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RESEARCH ARTICLE

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Will climate change cause the global peatland to expand or contract? Evidence from the habitat shift pattern of *Sphagnum* mosses

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Abstract

Peatlands play a crucial role in the global carbon cycle. *Sphagnum* mosses (peat mosses) are considered to be the peatland ecosystem engineers and contribute to the carbon accumulation in the peatland ecosystems. As cold-adapted species, the dominance of *Sphagnum* mosses in peatlands will be threatened by climate warming. The response of *Sphagnum* mosses to climate change is closely related to the future trajectory of carbon fluxes in peatlands. However, the impact of climate change on the habitat suitability of *Sphagnum* mosses on a global scale is poorly understood. To predict the potential impact of climate change on the global distribution of *Sphagnum* mosses, we used the MaxEnt model to predict the potential geographic distribution of six *Sphagnum* species that dominate peatlands in the future (2050 and 2070) under two greenhouse gas emission scenarios (SSP1-2.6 and SSP5-8.5). The results show that the mean temperature of the coldest quarter, precipitation of the driest month, and topsoil calcium carbonate are the main factors affecting the habitat availability of *Sphagnum* mosses. As the climate warms, *Sphagnum* mosses tend to migrate northward. The suitable habitat and abundance of *Sphagnum* mosses increase extensively in the high-latitude boreal peatland (north of 50°N) and decrease on a large scale beyond the high-latitude boreal peatland. The southern edge of boreal peatlands would experience the greatest decline in the suitable habitat and richness of *Sphagnum* mosses with the temperature rising and would be a risk area for the transition from carbon sink to carbon source. The spatial–temporal pattern changes of *Sphagnum* mosses simulated in this study provide a reference for the development of management and conservation strategies for *Sphagnum* bogs.

KEYWORDS
bog, carbon sink, climate warming, MaxEnt, peat moss

1 | INTRODUCTION

Peatlands cover approximately 3% of the world's land area, but store almost 30% of total global soil organic carbon stock, and are an essential ecosystem for mitigating climate change (Crump, 2017; Gorham, 1991; Yu et al., 2010). Peatlands are mostly found in high latitudes of the Northern Hemisphere, where temperatures are rising faster than in the rest of the world. Based on up-to-date knowledge, climate-induced changes in peatland vegetation phenology and composition would compromise the carbon sink function of peatlands (Antala et al., 2022; Dieleman et al., 2015; Larmola et al., 2013; Oke & Hager, 2020; Walker et al., 2016). Peatland vegetation is very sensitive to climate change, especially bryophytes (Gignac & Vitt, 1994). Studies on the distribution and abundance of peatland bryophytes in relation to climate are thought to be useful in predicting the potential effects of global warming on peatland ecosystems (Gignac & Vitt, 1994). *Sphagnum* L. (peat mosses) have unique physiological and biochemical characteristics as well as methanotrophic symbionts that contribute to carbon accumulation in the peatland ecosystems (Freeman et al., 2001; Raghoebarsing et al., 2005; Rydin et al., 2006). They are the dominant components of the peatland ecosystem and contribute up to 50% of the organic soil carbon in many boreal peatlands (Gajewski et al., 2001; Oke & Hager, 2017). The response of *Sphagnum* mosses to climate change is closely related to the future trajectory of carbon fluxes in peatlands.

Sphagnum mosses as the peatland ecosystem engineers typically grow in bogs (ombrotrophic peatlands) and poor fens (oligotrophic peatlands or poor minerotrophic peatlands) (Shaw, Devos, et al., 2016; van Breemen, 1995; Vitt & House, 2021). They have an astonishing ability to create and then uniquely thrive in nutrient-poor, acidic, and waterlogged conditions (Glime, 2017; Jones et al., 1994; Rydin et al., 2006; Weston et al., 2018). Due to the lack of stomata and water-conducting tissues, the growth, community composition and vitality of *Sphagnum* mosses are strongly dependent on environmental factors such as temperature (Carrell et al., 2019; Jassey & Signarbieux, 2019; Robroek et al., 2007), pH (Gignac & Vitt, 1990), water table depth (Gignac & Vitt, 1994; Oke & Hager, 2020; Vitt et al., 2003) and atmospheric CO_2 (Toet et al., 2006). Alterations in any of these factors caused by climate change may alter existing distribution patterns of *Sphagnum* mosses and feedback to peatland ecosystem functioning. Hence, predicting potential changes in the geographic distribution of *Sphagnum* species that dominate peatlands under future climate scenarios is essential for understanding the response of the peatland ecosystem to global warming.

As the climate warms, most species tend to shift to higher latitudes or elevations (Parmesan, 2006; Sun et al., 2020; Thurm et al., 2018). This would be a big challenge for the cold-adapted species (Wei et al., 2021). *Sphagnum*-dominated peatlands will be at increased risk of invasion by vascular plants due to elevated temperature, the lower water table and increased nitrogen deposition (Dieleman et al., 2015; Hogg et al., 1995; Tomassen et al., 2004). The expansion of vascular plants will threaten the dominance of *Sphagnum* species in peatlands, and put the carbon sink capacity of peatlands and the C already stored at risk (Comont et al., 2006; Gogo et al., 2011; Norby et al., 2019). Changes in the geographic distribution and composition of species driven by climate change are closely linked to the fate of peatland ecosystems. Recent species distribution models (SDMs) for *Sphagnum* species or *Sphagnum* bogs have focused on suitable habitat projections on country-wide and continental-wide scales (Campbell et al., 2021; Cerrejón et al., 2020; Cong et al., 2020; Oke & Hager, 2017). Oke and Hager (2017) modeled the distribution and expansion of four *Sphagnum* species in North American peatlands which were tightly influenced by the future climate scenarios. They proposed that projected global warming would be effectively balanced by the expected increase in precipitation, leading to higher productivity of *Sphagnum* mosses. However, the suitable areas for *Sphagnum* bogs in China would experience a large-scale decline in the future (Cong et al., 2020). The distribution pattern of *Sphagnum* mosses in local regions may not adapt to other regions due to the limitation of regional climate (Oke & Hager, 2017) and we cannot infer the future global distribution pattern of *Sphagnum* mosses.

For bryophytes that dominate peatland surfaces, water and soil nutrients are considered to be the main environmental factors limiting their growth (Hájek, 2014). Many studies have revealed that climatic factors related to precipitation, such as annual water balance, the precipitation of driest month, and annual precipitation, are important indicators of *Sphagnum* moss distribution and richness (Campbell et al., 2021; Cong et al., 2020; Oke & Hager, 2017; Popov, 2016, 2018). In addition, the physical and chemical properties of soil such as pH, cation content, and soil nutrients will affect the growth and dispersal of *Sphagnum* mosses (Chapin et al., 2004; Gignac & Vitt, 1990; Gogo et al., 2011; Hájek, 2014; Vicherová et al., 2015). However, previous studies on *Sphagnum* moss distribution models only considered climatic variables as predictors.

The genus *Sphagnum* includes 250–450 species (Shaw, Schmutz, et al., 2016), but less than 50 species have contributed to large-scale peat formation. These species usually occur sympatrically (same geographic area) and dominate in northern peatlands (Gunnarsson, 2005). The sympatric occurrence of multiple *Sphagnum* species that dominate peatlands can, to some extent, reflect the presence of *Sphagnum*-dominated peatlands (Oke & Hager, 2017). Effective representation of the geographic distribution of *Sphagnum* species that dominate peatlands can provide an important reference for understanding the response of peatland ecosystems to climate warming. In this study, we used the MaxEnt model to simulate the potential habitats of six *Sphagnum* species dominant in peatlands and predict their potential global distribution shifts under future climate scenarios. We aim to predict the trends and extent of changes in suitable habitats of *Sphagnum* mosses under future climate scenarios and explore the global distribution patterns of the vulnerable habitats.

2 | MATERIALS AND METHODS

2.1 | Species occurrence record

We obtained occurrence records of six *Sphagnum* species that are dominant in peatlands from the Global Biodiversity Information Facility (https://www.gbif.org/), the Consortium of North American Bryophyte Herbaria (https://www.bryophyteportal.org), the Smithsonian National Museum of Natural History (https://naturalhistory.si.edu/), the National Specimen Information Infrastructure database (http://www.nsii.org.cn), and the Chinese Virtual Herbarium (https://www.cvh.ac.cn). We also collected *Sphagnum* occurrence records from our field surveys in Africa, Asia, America, and Europe during the period of 2010–2021. We used Google Earth (https://earth.google.com/) to obtain the approximate latitude and longitude based on geographic location for specimens without precise geographic coordinates. Duplicate records in each grid cell (~10×10 km) were removed during analysis. Finally, 6519 occurrence records were used for modeling, including 784 of *Sphagnum angustifolium*, 795 of *Sphagnum fuscum*, 1536 of *Sphagnum magellanicum s. lato*, 668 of *Sphagnum rubellum*, 1430 of *Sphagnum papillosum*, and 1306 of *Sphagnum cuspidatum* (Figure S1). All the occurrence records used for modeling are archived in Dryad (Ma et al., 2022). *Sphagnum magellanicum s. lato* has recently been split into three narrow species, *Sphagnum divinum*, *Sphagnum magellanicum s. str.*, *Sphagnum medium*, all of which typically occur in peatlands (Hassel et al., 2018). Considering that the three species are very hard to distinguish because of their variable and soft morphological characters (Hill, 2020), a broad species concept for *S. magellanicum* was adopted in the present study.

2.2 | Environmental factors

Thirty-six environmental factors, including elevation, 19 bioclimatic variables, and 16 soil variables that would influence the distribution of *Sphagnum* mosses (Chapin et al., 2004; Hájek, 2014; Oke & Hager, 2017; Popov, 2016, 2018) were downloaded to model the current species distribution patterns. The elevation and 19 bioclimatic variables with 2.5 min spatial resolution (approximately 5 km^2) were obtained from the World Climate Database (version 2.0, http://worldclim.org/; Fick & Hijmans, 2017), and 16 soil variables were obtained from Harmonized World Soil Database (version 1.2, https://www.fao.org/soils-portal/).

For future climate scenarios, we used CNRM-CM6-1 climate system model released by the sixth phase of the Coupled Model Intercomparison Project (CMIP6) of IPCC6 report (Voldoire et al., 2019). The shared socioeconomic pathways (SSPs) of CMIP6 are considered to be the more reasonable future climate scenarios than the representative concentration pathway of CMIP5 (Su et al., 2021). Here we selected SSP1-2.6 and SSP5-8.5 future climate scenarios to represent the lowest and highest levels of greenhouse gas (GHG) emissions, respectively. Future climate data for average years 2041–2060 and 2061–2080 (hereafter referred to as 2050 and 2070, respectively) were selected in our study. The elevation and soil environmental parameters remained unchanged for SDMs analysis under future climate conditions. We resampled all of the environmental variables at a 2.5 min spatial resolution. To avoid overfitting of the model owing to the multi-collinearity of environmental variables, we examined the correlation between variables using ArcGIS10.2 and removed the variables with a correlation higher than 0.75. Finally, 21 environmental variables archived in Dryad (Ma et al., 2022) were selected for SDMs (Table 1).

2.3 | Species distribution modeling

We simulated the potential distribution of *Sphagnum* mosses using the maximum entropy model (MaxEnt version 3.4.0; http://www.cs.princeton.edu/; Phillips et al., 2006). In this study, 75% of occurrence data were used for model training, and the remaining 25% was randomly selected for model testing. To ensure that the model has adequate time to converge, the maximum number of background points was set to 10,000 and the algorithm was run with 3000 iterations, while other values were kept as default. Ten replications of each scenario were performed to assess the average results. The area under the curve (AUC), which is the area under the receiver-operating characteristic (ROC), was used to evaluate the accuracy of the model. The AUC values range from 0.5 to 1, with higher values indicating the better performance of the model: poor (0.5–0.6), fair (0.6–0.7), good (0.7–0.8), very good (0.8–0.9), and excellent (0.9–1.0) (Swets, 1988). The Jackknife test was used to assess the relative importance of the variables. We created binary distribution maps of suitable and unsuitable ranges selecting 0.2 as the appropriate threshold by weighing the Maximum Test Sensitivity Plus Specificity logistic threshold (MTSPS) of each specific model. Species richness (the number of different species per grid cell) was calculated by superposing all of the species ranges and the areas of potential gain, loss, and no change were calculated by superposing species ranges or species richness ranges under different climate scenarios.

2.4 | Geospatial analyses

ENMTools is a set of comparative similarity measures and statistical tests that allow quantitative comparison of ecological niche models. It can be used to measure niche and range overlap among species distributions (Jiao et al., 2016; Warren et al., 2008). We used ENMTools v1.3 (http://purl.oclc.org/enmtools) to measure niche and range overlap among potential distributions of six *Sphagnum* species. Pairwise similarity values of *I* derived from Hellinger distance would be calculated (Warren et al., 2008). Pairwise similarity values of *I* and the values of range overlap range from 0 to 1 (larger values mean more niche overlap and range overlap, respectively).

To examine the migration trend of each species' range, we calculated the direction and distance of centroid changes in the range of each species by comparing the centroids of current and future binary distribution maps using the GIS toolkit SDMtoolbox (Brown, 2014). This analysis was performed by reducing each species' distribution to a single central point (a centroid) and creating a vector file for depicting the magnitude and direction of distribution changes over time. Then we measured the potential distribution areas change for each species using SDMtoolbox and the output was based on the World Equal Area Cylindrical projection. The richness variation value and latitude of all the grid cells were obtained by ArcGIS 10.2, and we used Matlab R2021a (https://ww2.mathworks.cn) to count the number of the grid cells with the variation of species number more than 1 in each latitude zone, and then plotted the frequency distribution histogram of species richness changes in each latitude zone under future climatic scenarios.

TABLE 1 Permutation importance of environmental variables under current climate conditions

Symbol	Environmental variable	Percent contribution (%)					
		Sphagnum angustifolium	*Sphagnum cuspidatum*	*Sphagnum fuscum*	*Sphagnum magellanicum s. lato*	*Sphagnum papillosum*	*Sphagnum rubellum*
bio2	Mean diurnal range	1.5	0.3	1.1	0.5	2.8	2.7
bio7	Temperature annual range	3.3	1.9	1.9	2.9	2.9	2.3
bio11	Mean temperature of coldest quarter	34.2	16.2	33.4	22.3	22.7	25.0
bio12	Annual precipitation	0.9	0.4	0.3	0.8	0.1	0.5
bio14	Precipitation of driest month	37.3	71.0	34.5	61.0	59.0	52.7
bio15	Precipitation seasonality	2.4	0.7	0.9	0.5	0.9	1.7
ASL	Elevation	0.9	2.5	0.4	1.1	0.8	3.1
AWC_CLASS	Available water capacity range	0.7	0.4	0.2	0.3	0.8	0.3
T_BULK_DEN	Topsoil bulk density	0.2	0.2	0.4	0.5	0.5	0.1
T_CEC_CLAY	Topsoil cation exchange capacity (clay)	1.6	0.5	2.0	0.8	0.9	1.7
T_CLAY	Topsoil clay fraction	0.1	0.3	0.3	0.6	0.1	0.9
T_GRAVEL	Topsoil gravel content	0.6	0.9	0.1	0.9	0.9	0.6
T_SAND	Topsoil sand fraction	1.2	0.1	0.3	0.9	0.2	0.7
T_SILT	Topsoil silt fraction	3.2	0.2	1.1	0.5	0.6	0.4
T_PH_H_2O	Topsoil pH (H_2O)	2.6	1.4	1.5	1.5	1.0	1.3
T_OC	Topsoil organic carbon	1.6	0.2	5.4	1.1	1.6	0.7
T_TEB	Topsoil total exchangeable bases	0.2	0.1	0.2	0.1	0	0.2
T_$CaCO_3$	Topsoil calcium carbonate	3.2	2.0	8.6	3.5	2.3	2.4
T_$CaCO_4$	Topsoil gypsum	2.3	0.2	1.4	0.1	0.1	0.9
T_ESP	Topsoil sodicity (ESP)	1.5	0	4.3	0.1	0.1	0.9
T_ECE	Topsoil salinity (Elco)	0.6	0.6	1.7	0.1	1.5	1.0

Note: Gray background indicates the top five important environmental variables for each species.

3 | RESULTS

3.1 | The SDM and main variables

We obtained the SDMs for all six *Sphagnum* species with the average test AUC ranging from 0.903 to 0.936 (Figure S2), approving that the models performed well and generated excellent evaluations.

Niche and range similarity analysis showed high niche overlap and range overlap between each of the six *Sphagnum* species habitat models under current conditions. Hellinger's-based I niche similarity scores ranged between 0.75 and 0.98, and the values of range overlap ranged between 0.66 and 0.99 (Figure 1). Currently, suitable areas for *Sphagnum* mosses were found to be mainly distributed in large parts of Europe and North America, parts of Asia, the southeastern region of Australia, and the southwest coastal part of South America (Figure S3).

By listing the top five important environmental variables for each species, the mean temperature of the coldest quarter (Bio11), precipitation of the driest month (Bio14), and topsoil calcium carbonate (T_CaCO_3) showed the most important contributions in most species (Table 1). The cumulative contribution of the three variables was up to 74.7%–89.2%. These environmental variables were used to describe the multidimensional niche of each species (existence probability >0.2) (Figure 2), and the niches for six *Sphagnum* species were similar.

3.2 | Potential habitat changes of *Sphagnum* mosses under future climate scenarios

Changes in the distribution centroid showed that all the six *Sphagnum* species in the 2070s under different climate scenarios would shift northward (Figure 3). We predicted the six *Sphagnum* species to shift between 180 and 620 km under SSP1-2.6, while the six species would shift 680–940 km under SSP5-8.5. In general, the potential distribution area of *Sphagnum* would shift noticeably northward, and the distance of the shift would increase with the intensification of GHC emissions.

By superposing the current potential distribution of *Sphagnum* mosses with the potential distribution under future climate scenarios, the habitat shift patterns were obtained (Figure 4), which could reflect the changes in the potential distribution of *Sphagnum* with climate scenarios more directly. The results showed that the habitat shift patterns of the six *Sphagnum* species were relatively consistent under different future climate scenarios. The newly added suitable habitats were mainly distributed in the high latitudes of North America, Europe, and Asia. The loss area of suitable habitats was concentrated in the lower latitudes of the Northern Hemisphere and the Southern Hemisphere, mainly located in the large part of the United States, southern Europe, southeastern Asia, the coastal areas of South America, and southeastern Australia. Under the SSP1-2.6 scenarios, the lost habitat area would be 55.19–242.93 × 10^4 km^2 and 53.33–255.86 × 10^4 km^2 in the 2050s and 2070s, respectively, while the added habitat area would be 71.45–193.19 × 10^4 km^2 and 64.45–170.55 × 10^4 km^2, respectively. Under the SSP5-8.5 scenarios, the lost habitat area would be 69.67–320.31 × 10^4 and 103.65–474.66 × 10^4 km^2 in the 2050s and 2070s, respectively, while the added habitat area would be 102.87–229.57 × 10^4 km^2 and 150.36–346.73 × 10^4 km^2, respectively (Figure 5). Overall, in the future, habitat expansion of the six *Sphagnum* species would be concentrated in the high Northern Hemisphere latitudes and the contraction would be concentrated in the middle and low Northern Hemisphere latitudes and the Southern Hemisphere. Under the green development model (SSP1-2.6), the degree of expansion would decrease after the 2050s, and this situation of northern expansion and southern contraction would intensify over time under the high GHG emission scenario (SSP5-8.5).

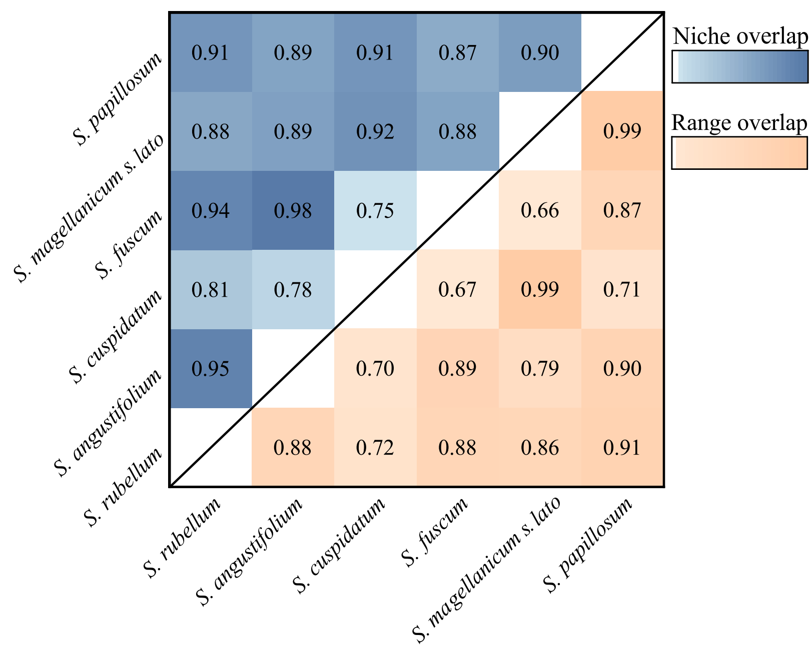

FIGURE 1 Niche and range overlap of six *Sphagnum* species. Pairwise similarity values of *I* and the values of range overlap (in the square) range from 0 to 1 (larger values mean more niche overlap and range overlap, respectively). [Colour figure can be viewed at wileyonlinelibrary.com]

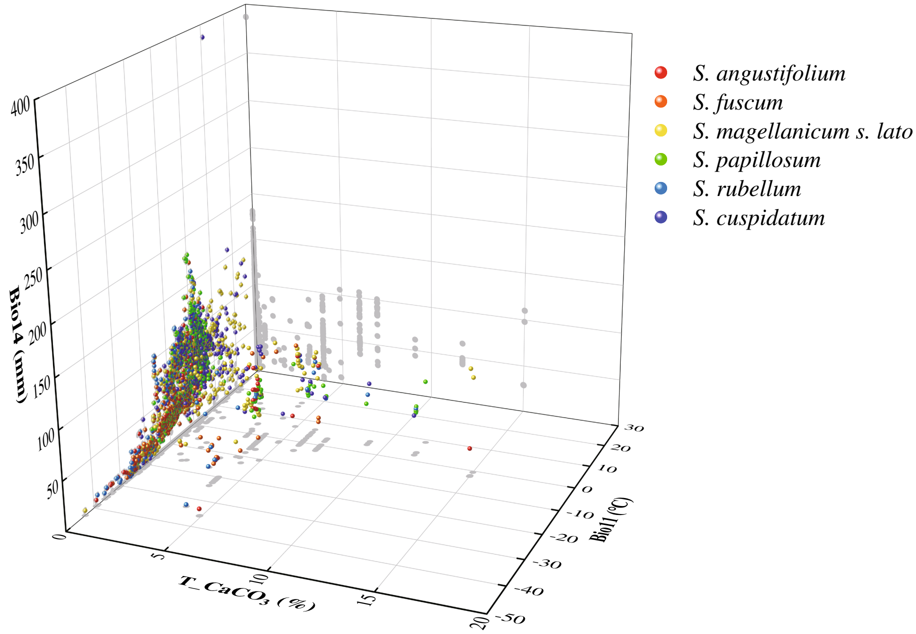

FIGURE 2 Ecological niches of six *Sphagnum* species. Bio11: The mean temperature of the coldest quarter; Bio14: Precipitation of the driest month; T_$CaCO_3$: Topsoil calcium carbonate. [Colour figure can be viewed at wileyonlinelibrary.com]

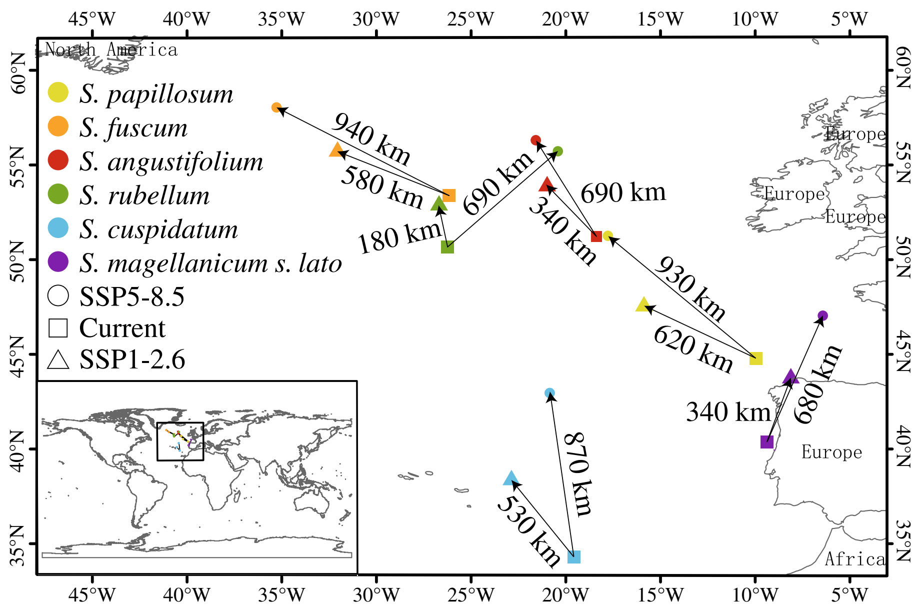

FIGURE 3 Centroid changes in the distribution of *Sphagnum* species in the 2070s under two future climate scenarios (SSP1-2.6 and SSP5–8.5). Each species' distribution was reduced to a single central point (a centroid). The arrows indicate the magnitude and direction of predicted distribution change through time. Map lines delineate study areas and do not necessarily depict accepted national boundaries. [Colour figure can be viewed at wileyonlinelibrary.com]

3.3 | Impact of climate change on potential species richness distributions

The global richness distribution of *Sphagnum* species that dominate peatlands was obtained by superposing the distribution data of six species (presence probability >0.2). The areas with high species richness were concentrated in North America and Europe under the present climatic scenarios (Figure S3). The hotspot of species richness showed a trend of northward movement under future climatic scenarios (Figure 6). The richness variations of all the grid cells showed that the richness variations distribution also presented a spatial pattern, and the spatial change pattern tended to be consistent across different climate scenarios. Under future climatic scenarios, the species richness of *Sphagnum* would increase in the area between 50°N and 70°N (the variation of species number is more than 1; Figures 6 and 7). By contrast, it would significantly decrease at latitudes below 50°N as a whole, especially between 40°N and 50°N.

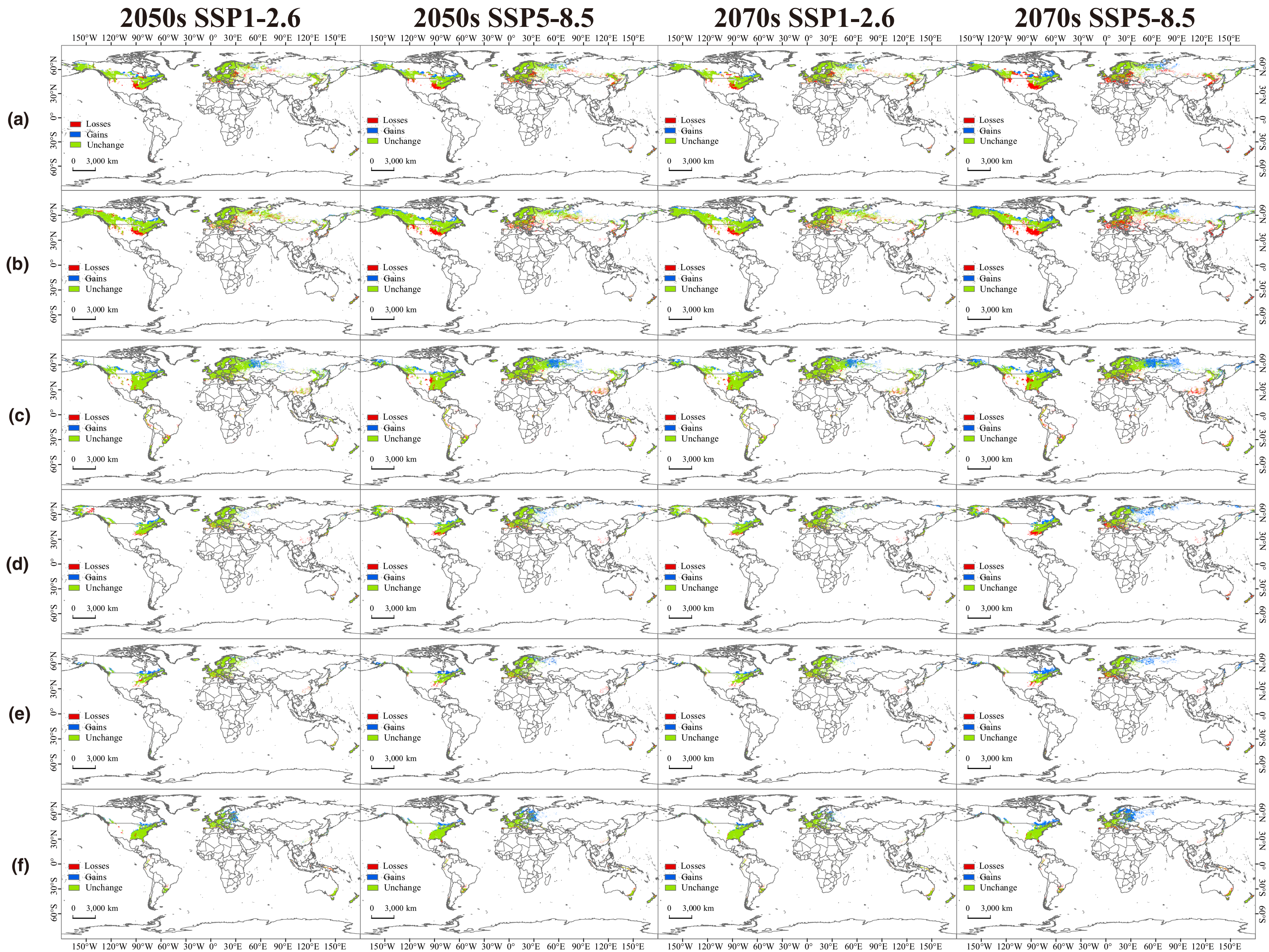

FIGURE 4 Changes in the potential geographical distribution under two future climate scenarios (SSP1-2.6 and SSP5-8.5) at two time points (2050 and 2070) compared with current distribution of *Sphagnum* species. (a) Species distribution model (SDM) for *Sphagnum angustifolium*; (b) SDM for *Sphagnum fuscum*; (c) SDM for *Sphagnum magellanicum s. lato*; (d) SDM for *Sphagnum rubellum*; (e) SDM for *Sphagnum papillosum*; (f) SDM for *Sphagnum cuspidatum*. Map lines delineate study areas and do not necessarily depict accepted national boundaries. [Colour figure can be viewed at wileyonlinelibrary.com]

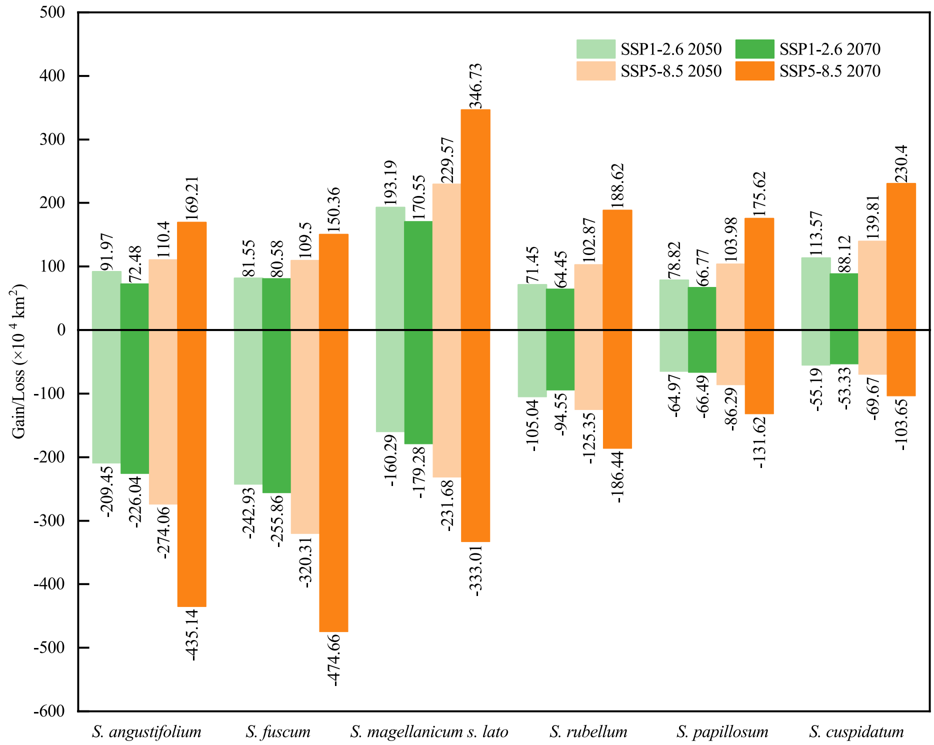

FIGURE 5 Predicted change in area for six *Sphagnum* species distribution under future climate scenarios compared with the current distribution. [Colour figure can be viewed at wileyonlinelibrary.com]

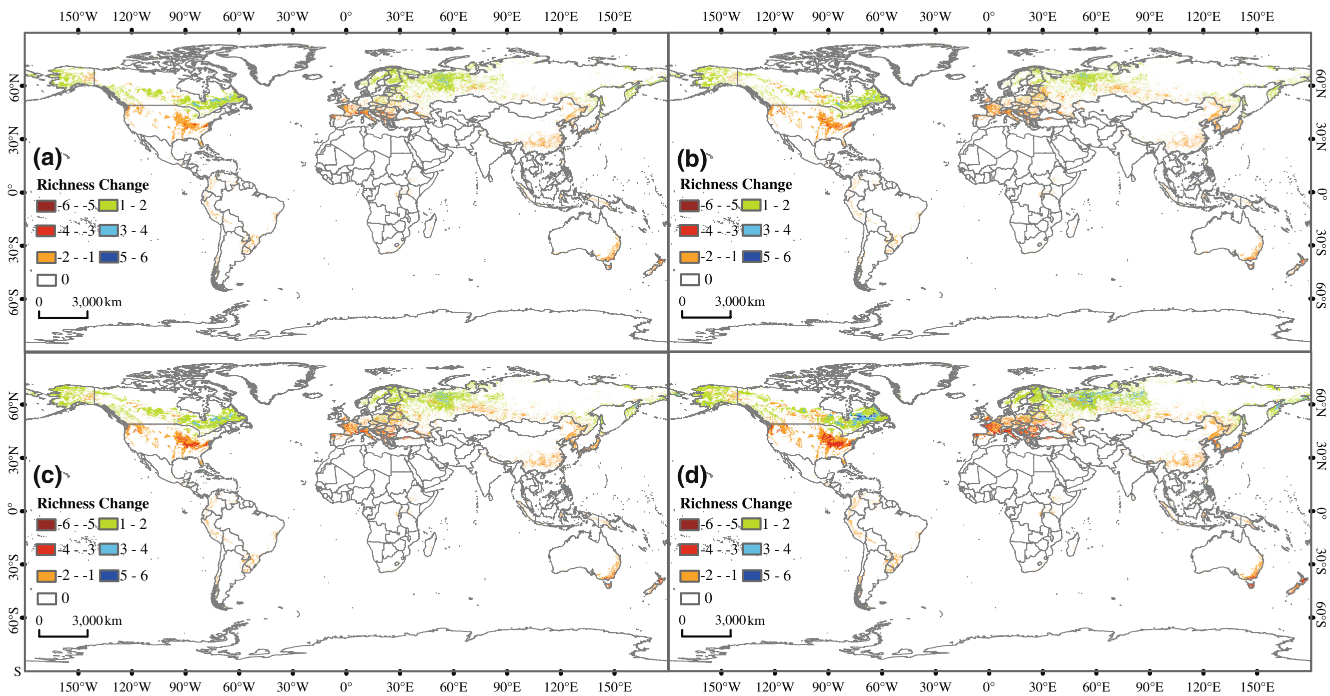

FIGURE 6 Richness change distributions of six *Sphagnum* species under future climate scenarios compared with the current richness distribution: (a) SSP1-2.62050; (b) SSP1-2.62070; (c) SSP5-8.52050; and (d) SSP5-8.52070. Different colors (from red to blue) indicate different species richness (the number of different species) change levels (from low to high, respectively). Map lines delineate study areas and do not necessarily depict accepted national boundaries. [Colour figure can be viewed at wileyonlinelibrary.com]

The potential richness variations of *Sphagnum* mosses differed to varying degrees under different climatic scenarios. By the 2050s, 20.44% and 26.47% of modern habitats would experience varying degrees of decline in species richness under the SSP1-2.6 and SSP5-8.5 projection scenarios respectively, with 1.28% and 2.97% of modern habitat experiencing loss of three or more species (Table 2). By the

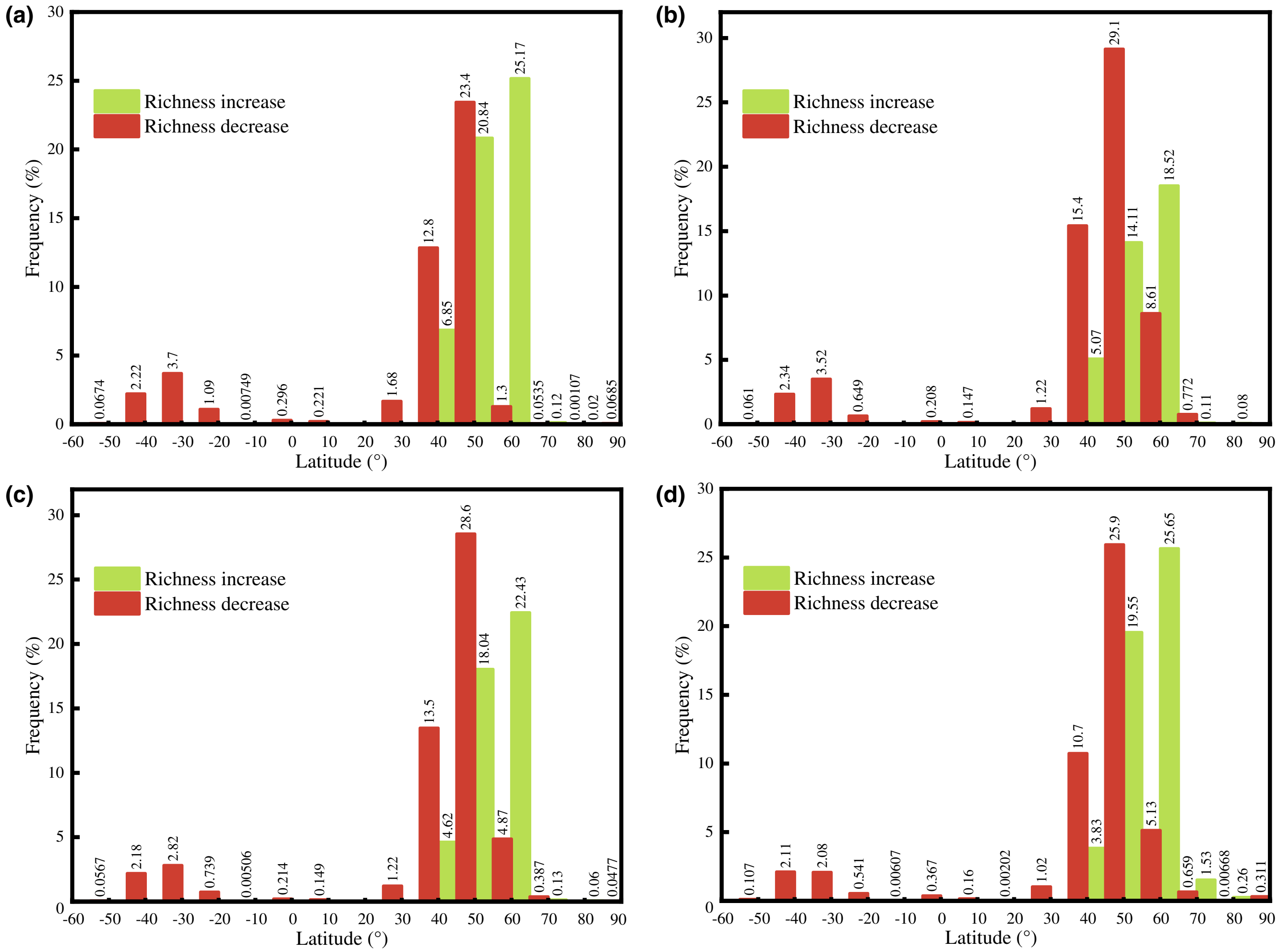

FIGURE 7 Frequency distribution histogram of *Sphagnum* species richness changes (the variation of species number is more than 1) at different latitudes under future climate scenarios: (a) SSP1-2.6 2050; (b) SSP1-2.6 2070; (c) SSP5-8.5 2050; and (d) SSP5-8.5 2070. [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 The area rates of species richness change under future climate scenarios compared with the current richness distribution

Richness change	−1 to −2	−3 to −4	−5 to −6	1–2	3–4	5–6
SSP1-2.6 2050	19.166%	1.255%	0.021%	26.017%	1.195%	0.001%
SSP1-2.6 2070	21.816%	1.484%	0.025%	22.047%	0.672%	0.001%
SSP5-8.5 2050	23.508%	2.868%	0.098%	29.050%	1.626%	0.006%
SSP5-8.5 2070	28.600%	6.425%	0.430%	34.203%	4.777%	0.716%

2070s, habitat areas experiencing species richness decline at mid-low latitudes would increase further. 23.33% and 35.46% of modern habitats would experience a decline in species richness under the SSP1-2.6 and SSP5-8.5 projection scenarios respectively. Under the SSP5-8.5 projection scenarios, up to 6.86% of modern habitats would lose three or more *Sphagnum* species, which are mainly distributed in the United States, southern Europe, southeastern Asia, and southeastern Australia.

4 | DISCUSSION

In this study, the SDMs of the six *Sphagnum* species that are dominant in peatlands showed a high degree of ecological niche and range overlap. The sympatric occurrence of multiple *Sphagnum* species that dominate peatlands can reflect the presence of *Sphagnum*-dominated peatlands to some extent (Oke & Hager, 2017). The species distribution under modern climatic scenarios in our study is consistent with the literature on the global distribution of dominant *Sphagnum* species in peatlands (Gunnarsson, 2005). This suggests that the potential distribution of the six species modeled in this study is highly representative of the distribution of *Sphagnum* species that dominate peatlands. Our results showed that all six species under current climatic scenarios were mainly distributed in North America and Eurasia. The areas with *Sphagnum* species richness greater than 2 were mainly concentrated in latitudes above 40°N in North America and above 45°N in Europe, which was consistent with the previous studies (Campbell et al., 2021; Gunnarsson, 2005; Oke & Hager, 2017). In addition, *Sphagnum*-dominated peatlands with a small range in the Southern Hemisphere were also realistically represented in this study, including the eastern coastal region of Australia and the southeastern coastal region of South America. The changes in the distribution suitability of *Sphagnum* species in these regions under future climate scenarios will reflect the potential for vegetation change in the relevant regions and the potential fate of peatlands.

4.1 | Expansion of *Sphagnum* mosses in high-latitude boreal peatlands

For adapting to global warming, the range of species tends to shift toward the poles or higher altitudes (Hughes, 2011; Parmesan, 2006; Sun et al., 2020; Thurm et al., 2018). Consistently, our results showed that the potential distribution of *Sphagnum* under future climate scenarios shifted noticeably northward, and as the emission scenario severity intensified, the distance of this shift increased. In addition, the habitat suitability and richness of *Sphagnum* in high latitudes (north of 50°N) would increase over a large area with global warming. Warmer climate, elevated precipitation, longer growing seasons and permafrost thaw are expected to increase the growth and productivity of *Sphagnum* in northern high-latitude peatlands (Bengtsson et al., 2021; Hájek et al., 2021; Küttim et al., 2019; Magnan et al., 2018). The fast-growing *Sphagnum* mosses can suppress competitively inferior non-*Sphagnum* bryophytes and seedlings of vascular plants, and expand in rich fens (Granath et al., 2010; Singh et al., 2019; Udd et al., 2016; van Breemen, 1995; Vicherová et al., 2017). As peatland ecosystem engineers, the establishment and spreading of *Sphagnum* in fens will speed up the succession from fens to bogs (Kolari, Korpelainen, et al., 2021; Singh et al., 2021; Väliranta et al., 2017). The shift from fens to bogs and accelerated *Sphagnum* moss expansion have recently been observed in Canada and some countries in Europe (Granlund et al., 2021; Gunnarsson et al., 2000; Hájek et al., 2015; Kolari, Sallinen, et al., 2021; Magnan et al., 2018, 2021; Paulissen et al., 2004; Robitaille et al., 2021). Our results implied that *Sphagnum* moss expansion would be prevalent in northern high-latitude peatlands under various future climate scenarios within the next few decades. Compared with fens, bogs, with a dominated population of decay-resistant *Sphagnum*, have lower plant productivity, slower decay rates, and less methane (CH_4) release, making it a more efficient carbon sink overall (Granath et al., 2010; Hornibrook & Bowes, 2007; Szumigalski & Bayley, 1996). As a result of climate-driven fen-bog transitions, peat accumulation would increase (Loisel & Yu, 2013; Magnan et al., 2021; Taillardat et al., 2020) but threaten fen specialized species. To protect the threatened species, many disturbance strategies have recently been proposed to prevent the invasion of *Sphagnum* species (Hájek et al., 2021; Singh et al., 2019, 2021). Here we reported the importance to reconsider the disturbance strategies that control the natural transformation of fens into bogs in the peatland ecosystem and reassess its global impact.

4.2 | *Sphagnum* moss decline beyond high-latitude boreal peatlands

In contrast to the northern high-latitude peatlands (north of 50°N), our study showed that the suitable habitat and abundance of *Sphagnum* mosses in the northern mid-low-latitude regions and Southern Hemisphere (south of 50°N) would decline or even disappear on a large scale in the future. For all terrestrial groups, the productivity maxima are at the equator and decrease toward the poles, with local maxima at about 45°N (Field et al., 1998). This peak is consistent with the highest productivity of *Sphagnum* at about 40–55°N (Gunnarsson, 2005). As temperature rises, the highest productivity of *Sphagnum* mosses would shift to higher latitudes. Our results showed that the southern edge of the boreal *Sphagnum* peatland range (between 40°N and 50°N) would experience the largest reduction in *Sphagnum* species richness compared with other latitudinal zones, including the *Sphagnum* peatlands in the United States, southern Europe, southern Siberia, and northeastern China. This is consistent with recent *Sphagnum* or *Sphagnum* bog distribution models in North America, Europe, and China (Campbell et al., 2021; Cong et al., 2020; Oke & Hager, 2017). Unlike the peatlands in high latitudes, the increase in evapotranspiration caused by increasing temperatures in northern mid and low latitude peatlands leads to negative annual moisture balance and lowered water tables (Schultheis et al., 2010). The height of *Sphagnum* mosses above the water table, which is a proxy for water availability, is the main factor controlling their productivity (Gunnarsson, 2005; Weltzin et al., 2001). Elevated temperature and the lower water table are expected to favour vascular plants and drive *Sphagnum* decline due to the loss of competitive advantage over vascular plants (Dieleman et al., 2015; Weltzin et al., 2000). The shift from *Sphagnum* moss dominance to vascular plant dominance in peatlands would alter soil nutrient content and pH conditions, and lead to increased ecosystem N availability, enhanced microbial respiration, increased decomposition rates and carbon stock degradation (Bragazza et al., 2006, 2013; Larmola et al., 2013; Oke & Hager, 2020). These changes may result in peatland shifting from carbon sinks to carbon sources and positive feedback to climate warming (Schultheis et al., 2010). Whether carbon released from the southern edge of the boreal peatlands will be offset by increased carbon fixation at higher latitudes will be one of the focuses of subsequent studies on the response of peatland ecosystems to climate warming.

Our study indicated that *Sphagnum* mosses in the Southern Hemisphere would face the same situation as those in the low northern latitudes, such as *Sphagnum* peatlands in Chile and Australia. In fact, some bogs have been found to be experiencing drought and shrinkage, and the specific flora and fauna associated with *Sphagnum* peatland will be under great threat in the future (Hughes, 2011; Whinam et al., 2003; Whinam & Copley, 2011). The *Sphagnum* peatlands in low latitudes of the Northern Hemisphere and in the Southern Hemisphere are not as extensive as at high latitudes of the

Northern Hemisphere. They still lack survey and monitoring and are more susceptible to disturbances such as moss harvesting, peat mining, burning, grazing, and forestry operations. Therefore, we suggest that relevant management agencies should actively carry out monitoring and protection of *Sphagnum* peatlands, conduct comprehensive field surveys, investigate the status of peatlands, establish nature reserves, and develop reasonable management strategies.

4.3 | Study uncertainty and improvement

Potential habitats of *Sphagnum* mosses simulated in this study provide an important reference for understanding the response of peatland ecosystems to climate warming on a global scale. Nevertheless, our results may be influenced by several factors. Firstly, the model certainty may be influenced by the accuracy and completeness of the species occurrence data (Rocchini et al., 2011). Second, we assumed that species were free to migrate to any suitable area. However, *Sphagnum* moss dispersal can be limited by wind direction and terrestrial barriers (Kyrkjeeide et al., 2016). Determining the migration rate of species can improve the accuracy of predictions in future studies. Third, here we only considered the effects of abiotic factors on species distribution. Species distribution is also influenced by biotic factors such as human activities and biotic interactions (Boulangeat et al., 2012). When all factors affecting species distribution are considered, suitable habitats for *Sphagnum* mosses may be decreased in some regions, such as the southern United States and southern China. Nevertheless, our results do provide important information on the potential distribution of *Sphagnum* mosses under future climate change.

5 | CONCLUSION

This study predicts the alteration pattern in the global distribution of *Sphagnum* species that dominate peatlands under future climate scenarios. *Sphagnum* mosses tend to migrate northward in the Northern Hemisphere under the future warming scenarios, and moving distance increases with time passing or the severity of emission scenarios. The suitable habitat and abundance of *Sphagnum* mosses increase massively in the high-latitude boreal peatland (north of 50°N) and decrease on a large scale beyond the high-latitude boreal peatland. This suggests that climate warming may lead to the local extinction of rich fens-dependent species in northern high-latitude peatlands, as well as the extinction of *Sphagnum* peatlands themselves at low latitudes in the Northern Hemisphere and the Southern Hemisphere. The specific flora and fauna associated with southern peatlands would also be highly threatened in the future. It is particularly noteworthy that the mid-latitude boreal peatlands (southern edge of boreal peatlands) would experience the greatest decline in suitable habitat and abundance of *Sphagnum* mosses with temperatures compared with other latitudinal zones. This region has accumulated carbon for centuries and millennia, but it may be a risk area for the transition from carbon sink to carbon source. The importance of this focus area for conservation and future research on peatland ecosystem response to climate warming must be paid attention to.

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CONFLICT OF INTEREST

All authors declare no conflict of interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.nvx0k6dw0 (Ma et al., 2022).

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