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

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Research Article

Keywords: climate change, Bryophytes, Maxent, habitat suitability, environmental variables

Posted Date: August 10th, 2021

DOI: https://doi.org/10.21203/rs.3.rs-311954/v1
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 $9.12 \times 10^5$ 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 pre processes 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 Assessment 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 km²). 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](http://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 ≤ HSI < 0.5); (2) Medium suitable habitats (MSH, 0.5 ≤ HSI < 0.65); and (3) High suitable habitats (HSH, HSI ≥ 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 $0.9608 \pm 0.038_{SD}$ (Table 2). The results suggested that the performance of Maxent model was excellent.

![Table 2](image)

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 $9.12 \times 10^5 \text{ km}^2$ (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* (Martinez-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: ×10^4 km²).

| 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 $9.12 \times 10^5 \text{ km}^2$ (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**

**Acknowledgments**

This research was funded by the National Natural Science Foundation of China (41690142; 41771076, 41671070). The logistical supports from the Cryosphere Research Station on the Qinghai-Tibet Plateau are especially appreciated.

**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"

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**Figures**
Figure 1

Study area and presence samples of Bryophytes
Figure 2

Potential distribution of Bryophytes under current climatic condition

![Diagram of Bryophytes distribution](image)

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%.

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