | Materials and Methods

2.1 | Study Sites

To obtain microbiomes conditioned to different origin temperatures (T_{origin}) in the field, microbiomes were sampled from four peatland sites (Table 1) spanning a latitudinal gradient across temperate, boreal, and subarctic zones. Each peatland site hosts an ongoing warming experiment or contains a natural elevated temperature source (i.e., geothermal site in Iceland).

Degerö Stormyr peatland (64°11′ N, 19°33′ E, altitude 270 m above sea level (a.s.l.), area 650 ha) is an oligotrophic minerogenic mixed mire system (pH 4.5) in the Kulbäckstiden Experimental Forest, northern Sweden (Noumonvi et al. 2023). The climate is cold-temperate-humid with a 30-year (1961–1990) mean annual air temperature of 1.2°C and a mean annual precipitation of 523 mm (Alexandersson, Karlström, and Larsson-McCann 1991). The highest and lowest monthly mean air temperature of 14.7°C and −12.4°C occur in July and January, respectively. A simulated climate change experiment was initiated

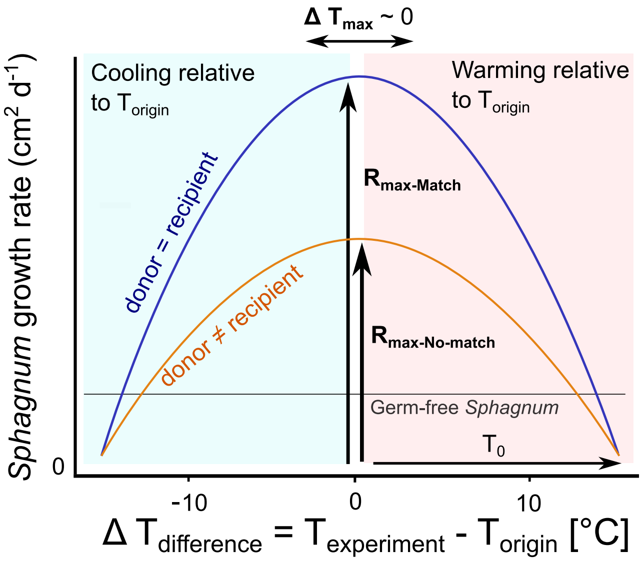

FIGURE 1 | Our first hypothesis is that the maximum growth rate of *Sphagnum* (R_{max}) is largest when the experimental temperature (T_{exp}) is equal to the origin temperature (T_{origin}) of the microbiome (H1: $\Delta T_{\mathrm{max}} \sim 0$). If the experimental temperature is below (cooling; light blue) or above (warming; light red) the origin temperature, we expect growth to decline. To test this, we fitted a temperature response model. Our second hypothesis is that *Sphagnum* growth (R_{max}) is largest when microbiome donor–recipient *Sphagnum* species pair matches, smaller when there is no matching and smallest when recipient *Sphagnum* has no microbiome (germ-free control); H2: $R_{\mathrm{max\text{-}match}} > R_{\mathrm{max\text{-}nomatch}} > R_{\mathrm{max\text{-}germ\text{-}free}}$.

TABLE 1 | Overview of sampled sites with an experimental warming treatment or a natural temperature gradient.

Location	Experiment or gradient	Biome	Peatland habitat	Mean annual temp (°C)	Growing season warming (°C)	Microbiome extracted from dominant *Sphagnum* spp.
E France 46°49′35″ N, 6°10′20″E	Experiment	Temperate	Poor fen/bog	7	2	*S. fallax*
N Sweden 64°11′N, 19°33′ E	Experiment	Boreal	Poor fen/bog	1.2	3.6	*S. lindbergii* *S. balticum*
W Iceland 64°41′09.2″N, 21°24′18.4″W	Gradient	Tundra	Poor fen	3.6 (1990–2016)	16[a]	*S.medium* *S.teres*
N USA 47°30.476′N, 93°27.162′W	Experiment	Temperate	Bog	3.3 (1961–2005)	9	*S. fallax*

[a] Difference in moss surface temperature between near-spring habitat (warm) and 5 m away (ambient).

in 1994 with the installation of chambers that raise air temperature by 3.6°C as measured 0.25 m above the *Sphagnum* layer (for details on warming chambers and the experimental set-up please see Granberg et al. (2001) and Wiedermann et al. 2007). The warming experiment was conducted in a poor fen lawn area dominated by the mosses *Sphagnum balticum* (Russ.) C. Jens., *S. majus* (Russ.) C. Jens., and *S. lindbergii* Schimp, sedges *Eriophorum vaginatum* L. and *Trichophorum cespitosum* L. and dwarf shrubs *Vaccinium oxycoccos* L. and *Andromeda polifolia* L. (Wiedermann et al. 2007).

Frasne peatland (46°49′N, 6°10′ E, altitude 840 m (a.s.l.), area 7 ha) is a *Sphagnum*-dominated bog-fen complex (pH 3.7–4.3) in the Jura Mountains in eastern France. This peatland is one of the four sites of the French Peatland Observation Service (Gogo et al. 2021). The annual air temperature is 7°C with cold winters (mean air temperature −1.4°C) and mild summers (mean air temperature 14.6°C), and the annual precipitation is 1300–1500 mm (Jassey, Chiapusio, et al. 2011). Open top chambers were installed in 2008 across the peatland complex to simulate climate warming with an increase of the annual air temperatures by 2°C (experimental design described in detail in Laggoun-Défarge et al. 2008; Delarue et al. 2011 and Jassey, Gilbert, et al. 2011). Dominant moss species in the experimental area were *S. fallax* (in the fen), *S. magellanicum* agg./*S. divinum* (in the bog), while vascular plants are distributed sporadically across bog-fen area, including *E. vaginatum*, *Andromeda polifolia*, *V. oxycoccos*, and *Calluna vulgaris*.

The Icelandic site (64°41′09.2′′N,21°24′18.4′′W) is a ca. 10 ha area with patches of fen habitat along streams and in depressions, located 46 m a.s.l. in a geothermal area. This area has an oceanic climate, with cold summers and mild winters; average annual temperature and precipitation are 3.6°C and 810 mm, respectively (1990–2016, Icelandic Met Office, https://en.vedur.is/). The site has no trees and is characterized by a few alkaline hot springs that have a constant outflow of boiling water with a pH > 7. Along the warm streams there are mats and cushions of *Sphagnum teres*, *S. warnstorfii*, *S. subnitens*, *S. centrale*, and *S. medium*. The *S. magellanicum* agg. is uncommon in Iceland (Lange, 1973), but here it is abundant. Temperatures at the moss surface (top 5 cm) range from 12°C 5 m away from the stream to 28°C close to the stream (0–30 cm). While vascular plants are in general sparse where mosses cover the surface, sedges such as *Carex nigra* are common.

S1-Bog (47°30.476′N,93°27.162′W, altitude 418 m (a.s.l.), area 8.1 ha) is a raised-dome, weakly ombrotrophic bog located in the Marcell Experimental Forest in northern Minnesota, USA. The S1-Bog is located in a sub-humid continental climate with an average annual air temperature of 3.3°C over the period from 1961 to 2005 and an average annual precipitation of 768 mm (Hanson et al. 2016). The S1-Bog hosts the SPRUCE (Spruce and Peatland Responses Under Climatic and Environmental Change, http://mnspruce.ornl.gov) experimental field site (for details on experimental design and site construction refer to Krassovski et al. 2015) that includes ten chambers in which the air and soil temperatures are manipulated by +0°C, +2.25°C, + 4.5°C, +6.75°C, and + 9°C in a regression design in which half of the plots also receive elevated CO_2. The experimental area is dominated by *Picea mariana* (Mill.) B.S.P. (black spruce) and *Larix laricina* (Du Roi) K. Koch (larch) in the tree canopy. At the bog surface, dominant *Sphagnum* species are *S. angustifolium* and *S. fallax* in wetter hollows and *S. divinum (formerly S. magellanicum)* in drier hummocks. Dominant vascular plants of the understory include ericaceous shrubs *Rhododendron groenlandicum* (Oeder) Kron and Judd (Labrador tea) and *Chamaedaphne calyculata* (L.) Moench. (leatherleaf; Hanson et al. 2016).

2.2 | Field Sampling

Overall, five dominant *Sphagnum* species (hereafter referred to as *donors*) were harvested from plots that were either exposed to *ambient* or *warming* conditions at the four established field experiments or along natural gradients (Table 1, Figure 2).

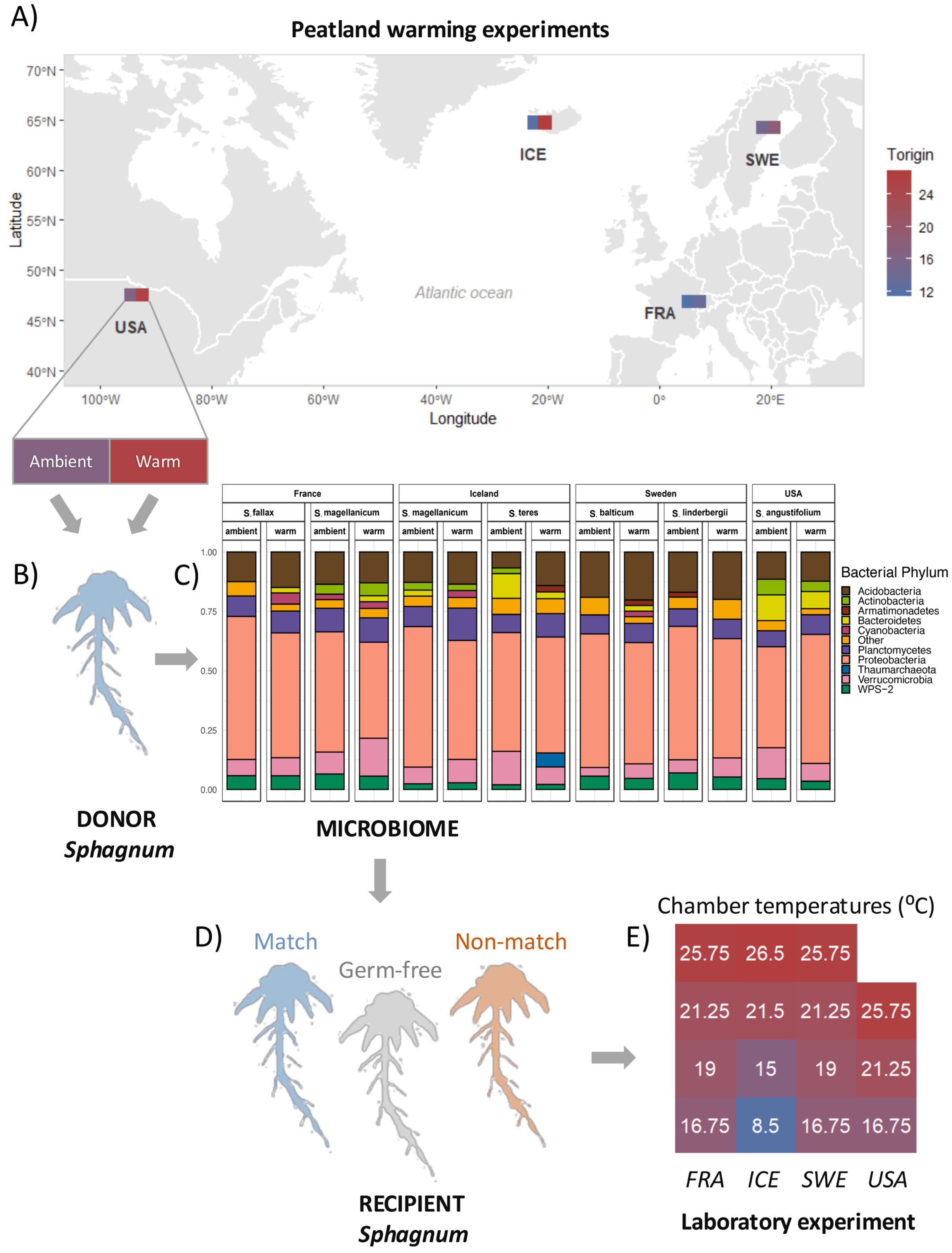

FIGURE 2 | Experimental design schematic. (A) Map depicting geographic locations for four selected peatland sites in: France (FRA), Sweden (SWE), Iceland (ICE), and the United States of America (USA). Map lines delineate study areas and do not necessarily depict accepted national boundaries. T_{origin} is the 2-week mean of soil temperatures at 5-7 cm depth prior to sampling at *ambient* and *warmed* (open-top chamber) plots at each field site. (B) Five *Sphagnum* donor species were collected from ambient and warmed plots at each site with: (B) In total, five *Sphagnum* donor species were collected from ambient and warmed plots across all sites. (C) Microbiomes of field collected *Sphagnum* material (donors) were taxonomically characterized (D) transplanted into *matching* (N=252) or *non-matching* species (N=629) or germ-free (N=256; Table S2) *Sphagnum* recipients. (E) Recipient *Sphagnum* mosses are placed into growing chambers with different temperature settings (T_{exp}; Table S2) and incubated for 4 weeks while performing weekly growth measurements.

Dominant *Sphagnum* species varied across experimental sites (Tables 1 and S1), and not all *Sphagnum* species were present at all four sites. Origin temperature of the microbiome (T_{origin}) was measured as the 2-week mean of soil temperatures at 5–7 cm depth prior to sampling of the ambient and warmed plots at each field site. By using a 2-week temperature mean, we assume that the microbiome acclimates to its thermal environment on sub-monthly timescales (see for example Trivedi et al. 2022). At peatland sites in France and Sweden, warming experiments employing open top chambers resulted in an increase of +2°C and + 3.6°C above ambient temperature, respectively. At the USA peatland, as part of the SPRUCE experiment, the plots sampled in this study were warmed by 4.5°C and 9°C relative to ambient conditions. In Iceland, the edge of the natural hot springs with +15°C difference compared to ambient represented the "warm" microbiome origin. Live green *Sphagnum* mosses were collected from the plots in June 2019, placed in sterile bags, shipped to Oak Ridge National Laboratory on ice, and refrigerated until the start of experiments.

2.3 | Microbiome Isolation and the Experimental Design of the Warming Treatment

Microbiomes were isolated from field-collected *Sphagnum* (Figure 2B) following methods in Carrell et al. (2022) by dicing 100 g of *Sphagnum* tissue with a sterile razor blade. Tissue was then pulverized with a mortar and pestle and suspended in 1/10th strength phosphate buffer solution (PBS). The suspension was filtered through Mira Cloth and centrifuged. The resulting microbial pellet was resuspended in 500 mL BG11-N medium at pH 5.5. Germ-free tissue cultures of recipient *Sphagnum* were previously established through clonal propagation from ethanol-sterilized spores collected from the S1 bog (Healey et al. 2023). Aliquots of 2-ml field-collected *Sphagnum* microbiomes were used to inoculate a single capitula of germ-free culture (*recipients*, Figure 2D) of: (1) *S. fallax*, (2) *S. divinum* or *S. medium*, and (3) *S. fuscum* in 12-well plates. Controls were single capitula of each species in 2-ml of sterile media (12 wells for each temperature treatment). Combinations of field-collected *Sphagnum* microbiomes and germ-free *Sphagnum* cultures that were either matching or non-matching donor–recipient pairs (Table S1), and controls were incubated for 4 weeks in growth chambers (Figure 2E) programmed to light–dark (12:12) cycles with ambient and incremental elevated temperatures (Figure 2E) mimicking future climate warming scenarios (IPCC report, 2022). The overall sample size for matching and non-matching donor–recipient microbiome pairs were 252 and 629, respectively, while the sample size for controls was 256. Please see Table S2 for the sample size of all donor–recipients and control combinations across different temperature treatments. Note that *S. medium* and *S. divinum* were matched pairs in this study as they are closely related. Previously both species were identified as *S. magellanicum* but have been separated into two species in 2018 (Hassel et al. 2018).

2.4 | *Sphagnum* Growth Measurements

Sphagnum growth was measured weekly by capturing images of capitula from the top of each plate and determining the surface area using imageJ software (following the same methodology as Carrell, Veličković et al. 2022 and accessible at Zivkovic et al. 2025). The proxy for growth was derived as the change in the surface area over time (Heck et al. 2021).

2.5 | Microbiome Composition Analyses

To characterize the field-collected *Sphagnum* microbiomes at the initiation of the experiment, DNA was extracted from 50 mg of *Sphagnum* tissue using the DNeasy PowerPlant Pro Kit (Qiagen). Extracted DNA was amplified and prepped for 16S rRNA amplicon sequencing with a two-step PCR approach following Cregger et al. (2018) that utilizes a mixture of custom 515F and 806R primers and a set of peptide nucleic acids to inhibit chloroplast and mitochondrial amplification. Microbial sequences were processed with QIIME2 (Bolyen et al. 2019). Paired sequences were demultiplexed, denoized, trimmed, and delineated into amplicon sequence variants (ASVs) with DADA2 (Callahan et al. 2016) and taxonomically classified with a Naïve Bayes classifier through the sklearn python package (Bokulich et al. 2018) trained on the SILVA database. The relationship of microbial beta diversity and *Sphagnum* field location was determined by permanova analysis of Bray–Curtis distances of each sample. The 16S rRNA amplicon sequences have been deposited in the BioProject database (http://ncbi.nlm.nih.gov/bioproject) under accession PRJNA1210807.

2.6 | Statistical Analyses

To compare *Sphagnum* host growth responses from microbiomes originating across the sites, growth rates were normalized by the site-specific maximum growth rate. Maximum growth rates were determined based on mean growth rates grouped by site, donor species, recipient species, and temperature difference between experimental treatment and origin ($\Delta T_{diff} = T_{exp} - T_{origin}$). We normalized growth rates to account for confounding site-specific factors such as nutrient or light availability.

To assess growth–temperature relationships, we fitted a nonlinear temperature function to normalized *Sphagnum* growth rates (*r*) using a generalized least squares method (adapted from Yan and Hunt 1999; fitted with a g*nls* function in the R *stats* package):

$$r = R_{max}\left(\frac{\left(T_0 + \Delta T_{max}\right) - \Delta T_{diff}}{T_0}\right)\left(\frac{\left(\Delta T_{max} - T_0\right) - \Delta T_{diff}}{-\,T_0}\right), \tag{1}$$

where R_{max}, ΔT_{max}, and T_0 are best-fit parameters. R_{max} represents the maximum growth rate, ΔT_{max} is the temperature difference between experimental and origin temperature at which the *Sphagnum* reaches the maximum growth rate R_{max}, and T_0 is the temperature difference relative to ΔT_{max} at which *Sphagnum* growth ceases (i.e., $r = 0$). The within-group error correlation structure was used in *gnls* to account for the correlation between observations within groups of site–donor pairs. We calculated the coefficient of determination (R^2) between model predictions and observations as a goodness of fit measure.

The temperature function was fitted separately for each treatment matching host and donor species, non-matching host and donor species, and controls. However, for control treatments, none of the model parameters were statistically significant. Therefore, we did not fit the temperature function to the control samples. Instead, we used mean normalized growth rates for control samples. Uncertainties of model parameters were quantified by fitting the temperature response function (or by calculating the mean for control samples) to 1000 bootstrap samples (i.e., resampling with replacement) of the dataset. Significant differences between fit parameters for subsets of matching and non-matching host and donor species, and of control samples were tested based on the sampling distributions derived by bootstrapping. Parameter estimates are significantly different if the 95% confidence interval of the distribution of fit parameter differences does not include zero.

TABLE 2 | Generalized least squares (GLS) model fit estimates for matched and non-matched *Sphagnum* host–microbiome pairs.

	Value	SE	t	p
Match				
$R_{\max}$	0.69	0.06	11.34	<0.001
T_0	21.17	2.02	10.46	<0.001
$\Delta T_{\max}$	0.31	0.88	0.35	0.73
Non-match				
$R_{\max}$	0.38	0.08	4.70	<0.01
T_0	20.43	2.79	7.32	<0.01
$\Delta T_{\max}$	−4.09	2.12	−1.93	0.06

Note: $R_{\max}$ represents maximum growth rates, $\Delta T_{\max}$ is the temperature difference between experimental and origin temperature at which the *Sphagnum* reaches the maximum growth rate, and T_0 is the temperature difference relative to $\Delta T_{\max}$ at which *Sphagnum* growth ceases. SE is a standard error within GLS models. $N_{\text{match}} = 21$, $N_{\text{non-match}} = 45$.

3 | Results

The growth of *Sphagnum* inoculated with a thermally conditioned microbiome achieved its maximum growth rate (R_{max}) when *Sphagnum* was grown at a temperature similar to the temperature origin of its microbiome. Cooling or warming of the recipient *Sphagnum*–microbiome relative to the origin temperatures of the inoculated microbiomes resulted in decreased growth of *Sphagnum*. Fitting normalized growth rates to temperature resulted in higher R^2 for the subset of samples that were inoculated with microbiomes (i.e., matched and non-matched pairs with 0.31 [$n=21$] and 0.29 [$n=46$], respectively) than for the uninoculated control samples ($R^2=0.02$, $n=11$). This finding suggests that growth acclimation of *Sphagnum* to temperature is mainly driven by microbiome acclimation to temperature. The highest maximum growth rates ($R_{\max}$) were observed when the microbiome was also inoculated into a matching host *Sphagnum* species (Table 2, Figure 4). Optimal growth rates of matched host–donor pairs were 48% larger than $R_{\max}$ of the non-matched host–donor pairs ($p<0.05$; Figures 3 and 4). Maximum growth rates of matched host–donor pairs were even larger (252%) compared to the mean of normalized growth rates of the controls ($p<0.05$; Figures 3 and 4). Non-normalized growth rates of *Sphagnum* showed that the presence of microbiome grown in ambient and warmed field conditions significantly increased *Sphagnum* growth compared to germ-free *Sphagnum* (Figure S1).

Maximum growth rates were observed for matched host–donor pairs when the treatment temperature was close to the origin temperature ($\Delta T_{\max}$: 0.3°C ± 0.9°C [±standard error], $p=0.73$) (Figure 4, Table 2). For non-matched host–donor pairs, maximum growth rates were observed when experimental temperatures were slightly cooler than origin temperatures ($\Delta T_{\max}$: −4.1°C ± 2.1°C, $p=0.06$, Table 2). These results indicate that *Sphagnum* growth is maximized when treatment temperatures are close to the origin temperatures of the microbiome (Figure 2A).

Microbiomes collected from *Sphagnum* across all sites were dominated by Proteobacteria (40.5%–60.4%), Acidobacteria (6.5%–19.5%), and Verrucomicrobia (3.3%–16.0%). At the

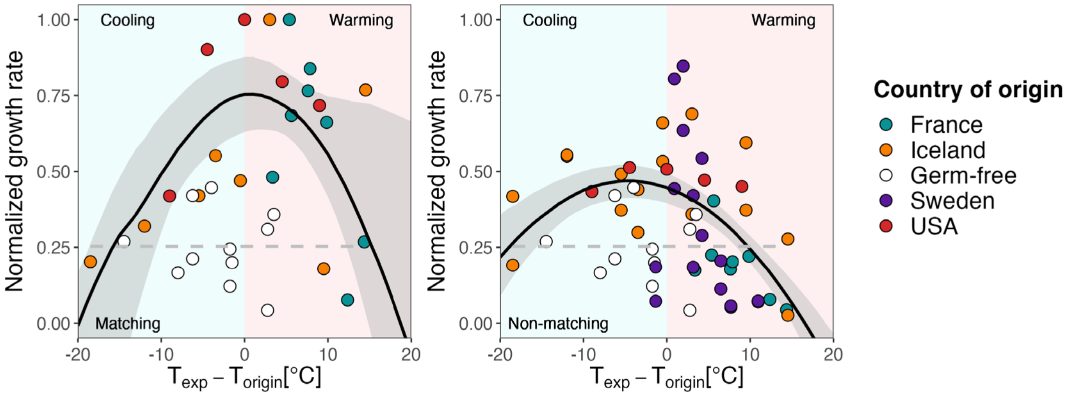

FIGURE 3 | Normalized *Sphagnum* growth as a function of the difference between experimental temperature (T_{exp}) and mean field temperature (T_{origin}) for matched microbiome donor-recipient *Sphagnum* pairs (left) and non-matched microbiome donor–recipient *Sphagnum* pairs (right) compared to germ-free *Sphagnum* (control, gray). Data for matched ($N=21$) and non-matched ($N=45$) are fitted using the temperature response function of plant growth and control is the mean value ($N=11$). Gray shaded areas indicate the 95% confidence interval of the fits.

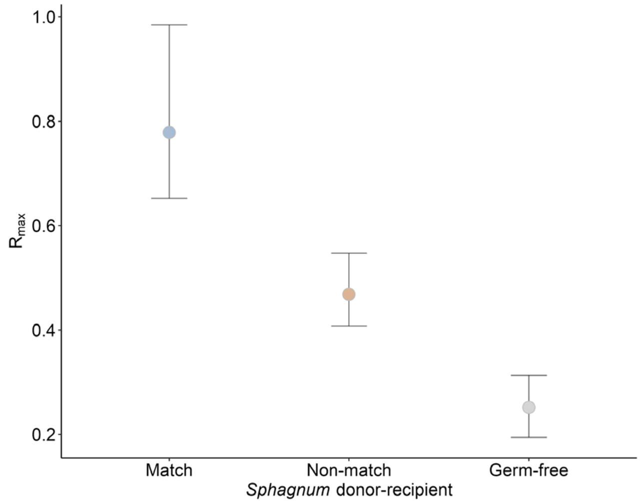

FIGURE 4 | Estimates of normalized optimal growth rate parameter (R_{max}) for matched, non-matched microbiome donor–recipient *Sphagnum* pairs and mean control (germ-free *Sphagnum*). 95% confidence intervals (CI) are shown as vertical lines and are derived from bootstrapping the original dataset 1000 times (i.e., 2.5th to 97.5th percentile).

bacterial family level all *Sphagnum* samples contained, *Acetobacteraceae* (11%–35%), *Acidobacteriaceae* (3.4%–11.6%), *Beijerinckiaceae* (0.5%–6.7%), *Caulobacteraceae* (2.6%–8.0%), and an uncultured bacterium belonging to the WD260 order of Gammaproteobacteria (2.5%–10.2%) (Table S3). Cyanobacteria were present in all samples and doubled from a relative abundance of 1.2% in ambient samples to 2.4% relative abundance in warm samples. Across all samples and sites, *Nostocaceae* increased in relative abundance with warming from 0.7% relative abundance in ambient samples to 2.2% relative abundance in warm samples. Similarly, *Beijerinckiaceae* relative abundance increased by 41% in warm field-collected microbiomes compared to ambient field-collected microbiomes (2.3%). Despite commonality in dominant bacterial families across sites and *Sphagnum* species, field-site strongly structured bacterial communities ($R^2 = 0.60$, $p < 0.001$).

4 | Discussion

Climate change poses a large threat to peatland ecosystem functioning and carbon sequestration. The ability of these systems to adapt to warming temperatures may depend not only on the plants themselves but on their associated microbiomes. Through a novel experimental approach combining field-collected microbiomes from diverse climatic zones with controlled laboratory conditions, we demonstrate three key findings about *Sphagnum*–microbiome interactions under warming conditions: (1) thermal acclimation of *Sphagnum* host–microbiome pairs occurs across a wide range of climatic zones, (2) microbiome-transferred thermal acclimation is host-species specific, and (3) in situ temperature conditions of the microbiome determine the thermal acclimation in *Sphagnum*. These findings provide new insights into the mechanisms underlying peatland resilience to climate change and highlight the importance of host–microbiome relationships in ecosystem adaptation.

Maximum *Sphagnum* growth was observed when host–microbiome pairs were grown at temperatures close to the temperature origin of the transplanted microbiome. A previous study on microbially driven thermal acclimation in *Sphagnum* at the SPRUCE peatland warming site showed similar results. Carrell et al. (2022) demonstrated that germ-free *S. fallax* grown with a microbiome conditioned by an in situ warming treatment (+9°C above ambient) exhibited increased growth when grown at elevated laboratory temperatures compared to the same host–microbiome pair grown at ambient temperatures. Our current study expands understanding of microbially driven thermal acclimation by extracting *Sphagnum* microbiomes from warming experiments and geothermal areas across a wide range of peatlands from diverse climate zones (temperate, boreal, and subarctic zones) and inoculating those microbiomes into three germ-free *Sphagnum* species grown across a range of laboratory temperatures matching field conditions. The field-acclimatized microbiomes were exposed to a wide range of in situ temperatures including short-term, whole ecosystem warming plots (< 5 years, USA), long-term, open-top chamber warming experiments (> 10 years, sites in Sweden and France), and natural geothermal origin sites (Iceland). While experimental warming raised the temperatures of *Sphagnum* to between +2°C and + 9°C above ambient, the geothermal microbiome from Iceland was conditioned under natural conditions at a stable temperature of 27°C on the edges of hot springs, which exceeds the growth temperature of *Sphagnum* in adjacent ambient plots by 15°C. Under such long-term, extreme growing conditions in geothermal areas, *Sphagnum*–microbiome interactions may have surpassed short-term acclimation and turned into long-term thermal adaptation. Long-term adaptation under extreme environmental conditions may lead to more complex coevolutionary processes and genomic interdependency in plant host–microbiome interactions (Bosch and McFall-Ngai 2011; Petipas, Geber, and Lau 2021). Thus, long-term exposure of the *Sphagnum* microbiome to climate change-induced warming could result in co-evolved adaptation, thereby extending the observed short-term microbe-mediated thermal acclimation effects on *Sphagnum*'s growth. The microbiome's capacity to more rapidly respond to environmental changes in comparison to the host (including temperature, Voolstra and Ziegler 2020) may support short-term acclimation of *Sphagnum* growth rates to warming even in the event of rapid climate change (as proposed by Trivedi et al. (2022) for plant adaptation).

Different traits specific to individual *Sphagnum* species and their associated microbiome may partially control responses of *Sphagnum* growth to climate warming. Here, we show that transferring the microbiome into the same (but germ-free) *Sphagnum* species (i.e., microbiome donor *Sphagnum* species matches to the recipient *Sphagnum* species) elicits a stronger growth response than when donor-recipient species are not matching. A potential explanation for such different effects is that each *Sphagnum* species, due to their niche preferences and their adaptation to local, abiotic, and biotic environments, may host a microbiome that is at least partially specialized to that host (Opelt et al. 2007; Bragina et al. 2013; Kolton et al. 2022) forming a unique community. *Sphagnum* and associated microbiomes form relationships that likely coevolved (Bosch and McFall-Ngai 2011) where both the environment and the plant host responses to the environment (Jassey, Chiapusio, et al. 2011, Jassey, Gilbert, et al. 2011; Jassey et al. 2013) shape the taxonomic and functional structure of the microbiome that in turn improves the plant fitness (Mendes et al. 2011). These *Sphagnum*–microbiome relationships promote plant growth through the provisioning of nutrients with the help of the microbial partners. Microbially driven processes like N_2 fixation and methane oxidation have been shown to support *Sphagnum* production and C accumulation in peatlands through improved nutrient and CO_2 supply (Berg, Danielsson, and Svensson 2013; Vile et al. 2014; Larmola et al. 2014; Raghoebarsing et al. 2005; Kip et al. 2010; Kolton et al. 2022; Petro et al. 2023). However, even in non-matched donor–recipient pairs significant increases in *Sphagnum* growth were observed, indicating that *Sphagnum* can also benefit from a non-species-specific *Sphagnum* microbiome. Microbe-conferred thermal tolerance of multiple host plants has previously been demonstrated (Lee et al. 2023; Ali et al. 2009), but this study is first to show microbiome-driven thermal transfer across different *Sphagnum* species. While the underlying molecular mechanisms remain unknown, microbe-driven transfer of thermal acclimation to *Sphagnum* may involve upregulation of heat shock proteins and downregulation of phytohormones (jasmonic acid; Carrell et al. 2022). In Carrell et al. (2022), the microbiome was transferred from and into the same *Sphagnum* species, but our study shows that similar mechanisms must exist even when *Sphagnum* donor-pairs mismatch and come from different geographical and climatic origins.

Our findings align with key results from plant–soil feedback (PSF) research while revealing unique aspects of moss–microbiome interactions. PSF studies have shown that plants condition their soil microbial communities, leading to feedbacks that impact subsequent plant growth (Bever, Westover, and Antonovics 1997; Van der Putten et al. 2013). The enhanced growth of *Sphagnum* with matched microbiomes suggests a positive feedback mechanism similar to vascular plants, but through direct host–microbiome associations rather than soil conditioning. While Kardol, Bezemer, and Van Der Putten (2006) demonstrated soil conditioning by early successional species resulted in positive feedbacks enhancing their growth through bulk soil communities, the *Sphagnum*–microbiome relationship involves microbes more intimately associated with the phyllosphere of the plant. The transferability of microbially conferred warming tolerance we observed aligns with studies showing soil communities can rapidly adapt to environmental stress and transfer tolerance to hosts. For example, Lau and Lennon (2012) found soil microbes could adapt to drought and enhance host plant fitness under water limited conditions. However, our finding that non-matched microbiomes conferred reduced but still positive benefits differs from PSF studies where non-native soil communities often produce neutral or negative effects (Kulmatiski et al. 2008). This difference may be due to the unique phyllosphere habitat of *Sphagnum* microbiomes compared to soil microbiomes or due to the evolution of conserved beneficial microbial functions in nutrient-poor and acidic *Sphagnum*-dominated peatland environment.

We found that in situ temperature conditions of the microbiome determine the thermal acclimation response in *Sphagnum*. Earlier work investigating *Sphagnum*'s heat and freezing tolerance (short-term exposure to extreme temperatures < 10°C and > 55°C) suggested that the least frost-tolerant *Sphagnum* plants (*S. magellanicum* and *S. fuscum*) typical of more southern, generally warmer peatlands while the *Sphagnum* plants (*S. balticum*, *S. subsecundum* and *S. teres*) typical of colder regions were more cold-resistant (Balagurova, Drozdov, and Grabovik 1996). Similarly, *Sphagnum* populations collected at low-elevation sites in the Alpine peatlands were more resistant to heat stress compared to those collected at high-elevation sites when exposed for four days to elevated temperatures of 36°C and 43°C (compared to ambient temperature of 25°C) (Gerdol and Vicentini 2011). Another experiment showed that *Sphagnum* plants from northern sites of Sweden were more affected by the increased temperature in the greenhouse experiment compared to those from south Sweden (Breeuwer et al. 2009). *Sphagnum* microbiome acclimation to the in situ origin temperature could have played a role in these studies and may be an important factor to consider in any thermal acclimation or adaptation studies of *Sphagnum*.

More recent evidence from in situ warming experiments indicates that climate warming is likely to have a major impact on plant–microbe interactions in the *Sphagnum* phytobiome (plant host + constituent microbiome + environment; Norby et al. 2019; Carrell et al. 2019; Petro et al. 2023). Elevated temperatures can directly impact the metabolic activity of *Sphagnum* leading to changes in the composition and quantity of exudates it releases (Sytiuk et al. 2023). These altered exudates can influence the structure and function of the *Sphagnum*–microbiome, as well as the abundance and activity of protists within the community (Jassey et al. 2013). Certain protists, such as testate amoeba, may exhibit increased predation on the microbial community due to the changes in exudate composition (Jassey et al. 2011). This shift in predation pressure can further influence the structure and function of the microbiome, potentially impacting *Sphagnum*'s fitness and overall performance. The intricate linkages between the microbiome, host, protists, and predation in *Sphagnum* ecosystems highlight the vulnerability of these complex interactions to elevated temperatures, emphasizing the need for a comprehensive understanding of this complex food web interaction in peatland ecosystems.

In some peatland warming experiments, *Sphagnum* abundance has been observed to decline at the expense of vascular plants (Norby et al. 2019, 2023; Jassey et al. 2011), while others have observed increased *Sphagnum* growth in response to summer warming (Dorrepaal et al. 2004). Other factors co-occurring with warming could have contributed to the diverging *Sphagnum* responses. For example, *Sphagnum* growth is sensitive to moisture with the largest productivity being observed in wet sites (McNeil and Waddington 2003). Warming has therefore been shown to enhance *Sphagnum* productivity in wet sites while having no effect or negatively affecting *Sphagnum* growth in dry sites (e.g., Buttler et al. 2015; Weltzin et al. 2003; Bengtsson et al. 2021). Similarly, Jassey and Signarbieux (2019) found *Sphagnum* photosynthesis to respond positively to warming during rainy periods while responding negatively to warming during dry periods. In a warmer climate, peatlands are expected to also experience drier conditions (Helbig et al. 2020; Swindles et al. 2019), which may limit the positive growth response of *Sphagnum* to warming. In our study, effects of climate change-driven extreme events (e.g., drought-induced decline in moisture availability, microbiome grazer population decline) were not studied. Thus, responses of *Sphagnum*–microbiome interaction to warming combined with changes in the frequency and intensity of precipitation or the duration of drought events (Dai 2013; Fischer and Knutti 2016; Martin 2018) may differ from the results reported here. Additionally, indirect effects of climate change induced temperature and moisture changes may alter the vegetation composition in peatlands. With increasing shrub cover (Weltzin et al. 2003), light availability due to shading is reduced for *Sphagnum* mosses (Norby et al. 2019, 2023; Jassey et al. 2011). The changes in the light environment should be considered too when assessing *Sphagnum*'s resilience to climate change. Our study indicates that the microbiome has the ability to acclimate to the thermal conditions of the environment and transfer this ability to *Sphagnum*, thus potentially moderating the negative effects on *Sphagnum*'s growth in a warming climate. Future studies should test if microbiomes adapted to large climate variability (including frequent droughts) can provide additional benefits to *Sphagnum* growth across multiple environmental conditions (temperature, moisture, and light).

Preliminary observations of our field-collected samples suggest potential warming-related variation in bacterial families commonly associated with N cycling, such as *Nostocaceae* (N_2 fixers) and *Beijerinckiaceae* (N_2 fixers and ammonia oxidizers). While limited replication prevents statistical validation of these patterns, these observations align with previous studies (Allison and Martiny 2008; Louca et al. 2018) and suggest the possibility of selection for microbial function rather than specific microbial species. The ecological principle of "functional redundancy" would predict that many microbial taxa, even members of the rare biosphere, could become active in mediating processes such as N_2 fixation depending on shifts in environmental conditions (Prosser 2012). Although cyanobacteria of the *Nostocaceae* are often the most abundant amongst diazotrophs of the *Sphagnum* microbiome, rare keystone members of the *Beijerinckiaceae* were shown to be the most active in fixing nitrogen and oxidizing methane in *Sphagnum* microbiomes of North American peatlands (Kolton et al. 2022). This is consistent with other systems such as coral (Doering et al. 2021) or *Drosophila melanogaster* (Moghadam et al. 2018) that report the abundances of specific taxa do not always correlate to the outcome of microbiome conferred tolerance. In a warming climate, changes in the local environment may cause a loss (Norby et al. 2019) or shifts in *Sphagnum* species within each niche (e.g., Robroek et al. 2007; Breeuwer et al. 2008). Incoming *Sphagnum* species could adopt an already (non-matching) existing microbiome in the surface peat which, if trends shown here hold true in the field, would be capable of providing growth benefits to *Sphagnum*.

Our findings demonstrate the importance of leveraging *Sphagnum*–microbiome relationships in plant response to temperature change, with implications for peatland resilience under future climate scenarios. The ability of microbiomes to both rapidly acclimate to warming conditions and confer benefits across *Sphagnum* species suggests multiple mechanisms for ecosystem adaptation. Future research should examine how these beneficial host–microbiome interactions persist under field conditions where multiple climate stressors co-occur, including drought, altered precipitation patterns, and changing light conditions due to vegetation shifts. Understanding these complex interactions will be crucial for predicting and potentially managing peatland responses to climate change, with implications for global carbon cycling and ecosystem stability.

Author Contributions

Tatjana Živković: conceptualization, data curation, formal analysis, investigation, methodology, validation, visualization, writing – original draft, writing – review and editing. **Alyssa A. Carrell:** conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing – review and editing. **Gustaf Granath:** conceptualization, funding acquisition, methodology, writing – review and editing. **A. Jonathan Shaw:** writing – review and editing. **Dale A. Pelletier:** funding acquisition, investigation, methodology, writing – review and editing. **Christopher W. Schadt:** writing – review and editing. **Dawn M. Klingeman:** methodology, writing – review and editing. **Mats B. Nilsson:** resources, writing – review and editing. **Manuel Helbig:** formal analysis, methodology, writing – review and editing. **Denis Warshan:** writing – review and editing. **Ingeborg J. Klarenberg:** writing – review and editing. **Daniel Gilbert:** resources, writing – review and editing. **Joel E. Kostka:** writing – review and editing. **David J. Weston:** conceptualization, funding acquisition, investigation, methodology, project administration, resources, supervision, validation, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.14714902 and in the BioProject database (http://ncbi.nlm.nih.gov/bioproject) under accession PRJNA1210807.

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Supporting Information

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