Assessing the Fate of Sphagnum Moss in the Hengduan Mountains under Climate Change

Ning Shi[1], Binghui Tian[1], Jinniu Wang[1], Xianlin Guo[1], Lin Zhang[2], Ning Wu[3], Huai Chen[1], Yan WU[1], and WenTao Du[4]

[1]Chengdu Institute of Biology, Chinese Academy of Sciences
[2]Institute of Tibetan Plateau Research, Chinese Academy of Sciences
[3]Chengdu Institute of Biology
[4]Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences, Lanzhou

June 7, 2023

Abstract

Climate change is one of the most serious challenges facing mankind. Sphagnum moss plays an important role in the carbon sink of peatland. Understanding the potential distribution of Sphagnum moss under climate change scenarios is critical for the conservation and rational exploitation of it. In this study, we divided the Hengduan Mountains (HDM) into east (EHDM) and west (WHDM) parts to see the difference between the whole and the parts, and understand the effects of integrity and connectivity of the landscape on species distribution. Since no enough occurrence data in EHDM, we applied the occurrence data in WHDM. Then, MaxEnt model was employed to predict the potential distribution of Sphagnum moss and computed the migratory paths of the distribution center points. We found precipitation in the coldest quarter, daily range of average temperature, isothermality and slope were the main factors affecting the suitable habitat for Sphagnum moss in HDM and WHDM. In HDM, the current potential suitable habitat is 2.6×104 km2, and will increase over 8 times and tend to shift northeastward and higher elevations in the future. In WHDM, the suitable area is 1.06×104 km2, but will decline exceeds 70% under most future climate scenarios, and tend to shift southward and lower elevations. Landscape integrity and connectivity have a great impact on the distribution of HDM Sphagnum moss species. Overall, our findings provide a reference for the conservation and management of Sphagnum moss.

Hosted file

964670_0_art_file_11034296_rvzx1z.docx available at https://authorea.com/users/626023/articles/647651-assessing-the-fate-of-sphagnum-moss-in-the-hengduan-mountains-under-climate-change

Assessing the Fate of Sphagnum Moss in the Hengduan Mountains under Climate Change

Ning Shi[1,2,3,†], Binghui Tian[1,4,†], Jinniu Wang[1,3,*], Xianlin Guo[1], Lin Zhang[5], Ning Wu[1], Huai Chen[1], Yan Wu[1], and Wentao Du[6]

[1]Chengdu Institute of Biology, Chinese Academy of Sciences, Chengdu 610041, China

[2]College of Life Sciences, University of Chinese Academy of Sciences, Beijing 100049, China

[3]Mangkang Biodiversity and Ecological Station, Tibet Ecological Safety Monitor Network, Changdu 854500, China

[4]College of Resources and Environmental Sciences, Gansu Agriculture University, Lanzhou 730000, China

[5]Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Beijing 100101, China

[6]Key Laboratory of Remote Sensing of Gansu Province, Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences, Lanzhou 730000, China

Corresponding author: J. N. Wang (wangjn@cib.ac.cn)

†These two authors contributed equally to this study.

Key Points:

- Precipitation in the coldest quarter is the most important factor affecting *Sphagnum* moss distribution in HDM and WHDM.
- *Sphagnum* moss will expand and shift northeastward and higher elevation in HDM, but shrink and shift southward and lower elevation in WHDM.
- Landscape integrity and study scale do impact significantly the modeling results about distribution of *Sphagnum* moss in HDM.

Abstract

Climate change is one of the most serious challenges facing mankind. *Sphagnum* moss plays an important role in the carbon sink of peatland. Understanding the potential distribution of *Sphagnum* moss under climate change scenarios is critical for the conservation and rational exploitation of it. In this study, we divided the Hengduan Mountains (HDM) into east (EHDM) and west (WHDM) parts to see the difference between the whole and the parts, and understand the effects of integrity and connectivity of the landscape on species distribution. Since no enough occurrence data in EHDM, we applied the occurrence data in WHDM. Then, MaxEnt model was employed to predict the potential distribution of *Sphagnum* moss and computed the migratory paths of the distribution center points. We found precipitation in the coldest quarter, daily range of average temperature, isothermality and slope were the main factors affecting the suitable habitat for *Sphagnum* moss in HDM and WHDM. In HDM, the current potential suitable habitat is 2.6×10^4 km^2, and will increase over 8 times and tend to shift northeastward and higher elevations in the future. In WHDM, the suitable area is 1.06×10^4 $km^{2,}$ but will decline exceeds 70% under most future climate scenarios, and tend to shift southward and lower elevations. Landscape integrity and connectivity have a great impact on the distribution of HDM *Sphagnum* moss species. Overall, our findings provide a reference for the conservation and management of *Sphagnum* moss.

Plain language summary

Sphagnum moss, as the engineer of peatland ecosystem, plays an important role in the carbon sink of peatland. Global changes and disturbances with human activities can affect species distribution in general. We used MaxEnt model to predict the potential distribution of *Sphagnum* moss in the Hengduan Mountains (HDM) and West Hengduan Mountains (WHDM). The results showed that the most important environmental factor affecting the distribution of *Sphagnum* moss species in HDM and WHDM was precipitation in the coldest season (Bio 19). As the climate warms, *Sphagnum* moss tended to shift northeastward and higher elevations in HDM, while tended to shift to southward and lower elevations in WHDM. Comparing the results of these two regions, we found that landscape integrity and connectivity have a great impact on the distribution of HDM *Sphagnum* moss species.

1. Introduction

Current and future climate warming is having and anticipated to continue influencing the natural environment and human well-being. Climate warming can lead to rapid changes in ecological communities, altering their interactions, ecosystem functions, and services (Beck et al., 2011; Gauthier et al., 2015; Jassey et al., 2013). The Intergovernmental Panel on Climate Change (IPCC) released the latest assessment report that climate change is getting faster than expected (IPCC, 2021). There is no doubt that temperature will continue to rise, and extreme climate events, such as heat extremes, stronger or longer-lasting droughts, and heavy precipitation events, may will become more frequent, severe, and even change the nature of extremes (IPCC, 2021; Schar et al., 2004). The impact of climate change on alpine regions is particularly pronounced compared to other regions of globe (IPCC, 2021; Ma et al., 2011; Wilmking and Juday, 2005). Boreal forests, tundra, and peatlands are the dominant terrestrial ecosystems across these regions, all of which are undergoing and will continue to experience dramatic changes as a result of climate warming (Bjorkman et al., 2018; Boulanger et al., 2017; Dise, 2009).

Boreal peatlands are one of the most important ecosystems on Earth, providing various important ecosystem functions, e.g., regulating and maintaining the hydrological cycle as well as carbon storage (Limpens et al., 2008). In China, most of the peatlands are mainly distributed in the northeast and southwest regions such as Lesser Khingan Mountains, Changbai Mountains and peripheral areas of the Sichuan Basin, while the Hengduan Mountains region (HDM) is one of the main peatland distribution areas in the southwest region, which is located in the southeast of the Qinghai-Tibet Plateau (Liu et al., 2020; Sun et al., 1998). In HDM, the area of peatland is about 4914 km^2, mainly included the Zoige peatlands (4605.3 km^2), Western Yunnan peatlands (103.9 km^2), Seda-Shiqu peatlands (96.5 km^2), Maerkang-Liangshan peatlands (17.5 km^2), Sanjiang peatlands (19.1 km^2) and Litang-Daocheng peatlands (71.9 km^2) (Liu et al., 2020; Sun et al., 1998). *Sphagnum* plants are widely distributed in HDM and play a special role in swamp forming and carbon production (Sun et al., 1998). The HDM is divided into east and west parts by the so called “mid-ridge” Shaluli Mountains, which stretch across the central part from upper north to down south. Its western part is mainly affected by the Indian summer monsoon, while the eastern is mainly influenced by the westerlies and the East Asian monsoon (Liu et al., 2020; Ono and Irino, 2004; Overpeck et al., 1996). Their complex hydroclimatic conditions and atmospheric circulation may lead to an extremely sensitive response to climate change in the HDM.

Climate-induced changes (e.g., temperature, precipitation, soil O_2 availability, and pH) in vegetation phenology and composition of peatland would affect peatlands expansion and carbon sink function (Antala et al., 2022; Bragazza et al., 2016; Larmola et al., 2013; Oke and Hager, 2020). Bryophytes are an important part of peatland ecosystems and are very sensitive to changing climatic conditions, and studying their distribution in relation to climate can help predict the potential impact of global warming on peatland ecosystems (Ma et al., 2022; Weston et al., 2015). *Sphagnum* moss is keystone species in northern peatlands, comprise up to 90% of peat (Hajek et al., 2011), and play a crucial role in carbon sequestration and maintaining the stability and resilience of peatlands (Turetsky et al., 2012). Therefore, the response of peat moss to climate change is closely related to the changes in future carbon fluxes and stability of peatland ecosystems.

The genus of *Sphagnum* is the only representative genus of Sphagnaceae, which consists of 250-450 species (Shaw et al., 2016), and there are currently 49 species in China (Zhu, 2022). They are a kind of moss with unique morphological, physiological, biochemical and developmental characteristics, known as the “ecosystem engineers” of peatlands, with special and irreplaceable ecological value, essential for ecosystem maintenance and global climate regulation (Beike et al., 2015; Freeman et al., 2001; Raghoebarsing et al., 2005). Although they have small individuals, they covered 1% of the Earth’s land area (1.5×10^6 km^2), and more than half of the peat worldwide comes from *Sphagnum* moss (Beike et al., 2015; Whitaker and Edwards, 2010). *Sphagnum* moss has very special hyaline cells (i.e., water cells) with hydathodes and spiral thickened cell walls, which have the functions of water storage, water conduction and support (Kostka et al., 2016). Because of its strong water-holding capacity and capillary action, it is able to accumulate moisture more than 20-40 times of its own dry weight, and is known as a "super sponge", which has a great impact on the ecosystem (Tveit et al., 2020; Zhu, 2022). In addition, it can provide a living place for the symbiosis of microorganisms such as methane anaerobes and cyanobacteria (Kostka et al., 2016). *Sphagnum* moss can fix carbon dioxide through photosynthesis like other plants, and effectively recover the greenhouse gas methane released from peatlands by methane anaerobic oxidation bacteria (Kostka et al., 2016; Zhu, 2022). Simulation experiments have shown that peat moss can reduce methane emissions by 93% in rewetting peatlands (Kostka et al., 2016; Kox et al., 2021). Furthermore, *Sphagnum* moss produces phenolic compounds and uronic acids, which are the two major secondary metabolites and have a strong inhibitory effect on the decomposition of organic matter, thus facilitating peat accumulation (Verhoeven and Toth, 1995; Zhu, 2022). The accumulation of peat alters the local hydrology and biogeochemistry of pore water, making environmental conditions generally more conducive to *Sphagnum* moss. However, due to the absence of stomata and water-conducting tissues, environmental factors such as temperature and water table depth (Carrell et al., 2019; Robroek et al., 2007a), can very easily affect *Sphagnum* moss. Any change in environmental factors caused by climate change is likely to alter the existing distribution pattern of *Sphagnum* moss and its feedback function to peatland ecosystems. So, there is a need for predicting the potential distribution changes of *Sphagnum* moss under different climatic scenarios, which is crucial for linking peatland responses to climate change with dominant plants distribution.

Warming-induced distributional shifts in plant species and communities have been proved by many studies, for example, some species tend to shift to higher latitudes and/or elevations (Bugmann, 2001; Naudiyal et al., 2021; Shi et al., 2022; Sun et al., 2020; Xiaodan et al., 2011). This is a great challenge for those cold-adapted species, especially in HDM with complex climate and topography. Warming is leading to changes in species distribution patterns and community composition, which are relevant to the fate of peatland ecosystems, especially in the boreal peatlands. Previous studies have shown that *Sphagnum* moss was influenced by the future climate scenarios, however, due to different scales, the results of changes in suitable distribution area existed differences (Campbell et al., 2021; Cerrejón et al., 2020; Cong et al., 2020; Ma et al., 2022; Oke and Hager, 2017). Due to the climatic differences between regions, the distribution pattern of *Sphagnum* moss in one local region may not adapted to others. Meanwhile, human activities have led to severe habitat loss and fragmentation, resulting in reduced landscape connectivity and the viability of species within the landscape (Fischer and Lindenmayer, 2007; Wu and Liu, 2014). Studies have shown that many native plants experience severe habitat loss and fragmentation, which is a major driver of plant species extinction (Ceballos et al., 2015; Fahrig, 2003; Huang, 2011; Lenoir et al., 2010). Hence, it is necessary to study the suitable distribution of *Sphagnum* moss in different size areas.

In this study, we used the MaxEnt model to forecast the potential suitable habitats of *Sphagnum* moss and assess its potential distribution change under different climate scenarios in HDM (Figure 1). Our aims were to (1) explore the key environmental factors that limiting the current and future potential distribution of *sphagnum* moss; (2) predict the trends and extent of changes in the distribution of potentially suitable habitats for *Sphagnum* moss under future climate scenarios and clarify the migration paths of central distribution points; and (3) to explore the effects of landscape integrity in HDM and its western part on species and migration under future climate scenarios.

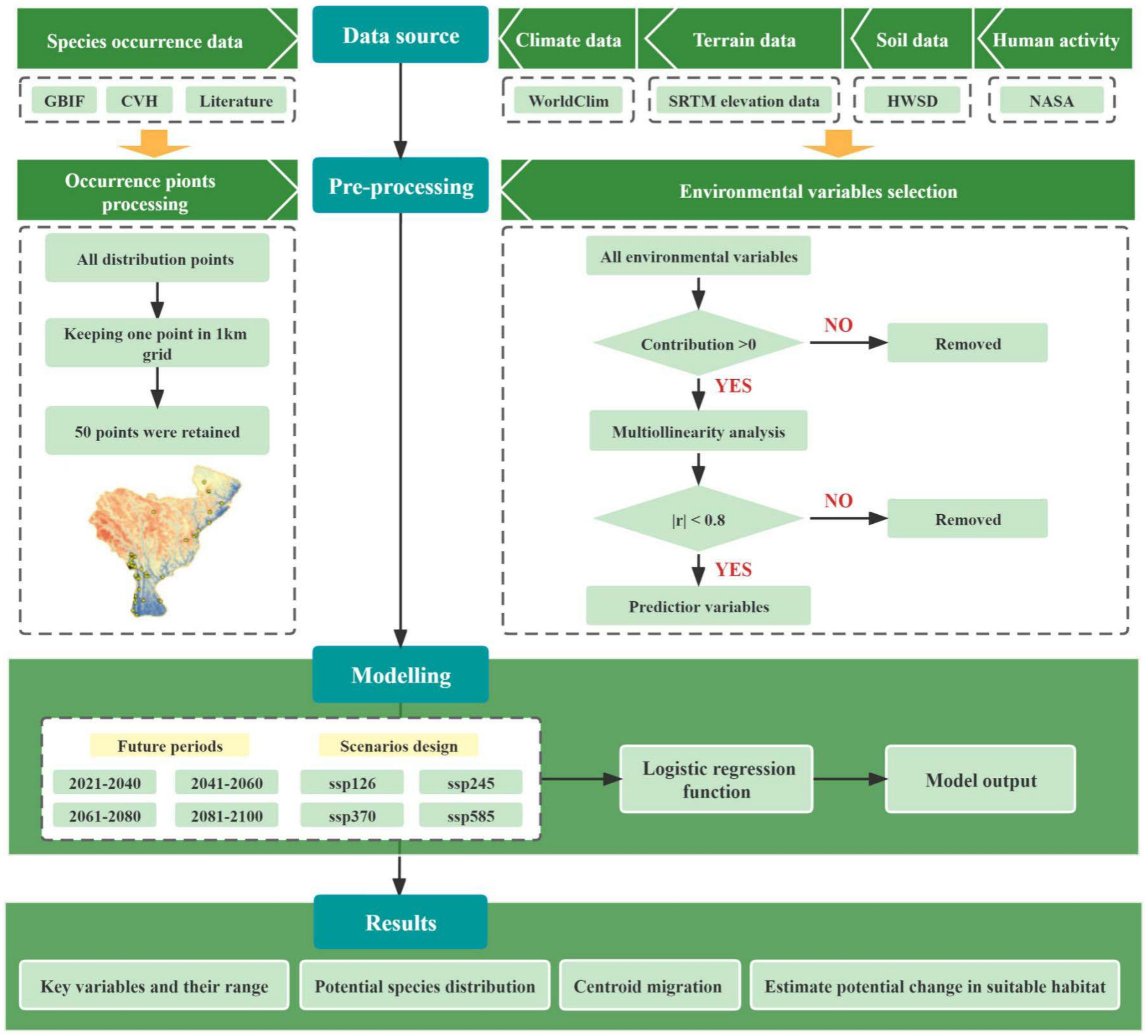


Figure 1. The conceptual framework of the study

2. Materials and Methods

2.1 Study area

The HDM lies between 24°40′ N to 34°00′ N and 96°20′ E to 104°30′ E, which is located in the southeastern Qinghai-Tibet Plateau, covering about 500,000 km^2 and consisting of a series of mountains and rivers running north-south (Li et al., 2014). From west to east, seven mountain chains (Boxoila Ling Mountains, Nu Mountains, Mangkang Mountains, Shaluli Mountains, Daxue Mountains, Qionglai Mountains, Minshan Mountains) and six rivers (Nu River, Lancang River, Jinsha River, Yalong River, Dadu River, Minjiang River) make up the main geographical features of this region (Li, 1987).The HDM is mainly controlled by two major climate systems, one of which is the westerly circumfluence, which carries less water vapor, and the other is the monsoon system, including the southwest monsoon from the Bay of Bengal, the southwest monsoon in the Indian Ocean and the southeast monsoon from the western Pacific, which bring the major precipitation (Niu et al., 2017). In addition, the plateau monsoon is also the main local circumfluence influencing the region (Niu et al., 2017). The barrier effect of the north-south mountains and the channel effect of the deep valleys make the precipitation variation and distribution characteristics in this region more complex (Cao et al., 2005). Generally, from mid-May to mid-October is the wet season, the precipitation accounts for more than 85% of the whole year, and mainly concentrated in June, July and August (Zhang, 1989). From mid-October to mid-May of the next year is the dry season, with less rainfall, long sunshine and large evaporation (Zhang, 1989). Furthermore, the climate has obvious vertical change. The average annual temperature of the plateau surface is 14~16℃, the coldest month is 6~9℃, and the average annual temperature of the valley can reach more than 20℃ (Yu et al., 2001).

The HDM is the richest in plant diversity with a vascular flora of about 12,000 species, and is the core of the south-central China biodiversity hotspot (Boufford, 2014; Myers et al., 2000; Xing and Ree, 2017). This region supports a high diversity of vegetation types due to complex geographic isolation, tectonic uplift, climate change, strong microhabitat divergence, and different migration and evolutionary history (Li and Li, 1993; Wu and Wang, 1983; Zhang et al., 2021). Due to the combined effects of Neogene cooling, orogeny and monsoon evolution, the vegetation of HDM not only has rich diversity, but also has obvious vertical zonality (Zhang et al., 2021). Generally, along the elevation from low to high, the typical vegetation includes evergreen broad-leaved forest, coniferous forest, alpine scrub, meadows and sparse vegetation zones. Alpine plants usually grow above treelines and below the nival belt, and scree slopes start at approximately 4400 m above the treeline (Li et al., 2014). We divided the entire study area into two sub-regions based on the boundaries of the mid-ridges (the Shaluli Mountains) and the influence of different monsoon systems: East Hengduan Mountains (EHDM) and West Hengduan Mountains (WHDM) (Figure 2).

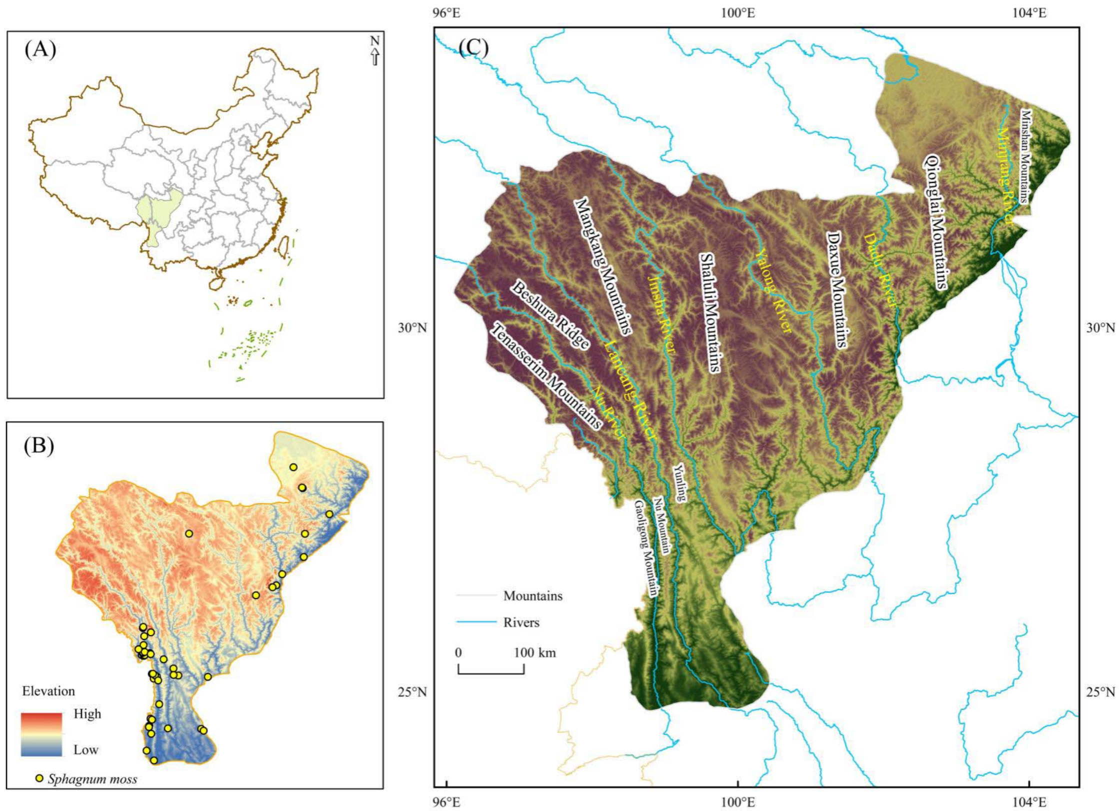


Figure 2. The presence points of *Sphagnum* moss in the study area

2.2 Data preparation

2.2.1 Species occurrence data

Species distribution data were obtained from (1) Global Biodiversity Information Facility (GBIF.org, https://www.gbif.org/), (2) Chinese Virtual Herbarium (CVH, http://www.cvh.ac.cn/), and (3) related published literature ((China National Knowledge Infrastructure, CNKI, https://www.cnki.net/; Web of Science, https://www.webofscience.com/). All 75 data points were carefully evaluated to exclude those that were out of the study area and duplicates based on ArcGIS 10.8, and then validated by Google Earth to eliminate possible errors. We also retained only one distribution point within the 1 km buffer according to the resolution of the environmental variable (30 arc-seconds) to avoid overfitting. Eventually, 50 distribution points were used for modeling, of which, 20, 15, and 15 presence points were located in grassland, shrub, and forest ecosystems, respectively. Regarding the two sub-regions, we found 41 presence points were located in WHDM totally, of which, 16, 11, and 14 presence points were located in grassland, shrub, and forest ecosystems, respectively. Only 9 distribution points were found in EHDM, since inadequate numbers of distribution points will cause the model with poor prediction accuracy and unreliable results, this study does not analyze the EHDM this sub-region.

2.2.2 Environmental data

The environmental factors that would influence the distribution of *Sphagnum* moss are as follows: (1) 19 bioclimatic variables (30 arc-seconds) (Booth et al., 2014) and 3 topographical variables were obtained from the WorldClim dataset (version 2.0, https://www.worldclim.org), (2) 18 top soil factors were downloaded from Harmonized World Soil Database (version 1.2, https://www.fao.org/), (3) 1 human influence variable was derived from National Aeronautics and Space Administration (NASA, https://sedac.ciesin.columbia.edu/).

For future climate scenarios, we selected the shared socioeconomic pathways (SSPs) of Coupled Model Intercomparison Project (CMIP6) which are considered more reasonable than the representative concentration pathway of CMIP5 (Eyring et al., 2015; Su et al., 2021). Future climatic information was obtained from the data of BCC-CSM2-MR, involved in four climate scenarios, namely, ssp1-2.6 (low forcing scenario with radiative forcing up to 2.6 W/m^2), ssp2-4.5 (moderate forcing scenario with radiative forcing up to 4.5 W/m^2), ssp3-7.0 (moderate to high forcing scenario with radiative forcing up to 7.0 W/m^2), ssp5-8.5 (high forcing scenario, radiative forcing up to 8.5 W/m^2). In addition, current climatic conditions were the average for 1970-2000, and future climate data for average years 2021-2040, 2041-2060, 2061-2080, and 2081-2100.

What's more, to ensure consistent spatial resolution, all environment variables are resampled at a resolution of 30 arc-seconds. To eliminate multicollinearity between environmental factors and improve the prediction accuracy of the model, we used Pearson correlation analysis to retain the variables with a correlation lower than 0.8, and among the environmental factors with correlation coefficients higher than 0.8, only one factor with higher contribution was retained of the two factors. Finally, a total of 20 environmental variables, including 7 bioclimatic variables, 3 topographic variables, 9 soil variables and 1 human influence variable were selected for SDMs (Table 1).

248 **Table 1.** Environmental factors used in this study and their contribution rate to the model outputs for *Sphagnum* moss

Region	Variable type	Variable code	Environment variable	unit	Percent contribution
HDM	Climate variable	Bio19	Precipitation of coldest quarter	mm	45%
		Bio12	Annual precipitation	mm	25.6%
		Bio2	Mean diurnal range	℃	11.4%
		Bio3	Isothermality	℃	6.5%
		Bio4	Temperature seasonality	℃	1.4%
		Bio15	Precipitation seasonality	mm	1.2%
		Bio5	Max temperature warmest month	℃	0.8%
	Terrain variable	slo	Slope	°	3.3%
		asp	Aspect	°	0.7%
		alt	Altitude	m	0.2%
	Soil variable	T_PH_H_2O	Topsoil pH (H_2O)	-log(H+)	1.1%
		T_ESP	Topsoil sodicity (ESP)	%	0.8%
		T_OC	Topsoil organic carbon	% weight	0.4%
		T_REF_BULK_DENSITY	Topsoil reference bulk density	kg/dm^3	0.3%
		T_SILT	Topsoil silt fraction	% wt.	0.2%
		T_CLAY	Topsoil clay fraction	% wt.	0.1%
		T_ECE	Topsoil salinity (Elco)	dS/m	0.1%
		T_GRAVEL	Topsoil gravel content	%vol.	0.1%
		AWC_CLASS	AWC range	Code	0.1%
	Human variable	FHP	Human influence index	—	0.5%
WHDM	Climate variable	Bio19	Precipitation of coldest quarter	mm	50.6%
		Bio2	Mean diurnal range	℃	12.7%
		Bio13	Precipitation of wettest month	mm	12.7%

	Bio3	Isothermality	℃	6%
	Bio11	Mean Temperature of coldest quarter	℃	4%
	Bio14	Precipitation of driest month	mm	3.2%
	Bio4	Temperature seasonality	℃	0.5%
	Bio15	Precipitation seasonality	mm	0.3%
Terrain variable	Slp	Slope	°	5.1%
	Alt	Altitude	m	0.1%
	Asp	Aspect	°	0.1 %
Soil variable	T_GRAVEL	Topsoil gravel content	%vol.	0.9%
	T_ECE	Topsoil salinity (Elco)	dS/m	0.5%
	T_ESP	Topsoil sodicity (ESP)	%	0.3%
	T_OC	Topsoil organic carbon	%weight	0.3%
	AWC_CLASS	AWC range	code	0.2%
	T_CEC_SOIL	Topsoil CEC (soil)	cmol/kg	0.1%
	T_CEC_CLAY	Topsoil CEC (clay)	cmol/kg	0.1%
	T_BS	Topsoil base saturation	%	0.1%
	T_GRAVEL	Topsoil gravel content	%vol.	0.9%
Human variable	FHP	Human influence index	—	2.2%

2.3 Species distribution modeling

In this study, maximum entropy model (Maxent 3.4.4, http://www.cs.princeton.edu/) was used to predict the distribution region of *Sphagnum* moss in HDM. 75% of species occurrence records were randomly selected for model training, and the remaining 25% as the test set to validating the model. We set the maximum number of iterations to 10,000 and leave the other values as defaults to ensure that the model has adequate time to converge, and the model was performed 10 replications to assess the average results.

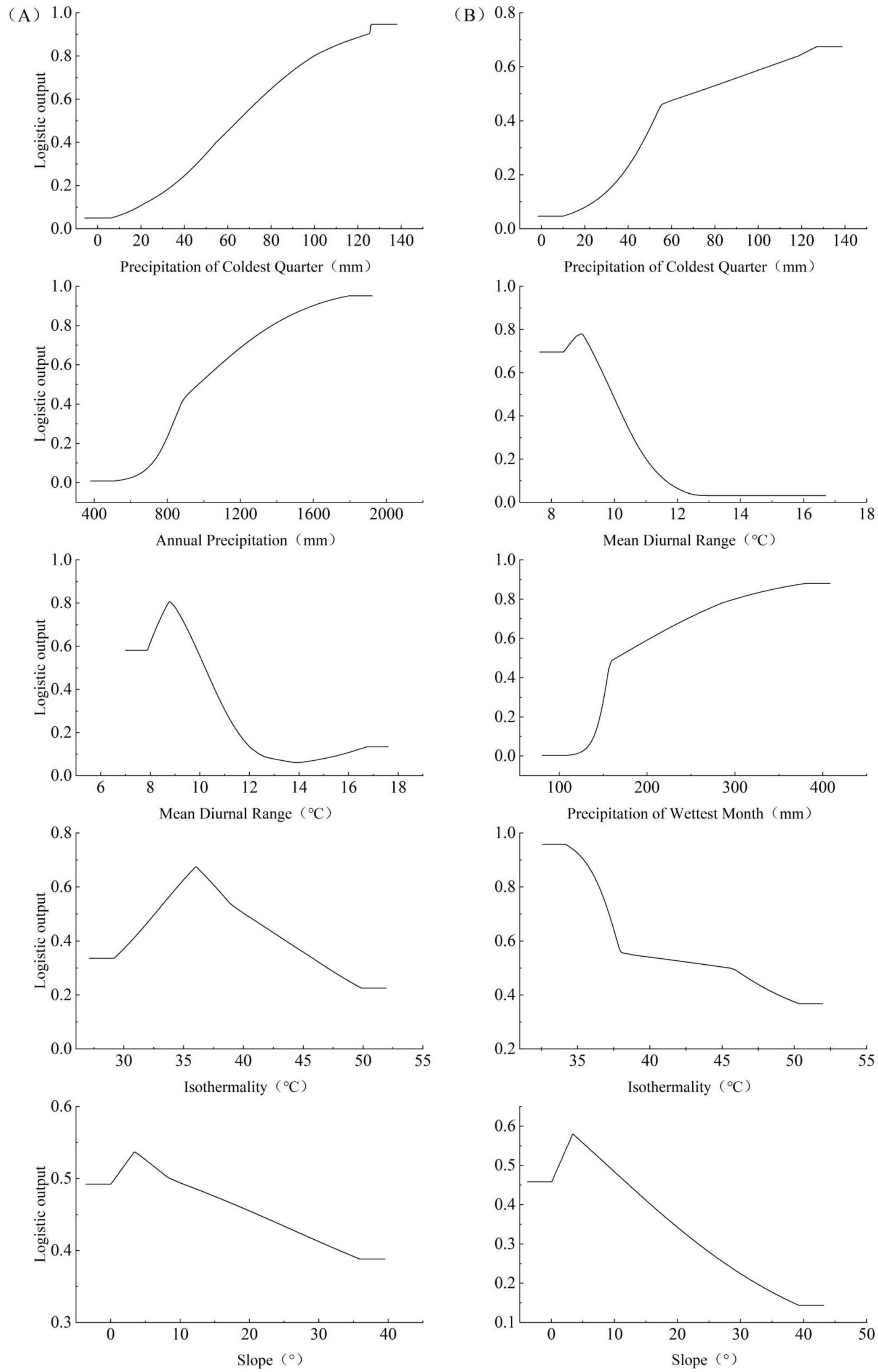
The area under the receiver operating characteristic (ROC) curve (AUC) was used to evaluate the accuracy of the model, which ranges from 0 to 1, with values closer to 1 indicating better model performance. According to the value of AUC, the model performance can be categorized as fair (0.6-0.7), good (0.7-0.8), very good (0.8-0.9), and excellent (>0.9) (Merow et al., 2013). The jackknife test was applied to identify the relative importance of the variables. The suitable habitat predictions were regrouped based on the logistic output, the threshold values below 0.3 were considered unsuitable, between 0.3 and 0.5 were low suitable, between 0.5 and 0.7 were moderate suitable, and greater than 0.7 were high suitable. By using the SDMtool tool, the centroid was calculated for the present and future four periods.

3. Results

3.1 Model performance and key environmental factors

The average test AUC ranging from 0.93 ~ 0.935 in HDM and 0.913 ~ 0.92 in EHDM in the current and future periods, indicating that the models were performed good and generated excellent evaluations.

The model results revealed that precipitation in the coldest quarter (45%), annual precipitation (25.6%), daily range of average temperature (11.4%) and isothermality (6.5%) were the dominant factors in *Sphagnum* species distribution in HDM. In addition to bioclimatic variables, slope (3.3%) also plays an important role in determining the distribution of *Sphagnum* (Table1). Since the cumulative contribution of these five predictors reached 91.8%, it is reasonable to assume that they provide the most important and useful information for predicting the distribution of *Sphagnum* in HDM. However, soil factors and human influence index have little effect on model output, the cumulative contribution rate of nine soil variables was 3.1%, while the contribution rate of human influence index was only 0.5%. A logical output value of environmental variables greater than 0.3 indicates that it is favorable for the growth of *Sphagnum* moss. According to the response curves of the key factors (Figure 3), it can be observed that when the logic output value is 0.3, the coldest quarter precipitation is 46.50 mm and the annual precipitation is 622.61 mm. With the greater precipitation, the probability of species existence increased. The mean diurnal temperature range is 6.83 ~ 11 °C and the range of isothermality is 26 ~ 51 °C (×100), whose increase led to the species presence probability an upward and then downward trend (Figure 3A). Gentle slope is beneficial to the survival of *Sphagnum*, in other words, the greater the slope, the lower the probability of its existence (Figure 3A).



290

291 **Figure 3.** The main environmental factors in HDM (A) and WHDM (B)

On the other hand, the main environmental factors affecting the distribution of *Sphagnum* species were precipitation in the coldest quarter (50.6%), daily range of average temperature (12.7%), precipitation in the wettest month (12.7%), isothermality (6%) and slope (5.1%) in WHDM (Table1). The accumulative contribution rate of these five environmental variables was 87.1%, indicating that they occupied dominant position for the distribution in WHDM. The results of model outputs showed that other factors such as soil and human activities have less influence on the distribution of *Sphagnum* moss. We can observe from the response curves of the variables that when the logical output value is 0.3, the coldest quarter precipitation is 45.61 mm and the wettest month precipitation is 150.97 mm, and there is an increasing trend in the probability of species presence with increasing precipitation (Figure 3). The daily range of average temperature suitable for the survival of *Sphagnum* moss ranged from 7.62 to 10.57℃, and the isothermality ranged from 32.54 to 51℃ (×100). In this range, the probability of the presence of *Sphagnum* moss appears to decrease sharply when the temperature reaches a certain critical value (Figure 3B). Similar to the condition in HDM, steep slopes are not conducive to the survival of *Sphagnum* moss in WHDM (Figure 3B).

We noticed that climate is the dominant factor affecting the potential distribution of *Sphagnum* species, followed by topography, soil and human activity factors (Table 1). Among all the factors, precipitation was the most important climatic factor affecting the potential distribution of *Sphagnum* species, followed by temperature. Comparing the model results in HDM and WHDM, we found that the most important factors were the precipitation in the coldest quarter, and only one factor (annual precipitation in HDM, precipitation of wettest month in WHDM) was different.

3.2 Potential habitats of *Sphagnum* under multiple climate scenarios

In HDM, the potential suitable habitats of *Sphagnum* are mainly distributed in the northwest of Yunnan Province near Gaoligong Mountain and Nu Mountain, and a small part is located in the Min River and Dadu River basin in Sichuan Province and the Nu River basin in southeastern Tibet under current climate scenario (Figure 4A). The total suitable habitat for *Sphagnum* is 2.6×10^4 km^2, which is about 7.51% of the total area. Among them, the area with high suitability is only 3.4×10^3 km^2, which accounts for less than 1%. The medium and low suitable habitat are slightly larger, but only 7.0×10^3 km^2 and 1.6×10^4 km^2, accounting for 1.98% and 4.57%, respectively (Figure 4A).

In WHDM, *Sphagnum* moss is mainly distributed near Gaoligong Mountain and Nu Mountain in the northwest of Yunnan Province under current climate scenario (Figure 4B). The total suitable area is 1.06×10^4 km^2, accounting for 5.8% of the total area. The high suitable area is very small, only 1.3×10^3 km^2, accounting for 0.7%. The middle suitable area is 2.95×10^3 km^2, accounting for 1.6%, and the low suitable area is 6.38×10^3 km^2, accounting for 3.5 % (Figure 4B).

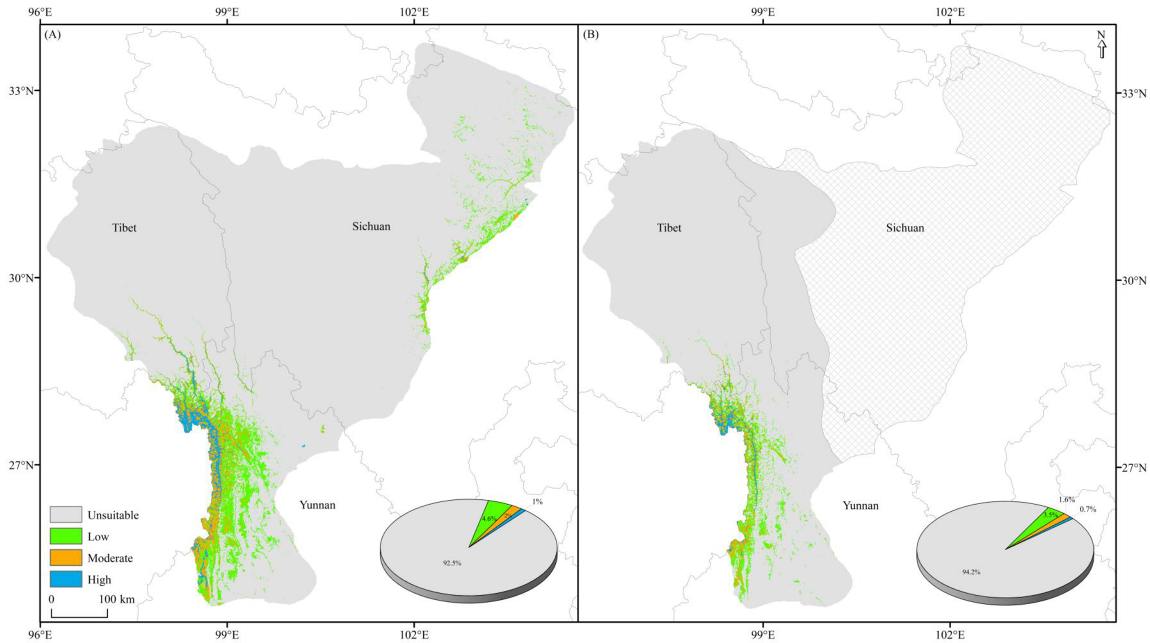


Figure 4. Potential distribution of *Sphagnum* under current climate scenarios in HDM (A) and WHDM (B)

In HDM, the suitable habitat of *Sphagnum* showed the tendency of expansion under different future climate scenarios, and the expansion area is greater than 8 times of the current suitable area, and the high suitable area is mainly concentrated in northeastern Yunnan Province (Figure 5). What's more, the area of medium and high suitable habitats accounted for more than 43% of the total suitable habitats, and the maximum area accounted for 81% under future climate scenarios (Figure 6A). We also found that the area of medium and high suitable habitat increased by 9.1 to 23.97 times compared to the current situation (Figure 6B). In 2061-2080 and 2081-2100, the highly suitable areas of *Sphagnum* gradually migrated northward. The area of medium to high suitable habitat has been increasing over time until it shrinks in period of 2081-2100 under three climate scenarios of ssp126, ssp245 and ssp370. Unexpectedly, under the high emission scenario, the area of medium to high suitable habitat for *Sphagnum* moss showed an increasing trend and had the largest area with 2.3×10^5 km^2 in period of 2081-2100 (Figure 6).

However, we observed that there is a decreasing trend of suitable habitat for *Sphagnum* under future climate change scenarios in WHDM, and the area with high suitability was mainly located near Gaoligong Mountains (Figure 7). Worryingly, the area of suitable habitat decline exceeds 70% under most future climate scenarios, and accounting for less than 2% of the WHDM area (Figure 7). Regardless of the period, the suitable habitat for *Sphagnum* was eventually significantly reduced in the high emission scenario (ssp585). In the further future (2081-2100), the suitable habitat for *Sphagnum* moss increases as the emission scenario intensifies and peaks the area with 1.48×10^4 km^2 under ssp370 scenario, and shrinks sharply the area with 2.49×10^3 km^2 as the emission scenario intensifies further (Figure 7, 8).In general, the medium and high suitable habitats accounted for less than 20% of the total suitable habitat area (Figure 8A). Compared with the current climate scenarios, the medium and high suitable habitats showed a significant decline trend except for the moderate emission scenario (ssp370) in 2081-2100, and most of the declines were greater than 80% (Figure 8B).

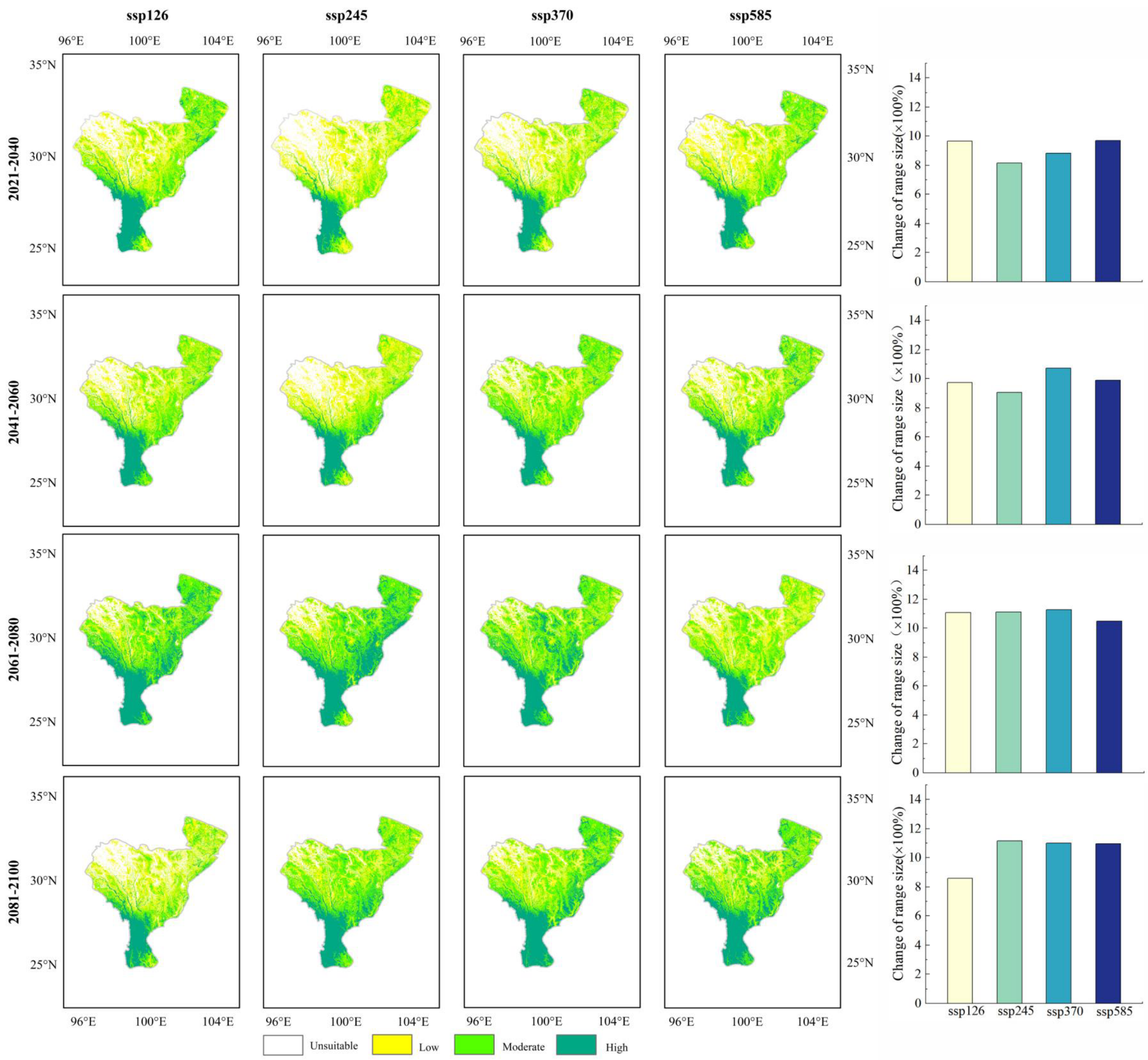


Figure 5. Potential distribution of *Sphagnum* under future climate change scenarios and the rate of area change for a suitable habitat in HDM

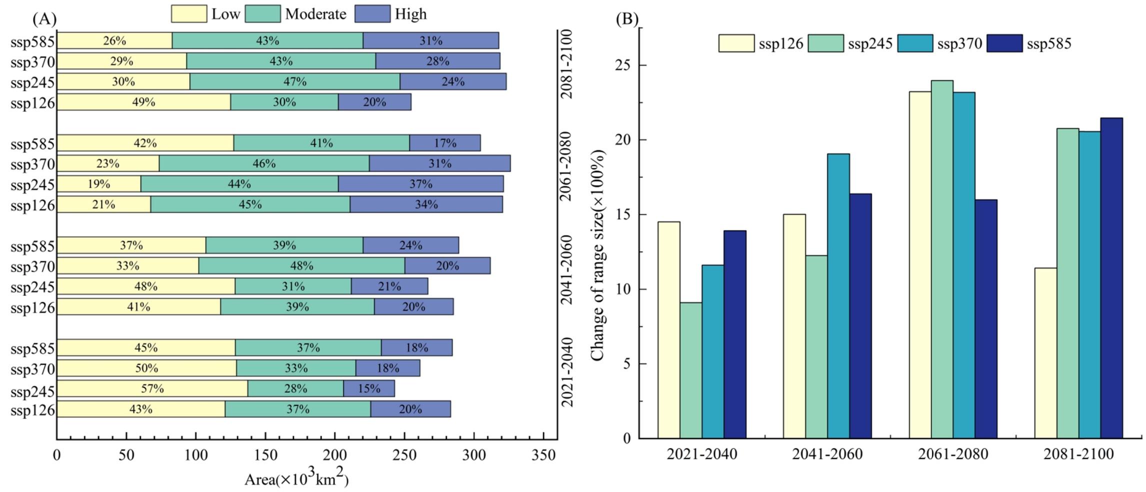


Figure 6. Area of potential suitable habitat for *Sphagnum* and its proportion (A) and the rate of change of area of medium and high suitable habitat (B) under future climate scenarios in HDM

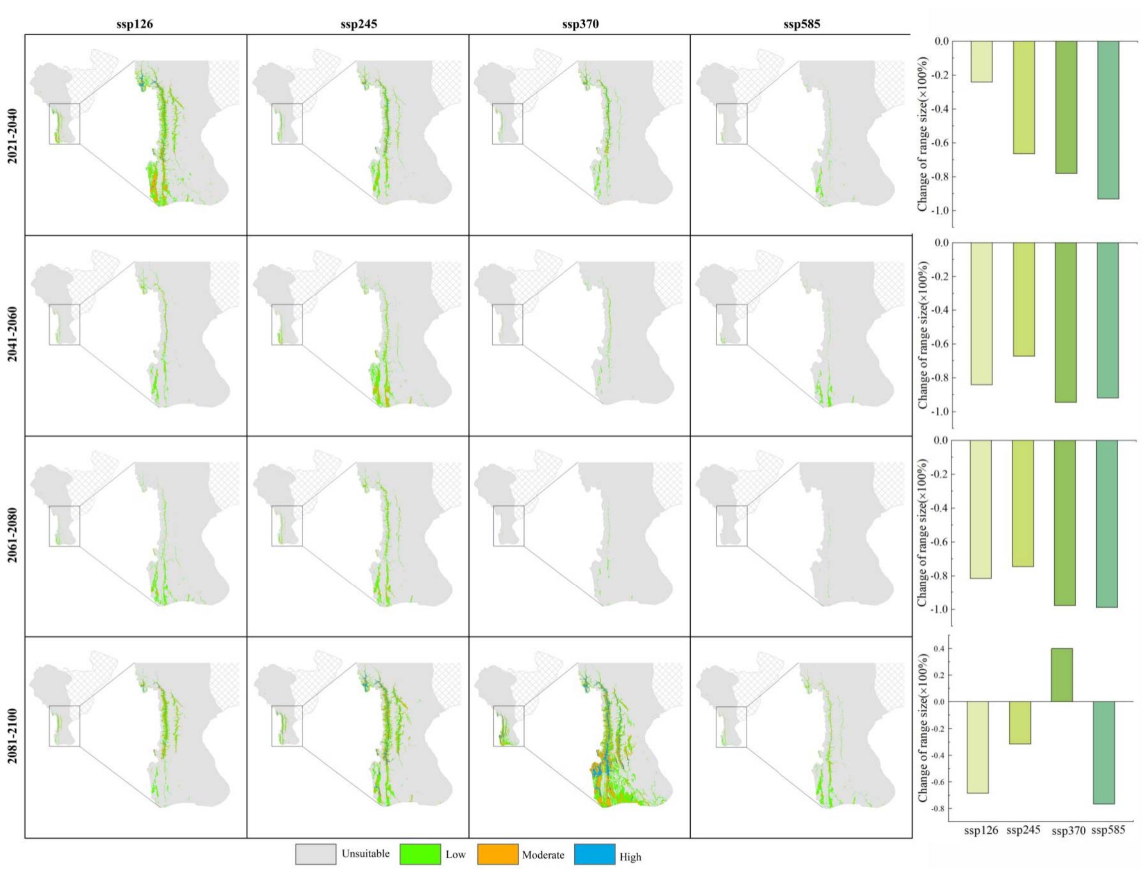


Figure 7. Potential distribution of *Sphagnum* under future climate change scenarios and the rate of area change for a suitable habitat in WHDM

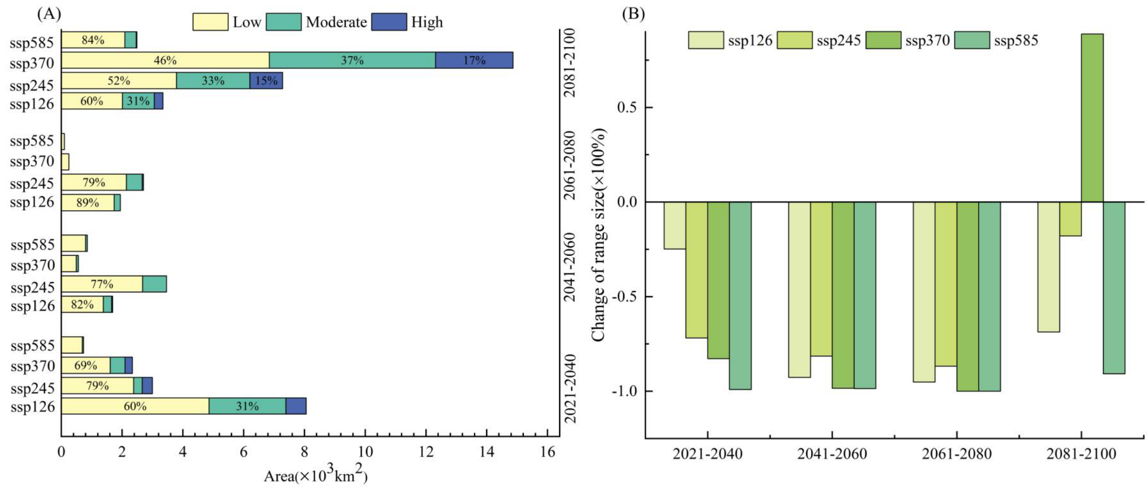


Figure 8. Area of potential suitable habitat for *Sphagnum* and its proportion (A) and the rate of change of area of medium and high suitable habitat (B) under future climate scenarios in WHDM

3.3 Impacts of climate change on centroid and altitude

In HDM, the future potential centroids of *Sphagnum* moss would shift northeastward 173.77 km, 274.40 km and 260.63 km under climate scenarios of ssp126, ssp245 and ssp585 in 2021-2040, as time goes by, the potential centroids position would only shift in a a very small area. However, under scenario of ssp370, the centroid would shift 124.35 km south in period of 2021-2040, and then 385.68 km to the northeast in period of 2041-2060, finally, the centroid location remains almost constant in next future (Figure 9A). In WHDM, the potential distribution centroids would shift noticeably northeastward and near Nu rivers. Under climate scenarios of ssp126 and ssp370, the centroids shift southward along the Nu rivers in period of 2021-2080 and then migrate northward. Under ssp245 and ssp585, the centroid migration is slightly different. It migrates southward during 2021-2060 and then shifts northward towards the river in 2061-2100 (Figure 9B). In general, changes in the distribution centroid showed that *Sphagnum* moss under different future climate scenarios would mainly shift northeastward in HDM, while in WHDM, mainly shift southward (Figure 9).

In future climate change scenarios, the mean elevation, minimum elevation and maximum elevation of suitable habitat for distribution of *Sphagnum* would shift upward, and the elevational range is extended in HDM (Table 2). Nevertheless, in WHDM, the results showed that the mean elevation is likely to shift downward, and in some future climate change scenarios, *Sphagnum* would like to inhabit a narrower elevational range as compared to its distribution under current climate scenario (Table 2). This is different from the distribution of *Sphagnum* moss in HDM.

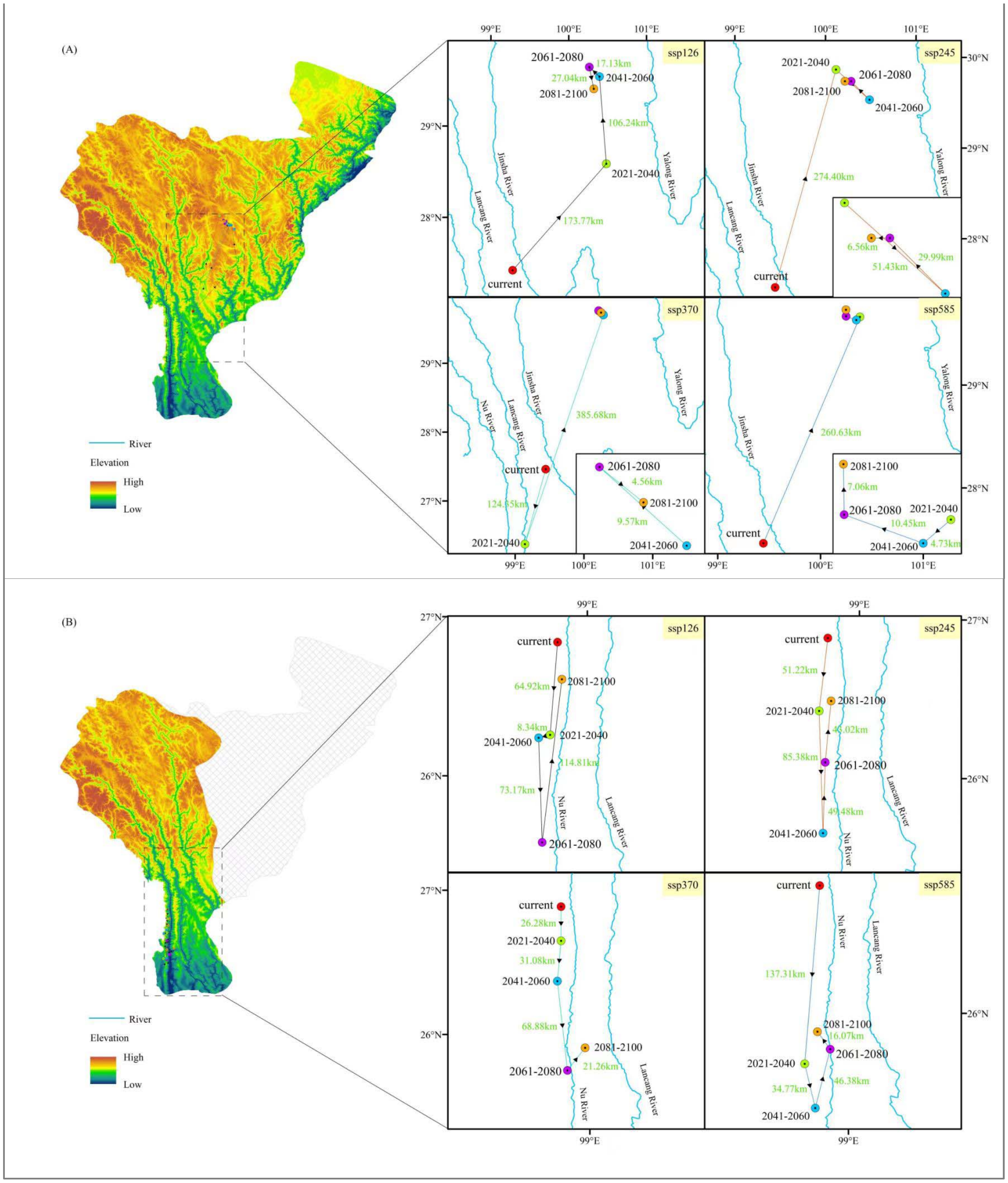


Figure 9. Centroid changes in the distribution of *Sphagnum* under future climate scenarios in HDM (A) and WHDM (B). The arrows indicate the magnitude and direction of predicted distribution change through time.

Table 2. Model projections for distribution in elevation (m±SD) among multiple climate scenarios in different periods for *Sphagnum*

Region	Periods	Gcm	Minimum		Maximum	Mean		SD
HDM	**Current**		709		4109	2632		716
	2021-2040	ssp126	1380		5181	3215	↑	992
		ssp245	771		4985	3254	↑	923
		ssp370	963		4816	3031	↑	904
		ssp585	940		4831	3325	↑	973
	2041-2060	ssp126	1011		5847	3471	↑	1059
		ssp245	826		4961	3269	↑	912
		ssp370	1449		5259	3598	↑	945
		ssp585	957		5027	3360	↑	1017
	2061-2080	ssp126	1188		5339	3690	↑	949
		ssp245	1783		5156	3717	↑	835
		ssp370	1401		5295	3636	↑	954
		ssp585	730		5455	3728	↑	964
	2081-2100	ssp126	1085		5371	3072	↑	1055
		ssp245	990		5346	3694	↑	978
		ssp370	1018		5297	3580	↑	924
		ssp585	1415		5406	3744	↑	879
WHDM	**Current**		1340		3873	2489		699
	2021-2040	ssp126	737		5530	1589		614
		ssp245	749	↔	2300	1598		333
		ssp370	938		5482	1673		504
		ssp585	1006	↔	1884	1523		286
	2041-2060	ssp126	841	↔	2202	1446		253
		ssp245	668	↔	2097	1225		375
		ssp370	976	↔	1922	1274		164
		ssp585	685		3685	1330		520
	2061-2080	ssp126	694		5586	1867		1303
		ssp245	686	↔	2169	1338		368
		ssp370	–	–	–	–	–	–
		ssp585	–	–	–	–	–	–
	2081-2100	ssp126	1079	↔	2674	1736		325
		ssp245	721		5528	1838		592
		ssp370	708		3124	1847		537
		ssp585	707		5561	1343		672

↔ Narrow range as compared with current range
↑Increase in elevation compared with current mean elevation

4. Discussion

Undoubtedly, the genus of *Sphagnum* species is one of the most important plant groups on earth, not just scarce ecological resources, with multi-functional and diverse service values, but value-added economic assets. As the climate warming and intensive human activities, the structure and function of terrestrial ecosystems have been disturbed severely. Peatland is a fragile natural wetland ecosystem, which is also special and irreplaceable. The negative effects of its degradation and destruction are alarming, such as intensifying greenhouse effects and leading to irreversible water loss and soil erosion (Cong et al., 2020). *Sphagnum* moss is very sensitive to climate change because of its simplistic gametophyte (Bates et al., 2005; Toet et al., 2006), and it is also a major component of peatland, so it is particularly vulnerable to be affected by climate change. In this study, the suitable habitat of *Sphagnum* moss was analyzed in detail, which is an important step in developing a feasible conservation strategy.

4.1 Climate preference of *Sphagnum* moss

The geographic distribution of species is influenced by a variety of environmental factors, such as climate, topography, soil, historical distribution, and human disturbance. Although human disturbance can have a great impact on the distribution of species, the human activity factors involved in this study only contain human activity footprints, which may not be enough to express the impact of human activities. Therefore, among the 20 environmental variables adopted in this model, precipitation in the coldest quarter (bio19) made the greatest contribution to the distribution model for *Sphagnum* moss both in whole HDM and WHMD, which means the factor plays a key role in its distribution. In addition, mean diurnal range (bio2) and isothermality (bio3) were two dominant variables affecting the habitat suitability of *Sphagnum* moss in a spatial range of different sizes. The previous studies at different regional and global scales have shown that the distribution of *Sphagnum* moss is mainly influenced by water and temperature (Ma et al., 2022; Oke and Hager, 2017). The reason why precipitation in the coldest season is the most important limiting factor may be that thicker snow in winter can protect spores from frost damage, and increased snow cover in combination with summer warming to improve soil water content (Jones et al., 1998), in addition, thicker snow has better adiabatic effect, and the soil temperature under it is less affected by air temperature fluctuations (Cline, 1997), so it can maintain non-freezing state in most of the winter, and soil microorganisms can carry out vigorous life activities, and finally promote nutrient mineralization (Brooks and Williams, 1999; Williams et al., 1998), thus providing sufficient water and nutrient for the growth and development of *Sphagnum* moss in the coming growing season (Bowman, 1992; Dorrepaal et al., 2004). Climate change radically alters the seasonal patterns of precipitation and temperature in northern latitudes (Fischer and Knutti, 2016; Santer et al., 2018; Wang et al., 2017), potentially affecting plant phenology and physiology (Sytiuk et al., 2022). *Sphagnum* moss prefers wet climate in general, because their photosynthesis can only be passively dependent on tissue water content, although they can store water, they cannot control its loss (Rydin and Jeglum, 2013; Titus et al., 1983; Weston et al., 2015). A suitable wet climate is achieved by reducing evaporation at low temperatures (Campbell et al., 2021). Nevertheless, precipitation variation from climate warming is bound to break this balance. In peatland, the level of the water table will affect the microenvironment where *sphagnum* moss grows, because it has no conduit tissue and root system, it will store water to the head through water pores to meet the needs of life activities (Robroek et al., 2007a). However, if the water table is too low, it will prevent the water transport to the head, resulting in changes in the ecosystem process (Robroek et al., 2007a; Robroek et al., 2009). More importantly, the water table is closely related to the precipitation, and changes in water table affect the hydrological cycle of peatland and aeration of surface peat soil. It has been shown that the reduction of peatland groundwater table will accelerate the decomposition and nutrient mineralization of peatland matrix, and eventually lead to the transformation of typical peatland plant communities into forests and serious degradation of peatland (Laiho et al., 1999; Robroek et al., 2007b; Sundstrom et al., 2000).

As for temperature, our results suggest that suitable climate for *Sphagnum* moss falls within a narrow range (Figure 3), which means it is sensitive to temperature changes. The quantity of heat in the environment is biologically important because of its physiological constraints on plant growth and survival (Campbell et al., 2021; Franklin, 1995). There are indications that photosynthesis of *Sphagnum* is sensitive to temperatures within a certain temperature range, and begins to be affected by temperature above 35℃ (Hanson et al., 1999; Haraguchi and Yamada, 2011), but if the moss can maintain moisture, the cooling effect of evaporation allows it to survive at higher temperatures (Dyukarev et al., 2009; Rydin, 1984), suggesting whose state of physiological function is related to the potential distribution range of *Sphagnum* moss (Weston et al., 2015). Nonetheless, *Sphagnum* moss productivity decreases as temperatures rise (Bragazza et al., 2016; Norby et al., 2019), and this decline is strongly associated with water availability (Jassey and Signarbieux, 2019). Additionally, warming also influences many primary and secondary metabolites of *Sphagnum*, such as polyphenols (Jassey et al., 2011; Sytiuk et al., 2022), which indirectly affects plant-microbial interactions, food web dynamics and nitrogen cycles within peatlands (Jassey et al., 2013), and these changes ultimately affect *Sphagnum* moss diffusion and distribution.

Slope was another key topographic factor besides climatic factors that had a strong effect on the distribution of *Sphagnum* moss in our study area. Slope gradient directly or indirectly affects plant functional groups by changing ecological factors such as local water, heat, light intensity and soil nutrient properties. Firstly, slope gradient can redistribute the solar radiation and precipitation, and therefore alters the soil temperature and soil moisture. (Qu et al., 2011). Besides, slope gradient affects soil erosion intensity and nutrient loss rate, resulting in differences in soil nutrients and ultimately affecting the distribution pattern of plants (Marini et al., 2007; Zhang et al., 2012). Swanson et al found that slope gradient had a significant effect on the spatial distribution of vegetation (Swanson et al., 1988). In temperate regions, the sunshine duration and the total amount of solar radiation that can be received by the places with different slope gradient are different, which is very important for the distribution of species. Surface runoff is an important part of peatland hydrology, and the change of slope may affect the habitat by influencing the average velocity of surface runoff, which may affect the growth environment of *Sphagnum* moss (Holden et al., 2008).

4.2 Changes of potential distribution for *Sphagnum* moss

The prediction maps reflected that future climate change will expand suitable habitat for *Sphagnum* moss in HDM (Figure 5), which in accordance with some previous research results that some researchers also found that *Sphagnum* moss is expanding rapidly in Canada and some countries in Europe (Granlund et al., 2022; Magnan et al., 2022). However, the suitable habitat of *Sphagnum* moss in China will face a massive reduction in the future (Cong et al., 2020), and Norby et al. found that under experimental warming conditions, the *Sphagnum* moss community experienced the rapid decline with sustained warming (Norby et al., 2019). The latest research found that the suitable habitat of *Sphagnum* moss increased massively in the high-latitude boreal peatland and decreased beyond the high-latitude boreal peatland at global scale (Ma et al., 2022). The effects of climate change on the distribution of *Sphagnum* moss does not follow a fixed pattern may be because the distribution of *Sphagnum* moss is influenced not only by regional climate, but also by local biotic (community composition, interspecific relationship) and abiotic factors (topography, microclimate, and soil properties). Our results indicated that the *Sphagnum* moss will experience a large-scale expansion under future climate scenarios in HDM. The efficient vegetative reproduction of *Sphagnum* moss allows it to occupy a large area quickly, and its spores have the ability to spread over long distances, which makes it possible to expand large areas (Sundberg, 2013; Zhu, 2022). Given *Sphagnum* moss is cold origin and prefers cool and wet climate (Cong et al., 2020), it has strong high-temperature resistance (Hanson et al., 1999; Haraguchi and Yamada, 2011), to survive facing the warmer and drier climate tendency in HDM (Xu et al., 2018), let along melting glaciers and thawing permafrost replenish water for it to a certain extent. Whilst, excessive warming and drought can make peatland ecosystems vulnerable (Jassey and Signarbieux, 2019), and peatland vegetation especially bryophytes is very sensitive to this change, so whether *Sphagnum* moss can maintain its current distribution is a great challenge in the further future.

For adapting to climate warming, the distribution area of many plant species generally tends to shift northward or higher elevations (Cong et al., 2020; Hanewinkel et al., 2013; Ma et al., 2022; Thuiller et al., 2006; Thurm et al., 2018). Consistently, our results showed that the potential distribution of *Sphagnum* moss shifted clearly northeastward and higher elevations in the future in HDM. Longer growing seasons, glacial ablation and thawing permafrost caused by climate warming are all likely to increase the growth and productivity of *Sphagnum* moss farther north or at higher elevations (Küttim et al., 2019; Magnan et al., 2018). *Sphagnum* moss as the ecosystem engineer of peatlands, its rapid growth can competitively inhibit the growth of other bryophytes and vascular plant seedlings (Granath et al., 2010; Udd et al., 2015; van Breemen, 1995), thus prompting the succession from fens to bogs (Singh et al., 2020; Väliranta et al., 2017). In comparison, bogs with *Sphagnum* moss as the dominant population are more efficient carbon sinks than the fens dominated by herbaceous plants because bogs have lower productivity, slower decay rates, and less methane emissions (Granath et al., 2010; Hornibrook and Bowes, 2007; Szumigalski and Bayley, 1996). Although the transition of fens to bogs induced by climate change may increase peat accumulation (Loisel and Yu, 2013; Magnan et al., 2022), specialized species in fens may be threatened. Therefore, it is crucial for taking measures to protect peatland to further protect threatened species.

There is evidence that human activity is the most and powerful destructive driver of the collapse of the marshes and has dramatically altered the original ecological balance (Davis and Froend, 1999; Hartig et al., 2002). For instance, the shift from peat bogs to forestry production has changed them from carbon sinks to carbon sources in northeastern China (Xing et al., 2015). Our results showed that *Sphagnum* moss will undergo tremendous shrinkage in the most climate scenarios in EHDM. We divide HDM into two parts based on its mid-ridge and tested effects of the integrity and connectivity of the landscape, which pointed out habitat destruction or shrinkage leads to a decline in the viability of the species (Fischer and Lindenmayer, 2007; Wu and Liu, 2014). The existence of available areas or boundaries can affect them by limiting resources and impairing dispersion (Henriques et al., 2016). In WHDM, *Sphagnum* moss tends to shift southward and lower elevations in the future, which is contrast the tendency in HDM. Moreover, the suitable habitat for *Sphagnum* moss were mainly distributed in the southwestern of Yunnan province, where the warm and wet climate of low altitude river valleys and lakes is conducive to the development of peat bogs (Jiang, 2019; Sun et al., 1998). From the figure 9B, we could find that *Sphagnum* moss moving southward but closer to the river system, because in the presence of sufficient water they can survive in the place with high air temperatures through the cooling effect of evaporation (Dyukarev et al., 2009; Rydin, 1984). The reduction of suitable habitat for *Sphagnum* moss in EHDM suggested that the overall habitat shrinkage causes changes in the spatial pattern of suitable habitat, and this change will affect the resource acquisition, migration and colonization of species, as well as the ecological process of ecosystem. So, maintaining landscape integrity is important for species to survive and disperse.

4.3 Limitations and implications

The simulation results of this study provide an important reference for the conservation and management of *Sphagnum* moss in HDM, whereas there may be several factors to limit our results. Primarily, the accuracy and completeness of species presence data may affect the certainty of the model (Rocchini et al., 2011), and this uncertainty did not take into account within the study. Secondly, we did not consider the effects of land use, biological interactions and other factors on species distribution. At last, we assume that *Sphagnum* moss is free from barriers and can migrate to any suitable area. Actually, *Sphagnum* moss is reproduced by spores spreading, which is dependent on water, therefore, dispersal limitation should be taken into consideration. When integrating these factors into the models, suitable habitats for *Sphagnum* moss may be declined in some areas. Anyway, this study does provide important information for *Sphagnum* moss potential suitable distribution under future climate change.

Sphagnum moss not only has a strong carbon storage function, but also has unique anticorrosive properties, adsorption capacity, cation exchange capacity, antioxidant function and antibacterial properties, and provide diverse ecosystem services, moreover, it has been widely used in agriculture, horticulture, environmental monitoring, sewage treatment and medicine and health fields (Beike et al., 2015; Gaudig et al., 2013; Gaudig et al., 2017; Krebs et al., 2017; Ma et al., 2017). In addition to climate change, *Sphagnum* moss also affected by the intensive human activities, such as peatland drainage, burning, grazing, trampling, large-scale peat and *Sphagnum* moss mining (Whinam et al., 2003).

Once they are destroyed, it is very difficult to restore them to their original state. So, it is shortsighted to sacrifice ecological resources for economic value. Given this, some *Sphagnum* species have been listed as protection directory (Zhu, 2022). Moreover, due to its sensitivity to the environment, in addition to in situ conservation, ex situ conservation is also necessary. It is suggested to establish a germplasm bank of *Sphagnum* moss to strengthen the priority conservation of *Sphagnum* moss genetic resources. Additionally, due to the lack of species diversity, distribution and ecological environment data, it is necessary to strengthen the comprehensive surveys of *Sphagnum* moss resource and environmental data. The most important thing is to stop human destruction immediately, and to and to meet the demand for products of *Sphagnum* moss in various fields, the screening and breeding of high quality of *Sphagnum* species should be carried out.

5. Conclusions

Climate change will greatly affect the distribution of plants. The present study explored the habitat assessment of *Sphagnum* moss and its spatial distribution under different climate change scenarios. The results suggest that *Sphagnum* moss presence is to a large extent governed by precipitation in the coldest quarter, and the potential suitable distribution areas of *Sphagnum* moss would increase and shift toward north and higher elevations in HDM, which is contrast to the tendency in WHDM. However, the expansion of *Sphagnum* moss in HDM does not mean it can always benefit from climate warming, there will be more serious challenges on longer time-scales. Suitable habitat for *Sphagnum* moss shrinkage in WHDM is indicated that its spatial distribution pattern is seriously affected by landscape integrity, and the distinct migration directions of *Sphagnum* moss in HDM and WHDM suggest that landscape fragmentation blocks the migration path to the most suitable habitat and instead moves to the more suitable areas within the landscape. It follows that the maintenance of landscape integrity is essential for species conservation. Furthermore, HDM has accumulated carbon for millennia, it risks turning from a carbon pool into a carbon source as human activity intensifies. To protect the peatlands and *Sphagnum* moss, anthropic destructive activities should stop at once. Finally, our study provides a scientific basis for the management and protection of *Sphagnum* moss.

Acknowledgments

This research was funded by the National Natural Science Foundation of China (31971436), CAS “Light of West China” Program (2021XBZG_XBQNXZ_A_007), State Key Laboratory of Cryospheric Science, Northwest Institute of Eco-Environment and Resources, Chinese Academy Sciences (SKLCS-OP-2021-06), Talented Young Scientist Program (Indian-18-008) by China Science and Technology Exchange Centre, Ministry of Science and Technology, and China Biodiversity Observation Networks (Sino BON).

Conflict of Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability Statement

The species occurrence data can be downloaded from supporting information, the bioclimatic data with 30 arc-second can be accessible in WorldClim dataset version 2.0 (current climate: https://worldclim.org/data/worldclim21.html; future climate data obtained from CMIP6 archive: https://worldclim.org/data/cmip6/cmip6_clim30s.html), the topographical data with 30 arc-second can be gained from https://worldclim.org/data/worldclim21.html , the soil data version 1.2 can be accessed from Harmonized World Soil Database (https://www.fao.org/soils-portal/soil-survey/soil-maps-and-databases/harmonized-world-soil-database-v12/en/), the human influence index data can be downloaded from National Aeronautics and Space Administration (NASA, https://sedac.ciesin.columbia.edu/data/set/wildareas-v2-human-influence-index-geographic).

References

Antala, M., Juszczak, R., van der Tol, C., and Rastogi, A. (2022). Impact of climate change-induced alterations in peatland vegetation phenology and composition on carbon balance. *Science of the Total Environment*, 827.

Bates, J. W., Thompson, K., and Grime, J. P. (2005). Effects of simulated long-term climatic change on the bryophytes of a limestone grassland community. *Global Change Biology*, 11, 757-769.

Beck, P. S. A., Juday, G. P., Alix, C., Barber, V. A., Winslow, S. E., Sousa, E. E., Heiser, P., Herriges, J. D., and Goetz, S. J. (2011). Changes in forest productivity across Alaska consistent with biome shift. *Ecology Letters*, 14, 373-379.

Beike, A. K., Spagnuolo, V., Lüth, V., Steinhart, F., Ramos-Gómez, J., Krebs, M., Adamo, P., Rey-Asensio, A. I., Angel Fernández, J., Giordano, S., Decker, E. L., and Reski, R. (2015). Clonal in vitro propagation of peat mosses (*Sphagnum* L.) as novel green resources for basic and applied research. *Plant Cell, Tissue and Organ Culture (PCTOC)* 120, 1037-1049.

Bjorkman, A. D., Myers-Smith, I. H., Elmendorf, S. C., Normand, S., Rüger, N., Beck, P. S. A., Blach-Overgaard, A., Blok, D., Cornelissen, J. H. C., Forbes, B. C., Georges, D., Goetz, S. J., Guay, K. C., Henry, G. H. R., HilleRisLambers, J., Hollister, R. D., Karger, D. N., Kattge, J., Manning, P., Prevéy, J. S., Rixen, C., Schaepman-Strub, G., Thomas, H. J. D., Vellend, M., Wilmking, M., Wipf, S., Carbognani, M., Hermanutz, L., Lévesque, E., Molau, U., Petraglia, A., Soudzilovskaia, N. A., Spasojevic, M. J., Tomaselli, M., Vowles, T., Alatalo, J. M., Alexander, H. D., Anadon-Rosell, A., Angers-Blondin, S., Beest, M. t., Berner, L., Björk, R. G., Buchwal, A., Buras, A., Christie, K., Cooper, E. J., Dullinger, S., Elberling, B., Eskelinen, A., Frei, E. R., Grau, O., Grogan, P., Hallinger, M., Harper, K. A., Heijmans, M. M. P. D., Hudson, J., Hülber, K., Iturrate-Garcia, M., Iversen, C. M., Jaroszynska, F., Johnstone, J. F., Jørgensen, R. H., Kaarlejärvi, E., Klady, R., Kuleza, S., Kulonen, A., Lamarque, L. J., Lantz, T., Little, C. J., Speed, J. D. M., Michelsen, A., Milbau, A., Nabe-Nielsen, J., Nielsen, S. S., Ninot, J. M., Oberbauer, S. F., Olofsson, J., Onipchenko, V. G., Rumpf, S. B., Semenchuk, P., Shetti, R., Collier, L. S., Street, L. E., Suding, K. N., Tape, K. D., Trant, A., Treier, U. A., Tremblay, J.-P., Tremblay, M., Venn, S., Weijers, S., Zamin, T., Boulanger-Lapointe, N., Gould, W. A., Hik, D. S., Hofgaard, A., Jónsdóttir, I. S., Jorgenson, J., Klein, J., Magnusson, B., et al. (2018). Plant functional trait change across a warming tundra biome. *Nature*, 562, 57-62.

Booth, T. H., Nix, H. A., Busby, J. R., Hutchinson, M. F., and Franklin, J. (2014). bioclim: the first species distribution modelling package, its early applications and relevance to most currentMaxEntstudies. *Diversity and Distributions*, 20, 1-9.

Boufford, D. E. (2014). Biodiversity hotspot: China's Hengduan Mountains. *Arnoldia* 72, 24-35.

Boulanger, Y., Taylor, A. R., Price, D. T., Cyr, D., McGarrigle, E., Rammer, W., Sainte-Marie, G., Beaudoin, A., Guindon, L., and Mansuy, N. (2017). Climate change impacts on forest landscapes along the Canadian southern boreal forest transition zone. *Landscape Ecology*, 32, 1415-1431.

Bowman, W. D. (1992). Inputs and storage of nitrogen in winter snowpack in an alpine ecosystem. *Arctic and Alpine Research*, 24, 211-215.

Bragazza, L., Buttler, A., Robroek, B. J. M., Albrecht, R., Zaccone, C., Jassey, V. E. J., and Signarbieux, C. (2016). Persistent high temperature and low precipitation reduce peat carbon accumulation. *Global Change Biology*, 22, 4114-4123.

Brooks, P. D., and Williams, M. W. (1999). Snowpack controls on nitrogen cycling and export in seasonally snow-covered catchments. *Hydrological Processes*, 13, 2177-2190.

Bugmann, H. (2001). A review of forest gap models. *Climatic Change* 51, 259-305.

Campbell, C., Granath, G., and Rydin, H. (2021). Climatic drivers of *Sphagnum* species distributions. *Frontiers of Biogeography*, 13.

Cao, J., He, D. M., and Yao, P. (2005). Research on the spatial distribution of rainfall and temperature in winter and summer over longitudinal range-gorge region (LRGR). *Advances in Earth Science*, 1176-1182.

Carrell, A. A., Kolton, M., Glass, J. B., Pelletier, D. A., Warren, M. J., Kostka, J. E., Iversen, C. M., Hanson, P. J., and Weston, D. J. (2019). Experimental warming alters the community composition, diversity, and N_2 fixation activity of peat moss (*Sphagnum fallax*) microbiomes. *Global Change Biology*, 25, 2993-3004.

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., Garcia, A., Pringle, R. M., and Palmer, T. M. (2015). Accelerated modern human-induced species losses: entering the sixth mass extinction. *Science Advances*, 1.

Cerrejón, C., Valeria, O., Mansuy, N., Barbé, M., and Fenton, N. J. (2020). Predictive mapping of bryophyte richness patterns in boreal forests using species distribution models and remote sensing data. *Ecological Indicators*, 119, 106826.

Cline, D. W. (1997). Snow surface energy exchanges and snowmelt at a continental, midlatitude Alpine site. *Water Resources Research*, 33, 689-701.

Cong, M., Xu, Y., Tang, L., Yang, W., and Jian, M. (2020). Predicting the dynamic distribution of *Sphagnum* bogs in China under climate change since the last interglacial period. *PLOS ONE*, 15, e0230969.

Davis, J. A., and Froend, R. (1999). Loss and degradation of wetlands in southwestern Australia: underlying causes, consequences and solutions. *Wetlands Ecology and Management*, 7, 13-23.

Dise, N. B. (2009). Peatland response to global change. *Science*, 326, 810-811.

Dorrepaal, E., Aerts, R., Cornelissen, J. H. C., Callaghan, T. V., and van Logtestijn, R. S. P. (2004). Summer warming and increased winter snow cover affect *Sphagnum fuscum* growth, structure and production in a sub-arctic bog. *Global Change Biology*, 10, 93-104.

Dyukarev, E. A., Golovatskaya, E. A., Duchkov, A. D., and Kazantsev, S. A. (2009). Temperature monitoring in Bakchar bog (West Siberia). *Russian Geology and Geophysics*, 50, 579-586.

Eyring, V., Bony, S., Meehl, G., Senior, C., Stevens, B., Ronald, S., and Taylor, K. (2015). Overview of the Coupled Model Intercomparison Project Phase 6 (CMIP6) experimental design and organisation. *Geoscientific Model Development Discussions*, 8, 10539-10583.

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology Evolution and Systematics*, 34, 487-515.

Fischer, E. M., and Knutti, R. (2016). Observed heavy precipitation increase confirms theory and early models. *Nature Climate Change*, 6, 986-991.

Fischer, J., and Lindenmayer, D. B. (2007). Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography*, 16, 265-280.

Franklin, J. (1995). Predictive vegetation mapping: Geographic modelling of biospatial patterns in relation to environmental gradients. *Progress in Physical Geography*, 19, 474-499.

Freeman, C., Ostle, N., and Kang, H. (2001). An enzymic 'latch' on a global carbon store. *Nature*, 409, 149-149.

Gaudig, G., Fengler, F., Krebs, M., Prager, A., Schulz, J., Wichmann, S., and Joosten, H. (2013). *Sphagnum* farming in Germany - a review of progress. *Mires and Peat*, 13.

Gaudig, G., Krebs, M., Prager, A., Wichmann, S., Barney, M., Caporn, S. J. M., Emmel, M., Fritz, C., Graf, M., Grobe, A., Pacheco, S. G., Hogue-Hugron, S., Holztrager, S., Irrgang, S., Kamarainen, A., Karofeld, E., Koch, G., Koebbing, J. F., Kumar, S., Matchutadze, I., Oberpaur, C., Oestmann, J., Raabe, P., Rammes, D., Rochefort, L., Schmilewksi, G., Sendzikaite, J., Smolders, A., St-Hilaire, B., van de Riet, B., Wright, B., Wright, N., Zoch, L., and Joosten, H. (2017). *Sphagnum* farming from species selection to the production of growing media: a review. *Mires and Peat*, 20.

Gauthier, S., Bernier, P., Kuuluvainen, T., Shvidenko, A. Z., and Schepaschenko, D. G. (2015). Boreal forest health and global change. *Science*, 349, 819-822.

Granath, G., Strengbom, J., and Rydin, H. (2010). Rapid ecosystem shifts in peatlands: Linking plant physiology and succession. *Ecology*, 91, 3047-56.

Granlund, L., Vesakoski, V., Sallinen, A., Kolari, T. H. M., Wolff, F., and Tahvanainen, T. (2022). Recent lateral expansion of *Sphagnum* bogs over central fen areas of boreal aapa mire complexes. *Ecosystems*, 25, 1455-1475.

Hajek, T., Ballance, S., Limpens, J., Zijlstra, M., and Verhoeven, J. T. A. (2011). Cell-wall polysaccharides play an important role in decay resistance of *Sphagnum* and actively depressed decomposition in vitro. *Biogeochemistry*, 103, 45-57.

Hanewinkel, M., Cullmann, D. A., Schelhaas, M.-J., Nabuurs, G.-J., and Zimmermann, N. E. (2013). Climate change may cause severe loss in the economic value of European forest land. *Nature Climate Change*, 3, 203-207.

Hanson, D., Swanson, S., Graham, L., and Sharkey, T. (1999). Evolutionary significance of isoprene emission from mosses. *American Journal of Botany - AMER J BOT*, 86.

Haraguchi, A., and Yamada, N. (2011). Temperature dependency of photosynthesis of *Sphagnum* spp. distributed in the warm-temperate and the cool-temperate mires of Japan. *American Journal of Plant Sciences*, 02.

Hartig, E., Gornitz, V., Kolker, A., Mushacke, F., and Fallon, D. (2002). Anthropogenic and climate-change impacts on salt marshes of Jamaica Bay, New York City. *Wetlands*, 22, 71-89.

Henriques, D. S. G., Borges, P. A. V., Ah-Peng, C., and Gabriel, R. (2016). Mosses and liverworts show contrasting elevational distribution patterns in an oceanic island (Terceira, Azores): the influence of climate and space. *Journal of Bryology*, 38, 183-194.

Holden, J., Kirkby, M., Lane, S., Milledge, D., Brookes, C., Holden, V., and McDonald, A. (2008). Overland flow velocity and roughness properties in peatlands. *Water Resources Research*, 44.

Hornibrook, E. R. C., and Bowes, H. L. (2007). Trophic status impacts both the magnitude and stable carbon isotope composition of methane flux from peatlands. *Geophysical Research Letters*, 34.

Huang, H. W. (2011). Plant diversity and conservation in China: planning a strategic bioresource for a sustainable future. *Botanical Journal of the Linnean Society*, 166, 282-300.

IPCC (2021). "Climate change 2021: The physical science basis. Contribution of working group I to the sixth assessment report of the Intergovernmental Panel on climate change."

Jassey, V. E. J., Chiapusio, G., Binet, P., Buttler, A., Laggoun-Defarge, F., Delarue, F., Bernard, N., Mitchell, E. A. D., Toussaint, M. L., Francez, A. J., and Gilbert, D. (2013). Above- and belowground linkages in *Sphagnum* peatland: climate warming affects plant-microbial interactions. *Global Change Biology*, 19, 811-823.

Jassey, V. E. J., Gilbert, D., Binet, P., Toussaint, M. L., and Chiapusio, G. (2011). Effect of a temperature gradient on *Sphagnum fallax* and its associated living microbial communities: a study under controlled conditions. *Canadian Journal of Microbiology*, 57, 226-235.

Jassey, V. E. J., and Signarbieux, C. (2019). Effects of climate warming on *Sphagnum* photosynthesis in peatlands depend on peat moisture and species-specific anatomical traits. *Global Change Biology*, 25, 3859-3870.

Jiang, M. J. (2019). Modern pollen vegetation/climate relationships in southwestern Yunnan, Yunnan Normal University.

Jones, M., Fahnestock, J., Walker, D., Walker, M., and Welker, J. (1998). Carbon dioxide fluxes in moist and dry arctic tundra during the snow-free season: responses to increases in summer temperature and winter snow accumulation. *Arctic and Alpine Research*, 30, 373-380.

Kostka, J. E., Weston, D. J., Glass, J. B., Lilleskov, E. A., Shaw, A. J., and Turetsky, M. R. (2016). The *Sphagnum* microbiome: new insights from an ancient plant lineage. *New Phytologist*, 211, 57-64.

Kox, M. A. R., Smolders, A. J. P., Speth, D. R., Lamers, L. P. M., Op den Camp, H. J. M., Jetten, M. S. M., and van Kessel, M. A. H. J. (2021). A novel laboratory-scale mesocosm setup to study methane emission mitigation by *Sphagnum* mosses and associated methanotrophs. *Frontiers in Microbiology*, 12.

Krebs, M., Gaudig, G., Matchutadze, I., and Joosten, H. (2017). *Sphagnum* regrowth after cutting. *Mires and Peat*, 20.

Küttim, M., Küttim, L., Ilomets, M., and Laine, A. (2019). Controls of *Sphagnum* growth and the role of winter. *Ecological Research*, 35.

Laiho, R., Sallantaus, T., and Laine, J. (1999). The effect of forestry drainage on vertical distributions of major plant nutrients in peat soils. *Plant and Soil*, 207, 169-181.

Larmola, T., Bubier, J. L., Kobyljanec, C., Basiliko, N., Juutinen, S., Humphreys, E., Preston, M., and Moore, T. R. (2013). Vegetation feedbacks of nutrient addition lead to a weaker carbon sink in an ombrotrophic bog. *Global Change Biology*, 19, 3729-3739.

Lenoir, J., Gegout, J. C., Guisan, A., Vittoz, P., Wohlgemuth, T., Zimmermann, N. E., Dullinger, S., Pauli, H., Willner, W., and Svenning, J. C. (2010). Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography*, 33, 295-303.

Li, B. L. (1987). On the boundaries of the Hengduan Mountains. *Mountain Research*, 74-82.

Li, X. H., Zhu, X. X., Niu, Y., and Sun, H. (2014). Phylogenetic clustering and overdispersion for alpine plants along elevational gradient in the Hengduan Mountains Region, southwest China. *Journal of Systematics and Evolution*, 52, 280-288.

Li, X. W., and Li, J. (1993). A preliminary floristic study on the seed plants from the region of Hengduan Mountain. *Acta Botanica Yunnanica*, 217-231.

Limpens, J., Berendse, F., Blodau, C., Canadell, J. G., Freeman, C., Holden, J., Roulet, N., Rydin, H., and Schaepman-Strub, G. (2008). Peatlands and the carbon cycle: from local processes to global implications: a synthesis. *Biogeosciences*, 5, 1475-1491.

Liu, L. J., Chen, H., Yu, Z. C., Zhu, D., He, Y. X., Liu, J. L., Zhu, Q. A., Liu, X. W., and Liu, L. F. (2020). Peatland development and carbon dynamics since the Last Glacial Maximum in the Hengduan Mountains Region. *Catena*, 190.

Loisel, J., and Yu, Z. (2013). Recent acceleration of carbon accumulation in a boreal peatland, south central Alaska. *Journal of Geophysical Research: Biogeosciences*, 118, 41-53.

Ma, J. H., Peng, T., and Li, D. H. (2017). Recent advances of *Sphagnum* palnt research in China. *Journal of Guizhou Normal University (Natural Sciences)*, 35, 114-120.

Ma, X. Y., Xu, H., Cao, Z. Y., Shu, L., and Zhu, R. L. (2022). Will climate change cause the global peatland to expand or contract? Evidence from the habitat shift pattern of *Sphagnum* mosses. *Global Change Biology*, 28, 6419-6432.

Ma, Z., Lei, X., Zhu, Q., Chen, H., Wang, W., Liu, S., Li, W., Fang, X., Zhou, X., and Peng, C. (2011). A drought-induced pervasive increase in tree mortality across Canada's boreal forests. *Nature Climate Change*, 1.

Magnan, G., Sanderson, N. K., Piilo, S., Pratte, S., Väliranta, M., van Bellen, S., Zhang, H., and Garneau, M. (2022). Widespread recent ecosystem state shifts in high-latitude peatlands of northeastern Canada and implications for carbon sequestration. *Global Change Biology*, 28, 1919-1934.

Magnan, G., van Bellen, S., Davies, L., Froese, D., Garneau, M., Mullan-Boudreau, G., Zaccone, C., and Shotyk, W. (2018). Impact of the Little Ice Age cooling and 20th century climate change on peatland vegetation dynamics in central and northern Alberta using a multi-proxy approach and high-resolution peat chronologies. *Quaternary Science Reviews*, 185, 230-243.

Marini, L., Scotton, M., Klimek, S., Isselstein, J., and Pecile, A. (2007). Effects of local factors on plant species richness and composition of alpine meadows. *Agriculture, Ecosystems & Environment*, 119, 281-288.

Merow, C., Smith, M. J., and Silander, J. A. (2013). A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography*, 36, 1058-1069.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., and Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403, 853-858.

Naudiyal, N., Wang, J. N., Ning, W., Gaire, N. P., Peili, S., Wei, Y. Q., Jiali, H., and Ning, S. (2021). Potential distribution of *Abies*, *Picea*, and *Juniperus* species in the sub-alpine forest of Minjiang headwater region under current and future climate scenarios and its implications on ecosystem services supply. *Ecological Indicators*, 121.

Niu, W. J., Gou, S., Liu, C., Li, D. L., Zhuang, W. H., and Liu, T. G. (2017). Spatio-temporal variation of droughts in Hengduan Mountains during 1979-2015. *Journal of Irrigation and Drainage*, 36, 97-103.

Norby, R. J., Childs, J., Hanson, P. J., and Warren, J. M. (2019). Rapid loss of an ecosystem engineer: *Sphagnum* decline in an experimentally warmed bog. *Ecology and Evolution*, 9, 12571-12585.

Oke, T., and Hager, H. (2017). Assessing environmental attributes and effects of climate change on *Sphagnum* peatland distributions in North America using single- and multi-species models. *PLOS ONE*, 12, e0175978.

Oke, T. A., and Hager, H. A. (2020). Plant community dynamics and carbon sequestration in *Sphagnum*-dominated peatlands in the era of global change. *Global Ecology and Biogeography*, 29, 1610-1620.

Ono, Y., and Irino, T. (2004). Southern migration of westerlies in the Northern Hemisphere PEP II transect during the Last Glacial Maximum. *Quaternary International*, 118, 13-22.

Overpeck, J., Anderson, D., Trumbore, S., and Prell, W. (1996). The southwest Indian Monsoon over the last 18000 years. *Climate Dynamics*, 12, 213-225.

Qu, Y. D., Su, Z. R., Li, Z. K., and Lin, Y. H. (2011). Effects of topographic factors on the distribution patterns of ground plants with different growth forms |in montane forests in North Guangdong, China. *Chinese Journal of Applied Ecology*, 22, 1107-1113.

Raghoebarsing, A. A., Smolders, A. J. P., Schmid, M. C., Rijpstra, W. I. C., Wolters-Arts, M., Derksen, J., Jetten, M. S. M., Schouten, S., Sinninghe Damsté, J. S., Lamers, L. P. M., Roelofs, J. G. M., Op den Camp, H. J. M., and Strous, M. (2005). Methanotrophic symbionts provide carbon for photosynthesis in peat bogs. *Nature*, 436, 1153-1156.

Robroek, B. J. M., Limpens, J., Breeuwer, A., and Schouten, M. G. C. (2007a). Effects of water level and temperature on performance of four *Sphagnum* mosses. *Plant Ecology*, 190, 97-107.

Robroek, B. J. M., Limpens, J., Breeuwer, A., van Ruijven, J., and Schouten, M. G. C. (2007b). Precipitation determines the persistence of hollow *Sphagnum* species on hummocks. *Wetlands*, 27, 979-986.

Robroek, B. J. M., Schouten, M. G. C., Limpens, J., Berendse, F., and Poorter, H. (2009). Interactive effects of water table and precipitation on net CO2 assimilation of three co-occurring *Sphagnum* mosses differing in distribution above the water table. *Global Change Biology*, 15, 680-691.

Rocchini, D., Hortal, J., Lengyel, S., Lobo, J. M., Jiménez-Valverde, A., Ricotta, C., Bacaro, G., and Chiarucci, A. (2011). Accounting for uncertainty when mapping species distributions: the need for maps of ignorance. *Progress in Physical Geography: Earth and Environment*, 35, 211-226.

Rydin, H. (1984). Some factors affecting temperature in *Sphagnum* vegetation: an experimental analysis. *Cryptogamie. Bryologie, lichénologie*, 5, 361-372.

Rydin, H., and Jeglum, J. (2013). "The biology of peatlands, second edition," Oxford University Press, Oxford.

Santer, B. D., Po-Chedley, S., Zelinka, M. D., Cvijanovic, I., Bonfils, C., Durack, P. J., Fu, Q., Kiehl, J., Mears, C., Painter, J., Pallotta, G., Solomon, S., Wentz, F. J., and Zou, C.-Z. (2018). Human influence on the seasonal cycle of tropospheric temperature. *Science*, 361, eaas8806.

Schar, C., Vidale, P. L., Luthi, D., Frei, C., Haberli, C., Liniger, M. A., and Appenzeller, C. (2004). The role of increasing temperature variability in European summer heatwaves. *Nature*, 427, 332-336.

Shaw, A. J., Schmutz, J., Devos, N., Shu, S., Carrell, A. A., and Weston, D. J. (2016). The *Sphagnum* genome project: a new model for ecological and evolutionary genomics. *Genomes and Evolution of Charophytes, Bryophytes, Lycophytes and Ferns*, 78, 167-187.

Shi, N., Naudiyal, N., Wang, J. N., Gaire, N. P., Wu, Y., Wei, Y. Q., He, J. L., and Wang, C. Y. (2022). Assessing the impact of climate change on potential distribution of *Meconopsis punicea* and its influence on ecosystem services supply in the southeastern margin of Qinghai-Tibet Plateau. *Frontiers in Plant Science*, 12.

Singh, P., Ekrtová, E., Holá, E., Štechová, T., Grill, S., and Hájek, M. (2020). Restoration of rare bryophytes in degraded rich fens: the effect of sod-and-moss removal. *Journal for Nature Conservation*, 59, 125928.

Su, B., Huang, J., Mondal, S. K., Zhai, J., Wang, Y., Wen, S., Gao, M., Lv, Y., Jiang, S., Jiang, T., and Li, A. (2021). Insight from CMIP6 SSP-RCP scenarios for future drought characteristics in China. *Atmospheric Research*, 250, 105375.

Sun, G. Y., Zhang, W. F., and Zhang, J. J. (1998). "The mire and peatland of the Hengduan Mountains region," Science Press, Beijing.

Sun, S., Zhang, Y., Huang, D., Wang, H., Cao, Q., Fan, P., Yang, N., Zheng, P., and Wang, R. (2020). The effect of climate change on the richness distribution pattern of oaks (*Quercus* L.) in China. *Science of The Total Environment*, 744, 140786.

Sundberg, S. (2013). Spore rain in relation to regional sources and beyond. *Ecography*, 36.

Sundstrom, E., Magnusson, T., and Hanell, B. (2000). Nutrient conditions in drained peatlands along a north-south climatic gradient in Sweden. *Forest Ecology and Management*, 126, 149-161.

Swanson, F. J., Kratz, T. K., Caine, N., and Woodmansee, R. G. (1988). Landform effects on ecosystem patterns and processes: geomorphic features of the earth's surface regulate the distribution of organisms and processes. *BioScience*, 38, 92-98.

Sytiuk, A., Hamard, S., Céréghino, R., Dorrepaal, E., Geissel, H., Küttim, M., Lamentowicz, M., Tuittila, E. S., and Jassey, V. E. J. (2022). Linkages between *Sphagnum* metabolites and peatland CO_2 uptake are sensitive to seasonality in warming trends. *New Phytologist*.

Szumigalski, A. R., and Bayley, S. E. (1996). Decomposition along a bog to rich fen gradient in central Alberta, Canada. *Canadian Journal of Botany*, 74, 573-581.

Thuiller, W., Lavorel, S., Sykes, M. T., and Araújo, M. B. (2006). Using niche-based modelling to assess the impact of climate change on tree functional diversity in Europe. *Diversity and Distributions*, 12, 49-60.

Thurm, E. A., Hernandez, L., Baltensweiler, A., Ayan, S., Rasztovits, E., Bielak, K., Zlatanov, T. M., Hladnik, D., Balic, B., Freudenschuss, A., Büchsenmeister, R., and Falk, W. (2018). Alternative tree species under climate warming in managed European forests. *Forest Ecology and Management*, 430, 485-497.

Titus, J. E., Wagner, D. J., and Stephens, M. D. (1983). Contrasting water relations of photosynthesis for two *Sphagnum* mosses. *Ecology*, 64, 1109-1115.

Toet, S., Cornelissen, J. H. C., Aerts, R., van Logtestijn, R. S. P., de Beus, M., and Stoevelaar, R. (2006). Moss responses to elevated CO_2 and variation in hydrology in a temperate lowland peatland. *Plant Ecology*, 182, 27-40.

Turetsky, M. R., Bond-Lamberty, B., Euskirchen, E., Talbot, J., Frolking, S., McGuire, A. D., and Tuittila, E. S. (2012). The resilience and functional role of moss in boreal and arctic ecosystems. *New Phytologist*, 196, 49-67.

Tveit, A. T., Kiss, A., Winkel, M., Horn, F., Hájek, T., Svenning, M. M., Wagner, D., and Liebner, S. (2020). Environmental patterns of brown moss- and *Sphagnum*-associated microbial communities. *Scientific Reports*, 10, 22412.

Udd, D., Sundberg, S., and Rydin, H. (2015). Multi-species competition experiments with peatland bryophytes. *Journal of Vegetation Science*, 27.

Väliranta, M., Salojärvi, N., Vuorsalo, A., Juutinen, S., Korhola, A., Luoto, M., and Tuittila, E. (2017). Holocene fen-bog transitions, current status in Finland and future perspectives. *The Holocene*, 27, 752–764.

van Breemen, N. (1995). How *Sphagnum* bogs down other plants. *Trends in Ecology & Evolution*, 10, 270-275.

Verhoeven, J. T. A., and Toth, E. (1995). Decomposition of *Carex* and *Sphagnum* litter in fens: effect of litter quality and inhibition by living tissue homogenates. *Soil Biology and Biochemistry*, 27, 271-275.

Wang, G., Wang, D., Trenberth, K. E., Erfanian, A., Yu, M., Bosilovich, Michael G., and Parr, D. T. (2017). The peak structure and future changes of the relationships between extreme precipitation and temperature. *Nature Climate Change*, 7, 268-274.

Weston, D. J., Timm, C. M., Walker, A. P., Gu, L. H., Muchero, W., Schmutz, J., Shaw, A. J., Tuskan, G. A., Warren, J. M., and Wullschleger, S. D. (2015). *Sphagnum* physiology in the context of changing climate: emergent influences of genomics, modelling and host-microbiome interactions on understanding ecosystem function. *Plant Cell and Environment*, 38, 1737-1751.

Whinam, J., Hope, G. S., Clarkson, B. R., Buxton, R. P., Alspach, P. A., and Adam, P. (2003). *Sphagnum* in peatlands of Australasia: their distribution, utilisation and management. *Wetlands Ecology and Management*, 11, 37-49.

Whitaker, D. L., and Edwards, J. (2010). *Sphagnum* moss disperses spores with vortex rings. *Science*, 329, 406-406.

Williams, M. W., Brooks, P. D., and Seastedt, T. (1998). Nitrogen and carbon soil dynamics in response to climate change in a high-elevation ecosystem in the Rocky Mountains, U.S.A. *Arctic and Alpine Research*, 30, 26-30.

Wilmking, M., and Juday, G. P. (2005). Longitudinal variation of radial growth at Alaska's northern treeline—recent changes and possible scenarios for the 21st century. *Global and Planetary Change*, 47, 282-300.

Wu, J., and Liu, Z. M. (2014). Effect of habitat fragmentation on biodiversity: a review. *Chinese Journal of Ecology*, 33, 1946-1952.

Wu, Z. Y., and Wang, H. S. (1983). "Physical geography of China: phytogeography (I)," Science Press, Beijing.

Xiaodan, W., Genwei, C., and Xianghao, Z. (2011). Assessing potential impacts of climatic change on subalpine forests on the eastern Tibetan Plateau. *Climatic Change*, 108, 225-241.

Xing, W., Guo, W., Liang, H., Li, X., Wang, C., He, J., Lu, X., and Wang, G. (2015). Holocene peatland initiation and carbon storage in temperate peatlands of the Sanjiang Plain, Northeast China. *The Holocene*, 26, 70-79.

Xing, Y., and Ree, R. H. (2017). Uplift-driven diversification in the Hengduan Mountains, a temperate biodiversity hotspot. *Proceedings of the National Academy of Sciences*, 114, E3444-E3451.

Xu, F., Jia, Y. W., Liu, C. W., Liu, J. J., and Zhang, W. H. (2018). Variation character of annual, seasonal and monthly temperature and precipitation. *Mountain Research*, 36, 171-183.

Yu, G., Tang, L., Yang, X., Ke, X., and Harrison, S. P. (2001). Modern pollen samples from alpine vegetation on the Tibetan Plateau. *Global Ecology and Biogeography*, 10, 503-519.

Zhang, C. S., Xie, G. D., Bao, W. K., Chen, L., Pei, X., and Fan, N. (2012). Effects of topographic factors on the plant species richness and distribution pattern of alpine meadow in source region of Langcang River, Southeast China. *Chinese Journal of Ecology*, 31, 2767-2774.

Zhang, Y., Qian, L., Spalink, D., Sun, L., Chen, J., and Sun, H. (2021). Spatial phylogenetics of two topographic extremes of the Hengduan Mountains in southwestern China and its implications for biodiversity conservation. *Plant Diversity*, 43, 181-191.

Zhang, Y. L. (1989). Climatic division of the Hengduan mountainous region. *Mountain Research*, 21-28.

Zhu, R. L. (2022). Peat mosses(*Sphagnum*): ecologically, economically, and scientifically important group of carbon sequestration plants. *Chinese Bulletin of Botany*, 57, 559-578.