Changes in Spatial Distribution of *Bryophytes* under CMIP6 Future Projections on the Qinghai-Tibet Plateau

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Abstract

Bryophytes play important roles in ecosystem due to their extensive geographical coverage on the Qinghai-Tibetan Plateau (QTP). While there are few studies attributing the potential distribution and landscape changes on the QTP in response to climate change. Based on climate data averaged of nine global climate models (GCMs) for shared socio-economic pathways SSP2-4.5 under current (the years 1970–2000) and future climate scenarios (the years 2021–2040, 2041–2060, 2061–2080, 2081–2100), and other environmental variables, this study has applied the maximum entropy (MaxEnt) model to assess the potential impact of climate change on the distribution of *Bryophytes* on the QTP. The key environmental factors which determined *Bryophytes's* habitats and range shifts were also examined. The results showed that *Bryophytes* occupied about 9.12×10^5 km^2 (35.43% of total QTP) at present, mainly accumulating in non-permafrost regions of southeast (SE) QTP. Niche suitability of the *Bryophytes* was dominated by soil moisture, ultraviolet-B radiation seasonality, temperature seasonality and precipitation of the coldest quarter. The occupied habitats of *Bryophytes* under future climate scenarios generally increased migrating towards Midwest and relatively higher elevation regions of QTP, where dedicated overall surface air warming and moistening, solar dimming. Additionally, the confusion matrix showed that most parts of the gained occupied habitats under future climate scenarios were low suitable habitats, and small parts for high suitable habitats, however reduced for the medium suitable habitats.

1. Introduction

The Qinghai-Tibetan Plateau (QTP), also called as “The Third Pole of the world”, is particularly vulnerable to climate change (IPCC 2019; Pepin et al., 2015; Thompson et al., 2018). Significant changes gleaned from long-term in-situ and satellite observations, and modeling results all have shown to happened, including vegetation phenology, treeline, vegetation greening, permafrost degradation, solar radiation and vegetation feedback with the climate warming over the QTP (Zhang et al., 2018; Yao et al., 2019; Kang et al., 2019).

Bryophytes, a group of early nonvascular land plants (Kenrick and Crane, 1997), are used as an ideal bio-indication of climate fluctuations as their specific eco-physiological and biological features (Tuba et al., 2011; Porada et al., 2016b;Becker Scarpitta et al., 2017). *Bryophytes* likewise held a key position in terms of carbon/nutrient cycling (Elbert et al., 2012; Lindo et al., 2013; Vicherová et al., 2020), grasslands biodiversity conservation (Boch et al., 2018), forest renewal (Kiebacher et al., 2016; Jiang et al., 2018; Ingerpuu et al., 2019), water and soil nutrients cycling and reserve (Soudzilovskaia et al., 2013) and environment pollution monitoring (Meyer et al., 2012; Wang et al., 2015). However, recent studies dedicate that changing climate would strongly affect ecosystem structure and function, biodiversity, species richness of Bryophytes, resulting in niches and geographical distribution shifts (Alatalo et al., 2015; Wang et al., 2019), and by the contrary, *Bryophytes*' niches changes will also alter the key ecosystem functions and sustainability processes (Lang et al., 2009; Hooper et al., 2012).

Bryophytes are widely distributed on the QTP (Gao et al., 2016). Thus, understanding the spatial distribution patterns and range shifts trends, and the key environmental factors, is helpful for protecting QTP ecosystems diversity, monitoring vegetation and climate changes, and guiding future field surveys of new *Bryophytes* species' occurrences, especially in unexplored areas. However, we largely overlooked the vast areas distribution of *Bryophytes* and the response of the spatial extent of their suitable habitats to climate change (Wu et al., 2002b; Liu and Bao 2006, Ingerpuu et al., 2019). Both researches and the red list of endangered *Bryophytes* in China approved that global warming will lead to diversity losses, or even endangered for *Bryophytes* of QTP (Cao et al., 2006; He et al., 2016). But Wu et al (2001) issued that despite the fact that a small part of *Bryophytes* disappeared with the uplift of QTP, in general, warming climate prompted the development and geographical distribution range in Hengduan mountains during past decades, although vast geophysical surveys and control experimental configurations about *Bryophytes* had been conducted (Wu et al., 2003a), but these ways are extremely costly and only available over relatively small areas.

The maximum entropy model (Maxent), an numerical tool that only combine limited species presence (or occurrence) data and environmental variables (Elith et al., 2006; Phillips et al., 2009), has come into particularly common used species distribution models (SDMs) (Elith et al., 2009) to gain species ecological and distributional evolutionary insights under changing climate (Muir et al., 2015; You et al., 2018; Zhang et al., 2018; Guo et al., 2019). Maxent modeling was also considered as a useful method for mapping geographical distribution and response to climate change for *Bryophytes* on a large scale. For example, Sérgio et al. (2007) compared three different approaches: genetic algorithm for rule-set production (GARP), maximum entropy (Maxent) and ecological niche factor analysis (ENFA) to modeling the potential distribution of *Bryophytes*, and the accuracy of Maxent dedicate the best; Désamoré et al. (2012) investigated the distribution and genetic diversity of *Bryophytes* under past and present climates conditions; Skowronek et al. (2018) mapped the distribution of *Bryophytes* combing with imaging spectroscopy data in Germany and Belgium; Song (2015) predicted the potential distribution of *Pottiaceae* in Tibet and explored the key ecological factors. However there are no reports to forecast the potential geographical distribution and range shifts of *Bryophytes* on the whole QTP, especially in clarifying the change of habitat suitability with climate change.

The objectives of this work were: (1) to explore the key environmental factors affecting the habitat suitability of *Bryophytes*; (2) to delineate the potential distribution of *Bryophytes* under current and future climatic scenarios; and (3) to identify the differential effects of climate warming on the potential distribution and habitat suitability of *Bryophytes*.

2. Materials And Methods

2.1. Study regions and occurrence records

The occurrences of *Bryophytes* were shown in Fig. 1, which were collected from the Global Biodiversity Information Facility (GBIF, www.gbif.org/). The occurrences for *Bryophytes* in GBIF were from of ten datasets, such as EOD-eBird Observation Dataset, plant Specimens from PE Herbarium in China and Chinese Institute of Biology etc. All the occurrences of *Bryophytes* had passed strict quality preprocesses by deleting and filtering spatially to ensure that there no duplicate point within 10 km × 10 km before Maxent was begun. Finally, a total of 250 samples, representing all known *Bryophytes* natural habitats on the QTP, saved as .csv file format, were generated for further modeling.

2.2. Environmental variables

Given that the habitat distribution of *Bryophytes* was influenced by climate condition, topography, soil properties, UV-B radiation and land cover. A database with 30 environmental variables was collected to model the patterns of *Bryophytes* over four future time periods (the years of 2021–2040, 2041–2060, 2061–2080 and 2081–2100). 19 climate data and 2 topographical factors were downloaded and generated from WorldClim database (https://www.worldclim.org/data/cmip6/) (Hijmans et al., 2005). The average for eight global climate models (GCMs): BCC-CSM2-MR, CNRM-CM6-1, CNRM-ESM2-1, CanESM5, IPSL-CM6A-LR, MIROC-ES2L, MIROC6, and MRI-ESM2-0 under shared socio-economic pathway245 (SSP2-4.5) were used to modeling, which were released from the 6 Coupled Model Intercomparison Project (CMIP6) and IPCC Accessment Report 6 (AR6). 4 UV-B radiation data from gIUV database (www.ufz.de/gluv/) (Beckmann et al., 2014); 3 soil properties came from Center for Sustainability and the Global Environment (www.sage.wisc.edu/atlas) (New et al., 2000); and 2 vegetation cover types were from EarthEnv (www.earthenv.org/ landcover) (Tuanmu et al., 2014).

Next, all above variables were resampling to a general spatial resolution of 30 s (ca. 1 km^2). Then we utilized Spearman's rank correlation to remove high spatially related bioclimatic variables based on previous reports of the factors potentially affecting *Bryophytes*, to avoid model over-fitting lead by multicollinearity of variables, (Graham, 2008), with which highly collinear variables were identified, i.e., r> |0.75| (Suppl. Table 1). Finally, 16 bioclimatic variables (Table 1) were used to model the habitat distribution modeling.

Table.1 Contribution of 16 environmental variables in Maxent modeling

Variable	Description	Percent contribution	Permutation importance
sm	Soil moisture	43.4	11.9
uvb2	UV-B seasonality	20.2	14.1
bio04	Temperature Seasonality (standard deviation × 100)	6.0	29.0
bio19	Precipitation of Coldest Quarter	4.5	11.3
bio01	Annual Mean Temperature	4.2	1.6
bio14	Precipitation of Driest Month	3.3	5.2
bio05	Max Temperature of Warmest Month	2.4	3.8
herb	Herbaceous vegetation	2.3	4.8
sph	Soil pH	2.3	1.9
bio12	Annual Precipitation	2.1	2.1
bio11	Mean Temperature of Coldest Quarter	2.0	0.7
bio15	Precipitation Seasonality (Coefficient of Variation)	1.9	2.9
asp	Aspect	1.6	2.4
shr	Shrubs vegetation	1.4	2.0
ele	Elevation	1.3	4.8
bio03	Isothermality (bio2/bio7) (× 100)	1.2	1.5

2.3. Species distribution modeling

MaxEnt software 3.4.0 k (available at www.cs.princeton.edu/*schapire/maxent) was used for habitat suitability simulation (Elith et al., 2006; Phillips et al., 2009). It only requires species occurrence locations and its related environmental variables. Of the 250 samples of *Bryophytes*, 75% were used for the model training, and 25% for model testing. The Jacknife analysis was performed to assess the contribution of each environmental variable for the potential habitat distribution.

The modeling output is a continuous habitat suitability index (HSI), ranging from 0 (unsuitable) to 1 (perfectly suitable). In order to accurately evaluate habitats, we defined unsuitable habitats (NSH) when HIS < 0.35 according to equate entropy of thresholded and original distributions. Then, the occupied habitats were reclassified into three classes: (1) Low suitable habitats (LSH, $0.35 \leq HSI < 0.5$; (2) Medium suitable habitats (MSH, $0.5 \leq HSI < 0.65$); and (3) High suitable habitats (HSH, $HSI \geq 0.65$).

The performance of MaxEnt was evaluated by Area Under the receiver operating characteristics Curve (AUC) value (Pearson et al., 2006). AUC value ranged from 0.5 (random) to 1.0 (perfect discrimination) (Swets, 1988; Weber, 2011).

2.4. Land-Cover Transition Matrix

A land-cover transition matrix was generated in ArcGIS 10.0 software to reflect the changes of four suitable types of *Bryophytes* from one climate scenario to another (Wan et al., 2015).

3. Results

3.1. Model performance

We determined AUC values for checking the model performance of all climate scenarios. The simulated results showed that the average AUC for the replicate runs of Maxent model under different climate scenarios was $0.9608_{mean} \pm 0.038_{SD}$ (Table 2). The results suggested that the performance of Maxent model was excellent.

Table 2
The average of AUC values under different periods.

Time periods	Mean AUC	Standard deviation
Current	0.964	0.040
2021–2040	0.961	0.038
2041–2060	0.961	0.036
2061–2080	0.958	0.038
2081–2100	0.960	0.038

3.2 Key environment variables and current distribution

The variable jack-knife results (Table 1) showed that soil moisture (sm, 43.4%), UV-B seasonality (uvb2, 20.2%), temperature seasonality (bio4, 6.0%) and precipitation of coldest quarter (bio19, 4.5%) had greater contribution to potential distribution modeling of *Bryophytes*. The permutation importance of these four variables reached 66.3%.

The occupied habitats under the current climatic conditions mainly distributed in non-permafrost region of southeast (SE) QTP (Song et al., 2015; Zou et al., 2016) (Fig. 2). According to the classified results of HSI, the total occupied habitat reached to 9.12×10^5 km^2 (covered 35.43 % of total QTP), among which 18.46% was LSH; next was MSH (13.21%), while HSH accounted for the smallest percentage (3.75%). Geographically, the larger proportion of occupied habitats distributed in three rivers valley and the Yalu

Tsangpo River basin. Moist condition and low UV-B radiation environment of these areas provided a suitable ecological corridor for *Bryophytes* (Martnez-Abaigar et al., 2003; Bartels et al., 2018).

3.3. Impact of climate change on Bryophytes

Variation of occupied areas of *Bryophytes* in four future time periods under SSP2-4.5 climate scenario was in accordance with total vegetation greening trend in QTP ecosystem with warming climate (Shen et al., 2016) (Fig. 3 and Fig. 4). With climate warming, degradation regions of permafrost and glacier in the central and western QTP would gradually become suitable for the growth of *Bryophytes*, and the potential occupied habitat of *Bryophytes* would migrate toward the Midwest of QTP (Fig. 3)

Note that the shifts ratios of different habitat types changed inconsistently (Fig. 4). Ratios of LSH and HSH showed increasing trends, however fall in MSH. Concluding from the transition matrix results of four suitable habitat types (Table 3), the gained area of LSH mainly came from NSH and MSH, and increased area of HSH was from MSH. Totally, majority of lost MSH was converted to LSH, yet a small part to HSH. However, the area of the former was much larger than the latter, which was also consistent with the overall increase in the potential distribution of *Bryophytes*.

Table 3
Dynamics of transition in four suitable types of *Bryophytes* on the QTP from Current to 2021–2040, 2021–2040 to 2041–2060, 2041–2060 to 2061–2080 and 2061–2080 to 2081–2100 (unit: $\times 10^4$ km^2).

Periods	Habitat Types	NSH	LSH	MSH	HSH
Current to 2021–2040	NSH	155.89	9.29	0.76	0.24
	LSH	6.33	35.30	5.64	0.23
	MSH	0.17	6.09	24.77	3.12
	HSH	0.01	0.06	1.71	7.80
2021–2040 to 2041–2060	NSH	159.75	2.61	0.04	0.00
	LSH	3.80	44.72	2.21	0.01
	MSH	0.03	2.82	29.04	1.00
	HSH	0.00	0.01	0.89	10.48
2041–2060 to 2061–2080	NSH	159.76	3.71	0.11	0.00
	LSH	3.46	43.69	2.99	0.02
	MSH	0.02	3.24	27.71	1.20
	HSH	0.00	0.01	1.18	10.29
2061–2080 to 2081–2100	NSH	159.66	3.57	0.01	0.00
	LSH	3.02	45.06	2.58	0.01
	MSH	0.12	2.52	28.27	1.08
	HSH	0.01	0.01	0.84	10.66

Both gained and lost occupied habitats of *Bryophytes* existed on the QTP as the temperature continues to rise. It could be inferred from Fig.5 that range shifts of *Bryophytes* correlated to elevations on the QTP, and gained habitats mainly migrate toward relatively higher elevations, while lost habitats happened at relatively low elevations.

4. Discussions

As an important bio-indication to climate monitoring, ecosystem biodiversity conservation, and soil nutrients cycling and reserving, less attention has been paid to changes about *Bryophytes'* niches and covers with climate warming on the QTP. Considering the global greenhouse gas emissions (SSP2-4.5), this paper delved the potential distribution, range shifts and key environmental variables of *Bryophytes* under current and future climate scenarios.

Geographically, the suitable habitats distributed in non-permafrost region of SE QTP and the area reached to 9.12×10^5 km^2 (covered 35.43% of total QTP). Without considering the biotic interactions, the different range shifts of *Bryophytes* species habitats mainly depended on habitat heterogeneity and environmental factors (Gao et al., 2016). In the larger scale, habitats with higher habitat heterogeneity were more conducive to the coexistence of species, which was shown in the spreading of gained *Bryophytes* to higher elevation regions, where usually more colder and wetter to be the considerable diversity (Sun et al., 2013; Zanatta et al., 2020). Additionally, the range shifts of *Bryophytes* were highly influenced by external environments and interactions of multiply factors due to the specific eco-physiological and biological features of *Bryophytes* (Mateo et al., 2013). Soil moisture, UV-B seasonality, temperature seasonality and precipitation of the coldest quarter were the four most predominant environmental factors by the Jackknife tests, and which were also compared with previous studies (Song et al., 2015; He et al., 2016; Tomiolo et al., 2018). Physiological of *Bryophytes* would change when exposed to UV-B seasonality, including changes of light quality, duration and intensity, in particular, a high UV-B radiation intensities at low temperatures, would be permanently damaged (Kallio and Valanne, 1975; Kershaw and Webber, 1986). Additionally, they preferred damp or humid habitats along with river (Levetin et al., 1996). So, it was common recognized that the peak photosynthetic activity of *Bryophytes* happened in early morning and late evening when the moisture conditions were most suitable (Bartels et al., 2018). In the meanwhile, the distribution and niches of *Bryophytes* were likewise coordinated by air temperature and its seasonal changes. Dilks and Proctor (1975) approved that there exist a relatively narrow temperatures extent for *Bryophytes* to obtain net photosynthesis. It seems that at high temperature, most *Bryophytes* on the QTP may suffer irreversible degradation or die (Weis et al., 1986; Löbel et al., 2018), but it could withstand much lower habitats in very cold climate for many years (Perera-Castro et al., 2020). Besides these three factors, precipitation defines *Bryophytes*' growth and distribution within those boundaries. Thus, we can inferred that extreme climate events might be the main factors for range shifts *Bryophytes* on the QTP (Zhu et al., 2017; Yao et al., 2018; Zhang et al., 2018).

Thus, there is a need for further studies to delve the larger variation in climate and more frequent climate extremes on Maxent model to improve the feedback of *Bryophytes* and niches to climate change. In addition to the climate change, the biomass and diversity of shrub and herbaceous vegetation (Jägerbrand et al 2012., Chen et al., 2017; Fergus et al., 2017), freeze-thaw cycles for frozen soil (Porada et al., 2016a; Higgins et al., 2018) and excessive grazing (Olden et al., 2016), can also affect the distribution of *Bryophytes*. Thus, future work should synthesis other crucial factors into Maxent modeling for *Bryophytes*.

5. Conclusions

In this study, changes in potential geographical distribution of *Bryophytes* under current and CMIP6 future projections on the QTP were projected using Maxent model based on species occurrences and relative environmental variables. The influences of environmental heterogeneity to habitats suitability were also analyzed. Our results indicated the occupied habitats of *Bryophytes* would increase slightly and move towards to the central and western regions with an overall surface air warming and moistening, solar dimming. The findings in this study can be used to clearly understand the distribution and range shifts of *Bryophytes*, and provide a basis for habitats and their biota conversation of *Bryophytes*, even conductive for monitoring climate and ecosystem change on the degradation regions of permafrost and glacier in the central and western QTP.

Declarations

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Competing Interests:

We declare no competing interests for our manuscript "Changes in Spatial Distribution of Bryophytes under CMIP6 Future Projections on the Qinghai-Tibet Plateau"

References

Alatalo JM, Jägerbrand AK, Molau U (2015) Testing reliability of short-term responses to predict longer-term responses of *Bryophytes* and lichens to environmental change. Ecol. Indic. 58: 77-85. https://doi.org/10.1016/j.ecolind.2015.05.050

Bartels S, Caners RT, Ogilvie J et al (2018) Relating *Bryophytes* Assemblages to a Remotely-Sensed Depth-to-Water in Boreal Forests. Front. Plant Sci. 9: 858. https://doi.org/10.3389/fpls.2018.00858

Becker Scarpitta A, Bardat J, Lalanne A et al (2017) Long-term community change: *Bryophytes* are more responsive than vascular plants to nitrogen deposition and warming. J. Veg. Sci, 28(6): 1220-1229. https://doi.org/10.1111/jvs.12579

Beckmann M, Václavík T, Manceur AM et al (2014) glUV: a global UV-B radiation data set for macroecological studies. Methods Ecol. Evol. 5(4): 372-383. https://doi.org/10.1111/2041- 210X.12168

Bibi S, Wang L, Li XP et al (2018) Climatic and associated cryospheric, biospheric, and hydrological changes on the Tibetan Plateau: a review. Int. J. Climatol. 38: e1-e17. https://doi.org/10.1002/joc.5411

Boch S, Allan E, Humbert JY et al (2018) Direct and indirect effects of land use on *Bryophytes* in grasslands. Sci. Total Environ. 644: 60-67. https://doi.org/10.1016/j.scitotenv.2018.06.323

Cao T, Zhu R, Guo SL, et al (2006) A brief report of the first red list of endangered *Bryophytes* in China. Bull. Botan. Res. 26: 756-762. (in Chinese) http://bbr.nefu.edu.cn/EN/Y2006/V26/I6/ 756

Chen Y, Niu S, Li PK et al (2017) Stand structure and substrate diversity as two major drivers for Bryophytes distribution in a temperate montane ecosystem. Front. Plant Sci. 8: 874. https://doi.org/10.3389/fpls.2017.00874

Désamoré A, Laenen B, Stech M et al (2012) How do temperate *Bryophytes* face the challenge of a changing environment? Lessons from the past and predictions for the future. Global Change Biol. 18(9): 2915-2924. https://doi.org/10.1111/j.1365-2486.2012.02752.x

Dilks TJK, Proctor MCF (1975) Comparative experiments on temperature responses of *Bryophytes*: assimilation, respiration and freezing damage. J. Bryol. 8(3): 317-336. https://doi.org/10.1179/jbr.1975.8.3.317

Elith J, Graham CH, Anderson RP et al (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography 29: 129-151. https://doi.org/10.1111/j.2006. 0906-7590.04596.x

Elith J, Leathwick JR (2009) Species distribution models: ecological explanation and prediction across space and time. Annu. Rev. Ecol. Evol. S. 40: 677-697. https://doi.org/10.1146/annurev.ecolsys.110308.120159

Fergus AJ, Gerighausen U, Roscher C (2017) Vascular plant diversity structures *Bryophytes* colonization in experimental grassland. J. Veg. Sci. 28(5): 903-914. https://doi.org/10.1111 /jvs.12563

Gao J, Zhang X, Zhang P et al (2016) Geographical distribution pattern of endemic *Bryophytes* in china. Chin. J. Ecol. 35: 1691-1696. (in Chinese) http://www.cje.net.cn/CN/Y2016/V35/I7/ 1691

Graham CH, Elith J, Hijmans RJ et al (2008) The influence of spatial errors in species occurrence data used in distribution models. J. Appl. Ecol. 45(1): 239-247. https://doi.org/10.1111/j.1365-2664.2007.01408.x

Guo C, Ma YZ, Meng HW et al (2018) Changes in vegetation and environment in Yamzhog Yumco Lake on the southern Tibetan Plateau over past 2000 years. Palaeogeogr. Palaeocl. 501: 30-44. https://doi.org/10.1016/j.palaeo.2018.04.005

Guo Y, Li X, Zhao ZF et al (2019) Predicting the impacts of climate change, soils and vegetation types on the geographic distribution of *Polyporus Umbellatus* in China. Sci. Total Environ. 648: 1-11. https://doi.org/10.1016/j.scitotenv.2018.07.465

He X, He KS, Hyvönen J (2016) Will *Bryophytes* survive in a warming world? Perspect. Plant Ecol. 19: 49-60. https://doi.org/10.1016/j.ppees.2016.02.005

Higgins KL, Garon-Labrecque MÈ (2018) Fine-scale influences on thaw depth in a forested peat plateau landscape in the Northwest Territories, Canada: Vegetation trumps microtopography. Permafrost Periglac. 29(1): 60-70. https://doi.org/10.1002/ppp.1961

Hijmans RJ, Cameron SE, Parra JL et al (2005) Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25(15): 1965-1978. https://doi.org/10.1002/joc.1276

Hooper DU, Adair EC, Cardinale BJ et al (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature 486, 105-108. https://doi.org/10.1038/nature11118

Ingerpuu N, Kupper T, Vellak K et al (2019) Response of *Bryophytes* to afforestation, increase of air humidity, and enrichment of soil diaspore bank. Forest Ecol. Manag. 432: 64-72. https://doi.org/10.1016/j.foreco.2018.09.004

Perera-Castro AV, Waterman MJ, Turnbull JD et al (2020) It is hot in the sun: Antarctic mosses have high temperature optima for photosynthesis despite cold climate. Front. Plant Sci. 11: 1178. https://doi.org/10.3389/fpls.2020.01178

Pörtner HO, Roberts DC, Masson-Delmotte et al (2019) IPCC special report on the ocean and cryosphere in a changing climate. IPCC Intergovernmental Panel on Climate Change (IPCC). Cambridge: Cambridge University Press.

Jägerbrand AK, Kudo G, Alatalo JM et al (2012) Effects of neighboring vascular plants on the abundance of *Bryophytes* in different vegetation types. Polar Sci. 6(2): 200-208. https://doi.org/10.1016/j.polar.2012.02.002

Jiang TT, Yang XC, Zhong YL et al (2018) Species composition and diversity of ground *Bryophytes* across a forest edge-to-interior gradient. Sci. Rep. 8(1): 11868. https://doi.org/10.1038/s41598-018-30400-1

Kang S, Zhang Q, Qian Y et al (2019) Linking atmospheric pollution to cryospheric change in the Third Pole region: current progress and future prospects. Nati. Sci. Rev. 6(4): 796-809. https://doi.org/10.1093/nsr/nwz031

Kallio P, Valanne N (1975) On the effect of continuous light on photosynthesis in mosses. In Fennoscandian tundra ecosystems. Springer, Berlin, pp 149-162.

Kenrick P, Crane PR (1997) The origin and early evolution of plants on land. Nature 389(6646): 33-39. https://doi.org/10.1038/37918

Kershaw KA, Webber MR (1986) Seasonal changes in the chlorophyll content and quantum efficiency of the moss *Brachythecium Rutabulum*. Trans. Brit. Bryol. Soc. 14(1): 151-158. https://doi.org/10.1179/jbr.1986.14.1.151

Kiebacher T, Keller C, Scheidegger C et al (2016) Hidden crown jewels: the role of tree crowns for *Bryophytes* and lichen species richness in sycamore maple wooded pastures. Biodivers. Conserv. 25(9): 1605-1624. https://doi.org/10.1007/s10531-016-1144-4

Lang SI, Cornelissen JH, Hölzer A et al (2009) Determinants of cryptogam composition and diversity in *Sphagnum*-dominated peatlands: the importance of temporal, spatial and functional scales. J. Ecol. 97(2): 299-310. https://doi.org/10.1111/j.1365-2745.2008.01472.x

Levetin E, McMahon K (1996). Plants and society. New York, Brown Publishers, pp 447.

Lindo Z, Nilsson MC, Gundale MJ et al (2013) *Bryophytes-cyanobacteria* associations as regulators of the northern latitude carbon balance in response to global change. Global Change Biol. 19(7): 2022-2035. https://doi.org/10.1111/gcb.12175

Liu J, Bao W (2006) Major *Bryophytes* patches biomass and relation with environmental factors in a coniferous forest of the eastern Qinghai-Tibetan plateau. Chin. Bull. Bot. 23(6): 684-690. (in Chinese). https://10.3969/j.issn.1674-3466.2006.06.010

Löbel S, Mair L, Lönnell N et al (2018) Biological traits explain *Bryophytes* species distributions and responses to forest fragmentation and climatic variation. J. Ecol. 106(4): 1700-1713. https://doi.org/10.1111/1365-2745.12930

Martnez-Abaigar J, Nez-Olivera E, Beaucourt N et al 2003. Different physiological responses of two aquatic *Bryophytes* to enhanced ultraviolet-B radiation. J. Bryol. 25(1): 17-30. https://doi.org/10.1111/1365-2745.12930

Mateo RG, Vanderpoorten A, Muñoz J et al (2013) Modeling species distributions from heterogeneous data for the biogeographic regionalization of the European *Bryophytes* flora. Plos One 8, e55648. https://doi.org/10.1371/journal.pone.0055648

Meyer C, Gilbert D, Gillet F et al (2012) Using "*Bryophytes* and their associated testate amoeba" microsystems as indicators of atmospheric pollution. Ecol. Indic. 13(1): 144-151. https://doi.org/10.1016/j.ecolind.2011.05.020

Muir PR, Wallace CC, Done T et al (2015) Limited scope for latitudinal extension of reef corals. Science 348(6239): 1135-1138. doi: 10.1126/science.1259911

New M, Hulme M, Jones P (2000) Representing twentieth-century space-time climate variability. part II: development of 1901-96 monthly grids of terrestrial surface climate. J. Climate 13(13): 829-856. https://doi.org/10.1175/1520-0442(2000)013<2217:RTCSTC>2.0.CO;2

Olden A, Raatikainen KJ, Tervonen K et al (2016) Grazing and soil pH are biodiversity drivers of vascular plants and *Bryophytes* in boreal wood-pastures. Agr. Ecosyst. Environ. 222: 171-184. https://doi.org/10.1016/j.agee.2016.02.018

Pearson RG, Raxworthy CJ, Nakamura M et al (2007) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. J. Biogeogr. 34(1): 102-117. https://doi.org/10.1111/j.1365-2699.2006.01594.x

Pepin N, Bradley RS, Diaz HF et al (2015) Elevation-dependent warming in mountain regions of the world. Nat. Clim. Change 5(5), 424-430. https://doi.org/10.1038/nclimate2563

Phillips SJ, Dudík M, Elith J et al (2009) Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. Ecol. Appl. 19(1): 181-197. https://doi.org/10.1890/07-2153.1

Porada P, Ekici A, Beer C (2016a) Effects of *Bryophytes* and lichen cover on permafrost soil temperature at large scale. The Cryosphere 10(5): 2291-2315. doi: 10.5194/tc-10-2291-2016

Porada P, Lenton TM, Pohl A et al (2016b) High potential for weathering and climate effects of non-vascular vegetation in the Late Ordovician. Nat. commun. 7(1): 12113. https://doi.org/10.1038/ncomms12113

Sérgio C, Figueira R, Draper D et al (2007) Modelling *Bryophytes* distribution based on ecological information for extent of occurrence assessment. Biol. Conserv. 135(3): 341-351. https://doi.org/10.1016/j.biocon.2006.10.018

Shen MG, Piao SL, Chen XQ et al (2016) Strong impacts of daily minimum temperature on the green-up date and summer greenness of the Tibetan Plateau. Global Change Biol. 22(9): 3057-3066. https://doi.org/10.1111/gcb.13301

Skowronek S, Van De Kerchove R, Rombouts B et al (2018) Transferability of species distribution models for the detection of an invasive alien *Bryophytes* using imaging spectroscopy data. Int. J. Appl. Earth Obs. 68, 61-72. https://doi.org/10.1016/j.jag.2018. 02.001

Song SS, Liu XH, Bai XL et al (2015) Impacts of environmental heterogeneity on moss diversity and distribution of *Didymodon (Pottiaceae)* in Tibet, China. Plos one, 10(7): e0132346. https://doi.org/10.1371/journal.pone.0132346

Soudzilovskaia NA, van Bodegom PM, Cornelissen JH (2013) Dominant *Bryophytes* control over high-latitude soil temperature fluctuations predicted by heat transfer traits, field moisture regime and laws of thermal insulation. Funct. Ecol. 27(6): 1442-1454. https://doi.org/10.1111/1365-2435.12127

Sun S, Wu Y, Wang G et al (2013) *Bryophytes* species richness and composition along an altitudinal gradient in Gongga Mountain, China. PloS one, 8(3): e58131. https://doi.org/10.1371/journal.pone.0058131

Swets JA (1988) Measuring the accuracy of diagnostic systems. Science 240(4857): doi:1285-1293.DOI: 10.1126/science.3287615

Thompson LG, Yao T, Davis ME et al (2018) Ice core records of climate variability on the Third Pole with emphasis on the Guliya ice cap, western Kunlun Mountains. Quaternary Sci. Rev. 188: 1-14. https://doi.org/10.1016/j.quascirev.2018.03.003

Tomiolo S, Ward D (2018) Species migrations and range shifts: A synthesis of causes and consequences. Perspect. Plant Ecol. 33: 62-77. https://doi.org/10.1016/j.ppees.2018.06.001

Tuanmu MN, Jetz W (2014) A global 1-km consensus land-cover product for biodiversity and ecosystem modelling. Global Ecol. Biogeogr. 23(9): 1031-1045. https://doi.org/10.1111/ geb.12182

Tuba Zoltán, Slack NG (2011) *Bryophytes* Ecology and Climate Change: The Ecological Value of Bryophytes as Indicators of Climate Change. Bryophytes ecology and climate change, England, Cambridge University Press, PP 3-12.

Vicherová E, Glinwood R, Hájek T et al (2020) Bryophytes can recognize their neighbours through volatile organic compounds. Sci. Rep. 10(1): 1-11. https://doi.org/10.1038/s41598 -020-64108-y

Wan L, Zhang Y, Zhang X et al (2015) Comparison of land use/land cover change and landscape patterns in Honghe National Nature Reserve and the surrounding Jiansanjiang Region, China. Ecol. Indic. 51: 205-214. https://doi.org/10.1016/j.ecolind.2014.11.025

Wang S, Zhang Z, Wang Z (2015) *Bryophytes* communities as biomonitors of environmental factors in the Goujiang karst bauxite, southwestern China. Sci. Total Environ. 538: 270-278. https://doi.org/10.1016/j.scitotenv.2015.08.049

Wang ZM, Ye W, Xing FW (2019) *Bryophyte* diversity on a tropical continental island (Hainan, China): potential vulnerable species and environmental indicators. J. Bryol. 41(4): 350-360. https://doi.org/10.1080/03736687.2019.1653557

Weber TC (2011) Maximum entropy modeling of mature hardwood forest distribution in four U.S. states. Forest Ecol. Manag. 261(3): 779-788. https://doi.org/10.1016/j.foreco.2010.12.009

Weis E, Santarius KA (1986) Heat sensitivity and thermal adaptation of photosynthesis in liverwort thalli. Oecologia 69(1): 134-139. https://doi.org/10.1007/BF00399049

Wu P, Wang M (2001) Relationship of the tropical elements of the *Bryophytes* between Hengduan Mts., southwest China and Taiwan province, southeast China. Guizhou Sci. 19(4): 6-9. (in Chinese)

Wu Y, Cheng G, Gao Q (2003a) *Bryophytes*'s Ecology Functions and Its Significances in Revegetation. J. Desert Res. 23: 9-14. (in Chinese)

Wu Y, Gao Q, Cheng, G et al (2002b) Response of Bryophytes to global change and its bio- indicatortation. J. Appl. Ecol. 13: 895-900. (in Chinese)

Yao J, Chen Y, Zhao Y et al (2018) Response of vegetation NDVI to climatic extremes in the arid region of Central Asia: a case study in Xinjiang, China. Theor. Appl. Climatol. 131(3-4): 1503-1515. https://doi.org/10.1007/s00704-017-2058-0

Yao T, Xue Y, Chen D et al (2019) Recent Third Pole's rapid warming accompanies cryospheric melt and water cycle intensification and interactions between monsoon and environment: multi-disciplinary approach with observation, modeling and analysis. Bull. Amer. Meteor. Soc., 100(3): 423-444. https://doi.org/10.1175/BAMS-D-17-0057.1

You J, Qin X, Ranjitkar S et al (2018) Response to climate change of montane herbaceous plants in the genus *Rhodiola* predicted by ecological niche modelling. Sci. Rep. 8: 5879. https://doi.org/10.1038/s41598-018-24360-9

Zanatta F, Engler R, Collart F et al (2020) *Bryophytes* are predicted to lag behind future climate change despite their high dispersal capacities. Nat Commun 11: 5601. https://doi.org/10.1038/s41467-020-19410-8

Zhang K, Yao L, Meng JS et al (2018) Maxent modeling for predicting the potential geographical distribution of two peony species under climate change. Sci. Total Environ. 634, 1326-1334. https://doi.org/10.1016/j.scitotenv.2018.04.112

Zhang Z, Chang J, Xu C et al (2018) The response of lake area and vegetation cover variations to climate change over the Qinghai-Tibetan Plateau during the past 30 years. Sci. Total Environ. 635: 443-451. https://doi.org/10.1016/j.scitotenv.2018.04.113

Zhu X, Wu T, Li R et al (2017) Impacts of Summer Extreme Precipitation Events on the Hydrothermal Dynamics of the Active Layer in the Tanggula Permafrost Region on the Qinghai-Tibetan Plateau. J. Geophys. Res. 122(21): 11559-11567. https://doi.org/10.1002/ 2017JD026736

Zou D, Zhao L, Sheng Y et al (2016) A New Map of the Permafrost Distribution on the Tibetan Plateau. The Cryosphere, 11:1-28. doi:10.5194/tc-2016-187

Figures

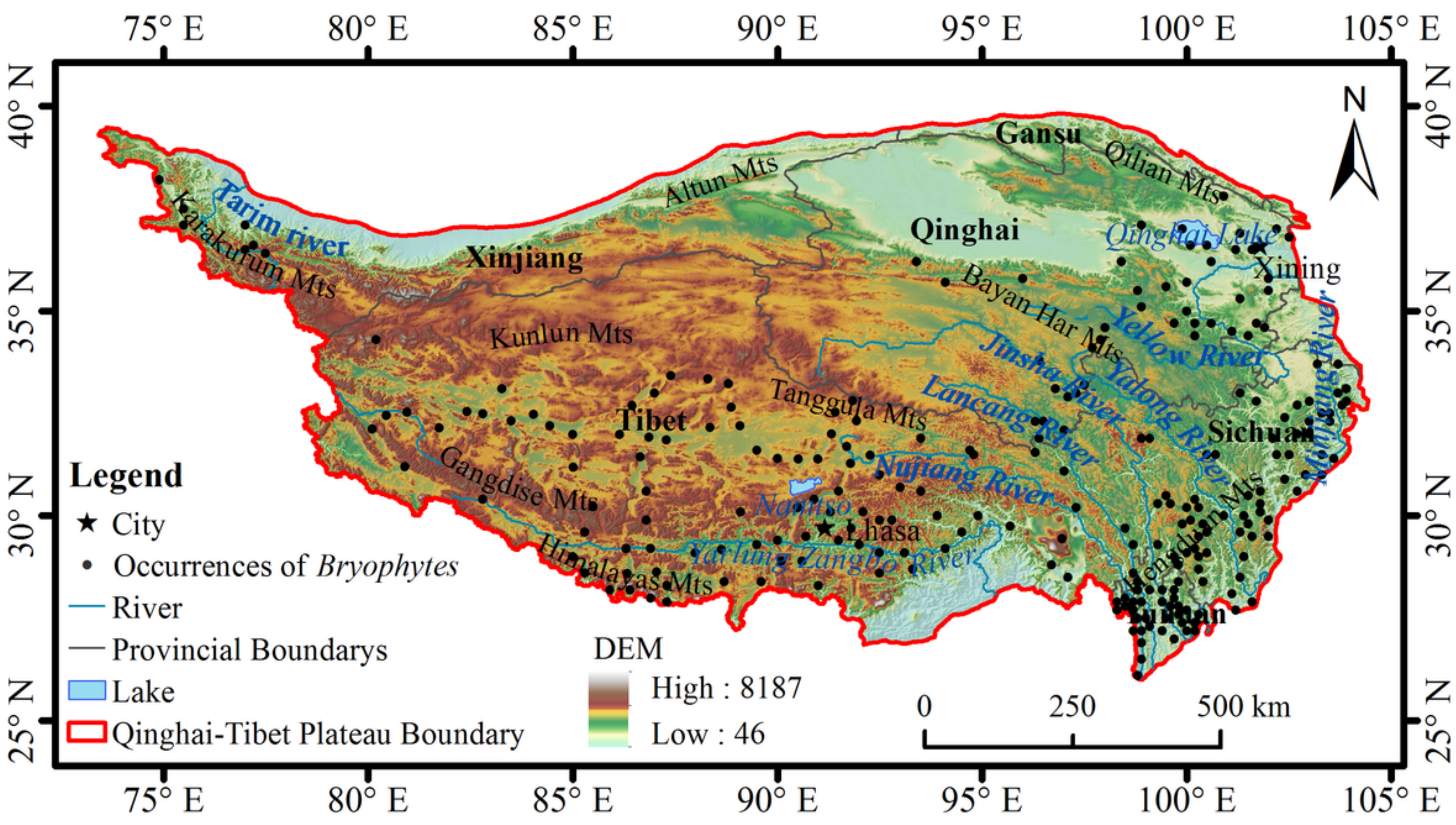

Figure 1

Study area and presence samples of Bryophytes

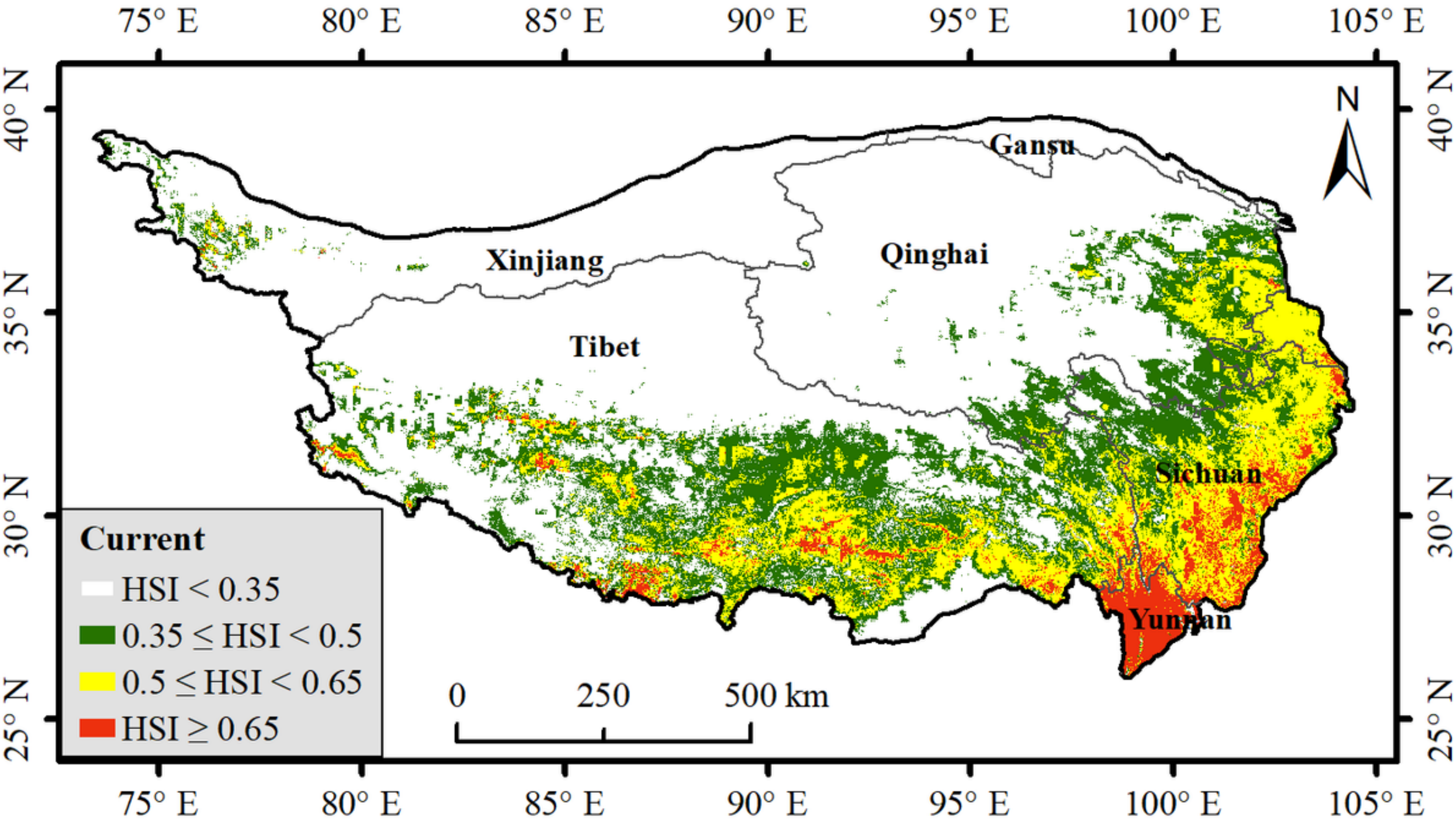

Figure 2

Potential distribution of Bryophytes under current climatic condition

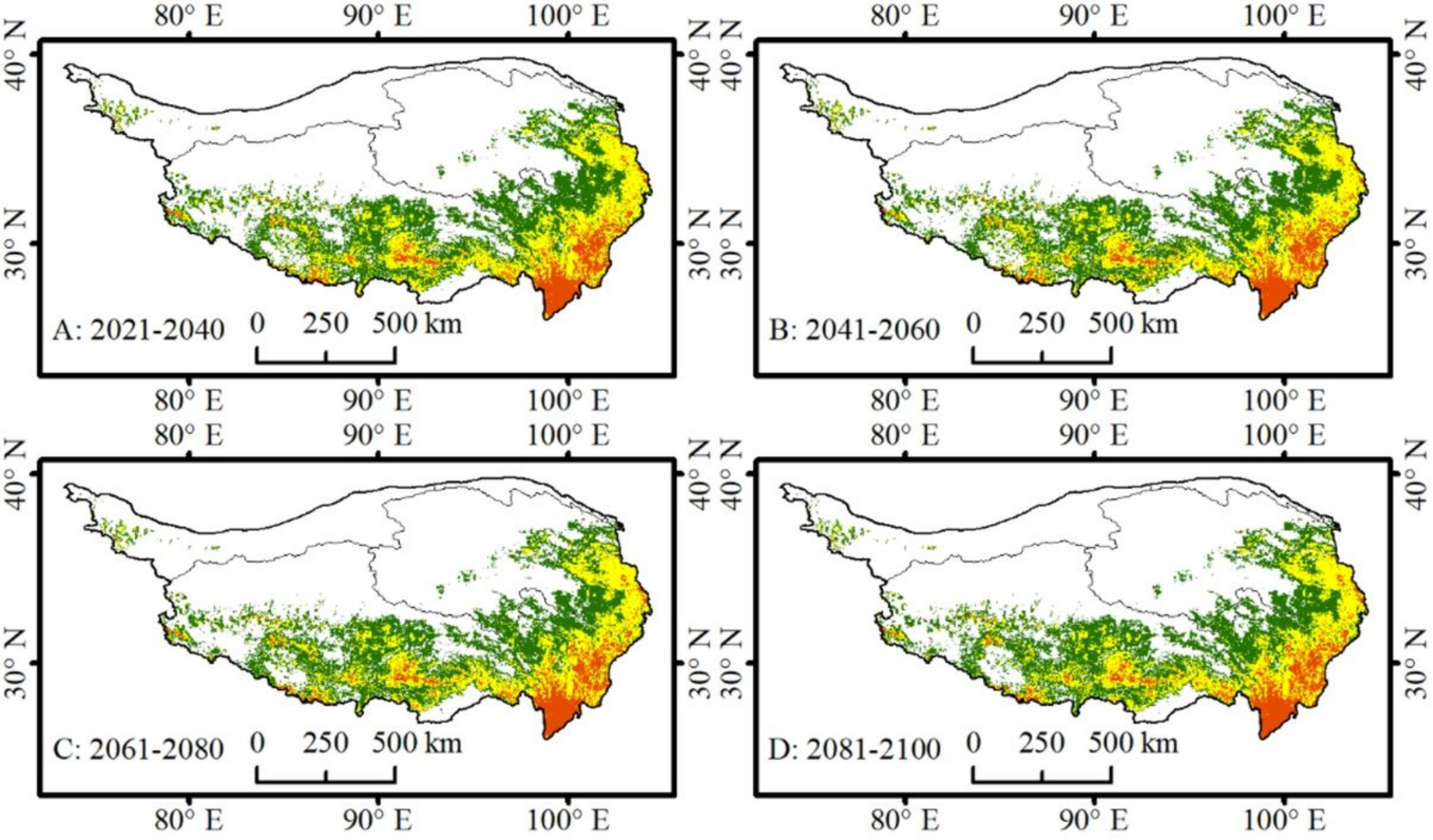

Figure 3

Occupied habitat maps of Bryophytes under future climate scenarios (the years of 2021-2040, 2041-2060, 2061-2080 and 2081-2100. The legends were same as Fig.2).

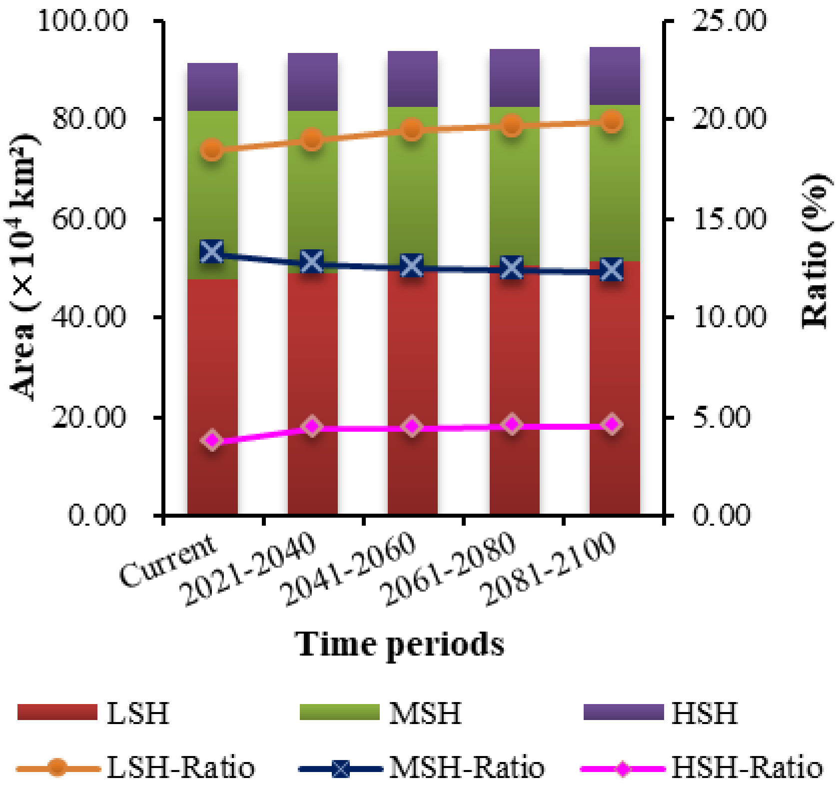

Figure 4

Variation of occupied areas and ratios of Bryophytes in different periods under SSP2-4.5 climate scenario for three habitat classes: LSH: Low suitable habitats; MSH: Middle suitable habitats; HSH: High suitable habitats.

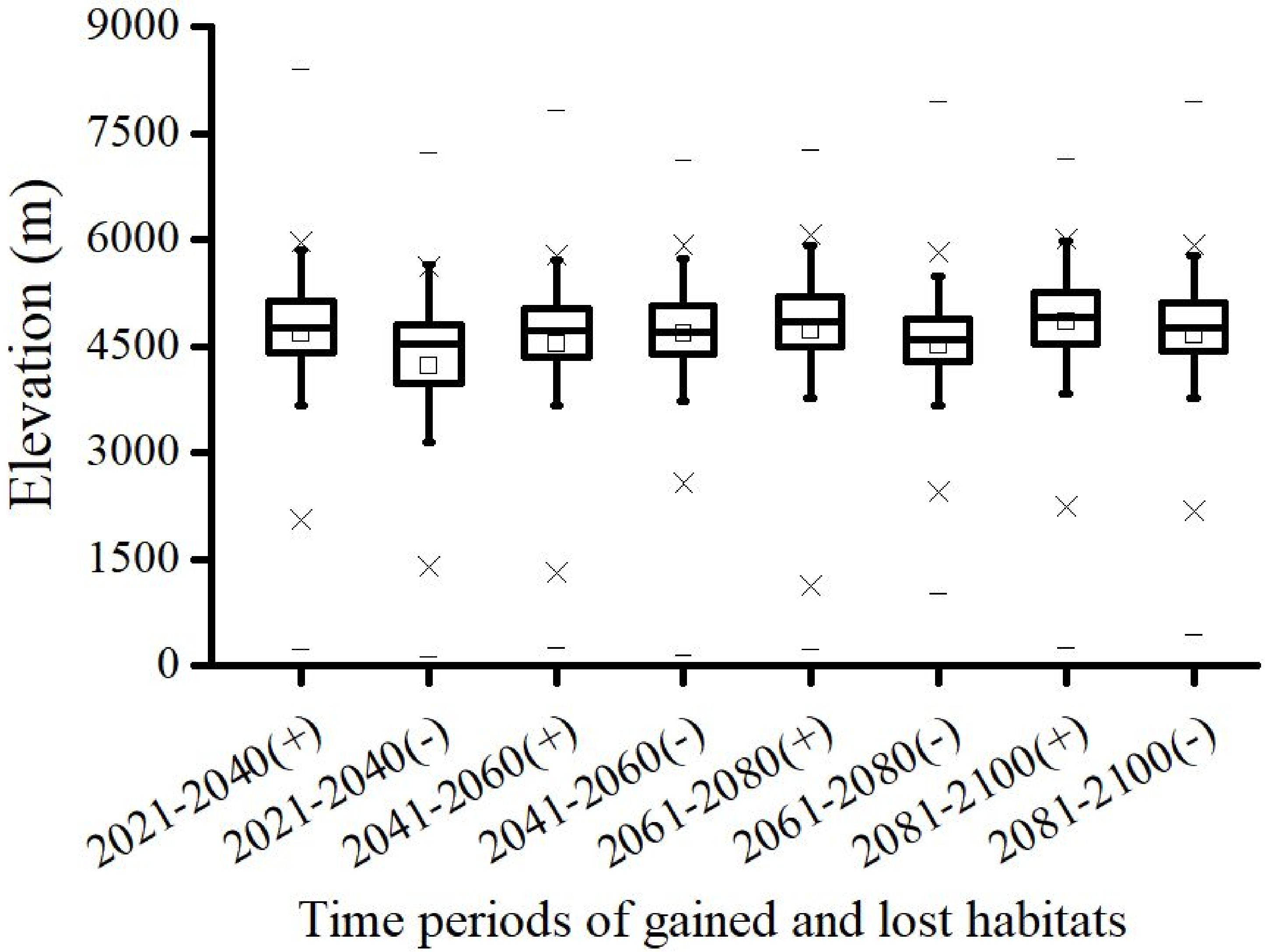

Figure 5

Box plot showed the elevation change in four future time periods. '+'and '-'represent the gained and lost habitats of Bryophytes relative to the former time period, respectively. The lower boundary of the box indicates the 25%, a line within the box marks the 50% (median), and the upper boundary of the box indicates the 75%.

Supplementary Files

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