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Research article

Exploring the distribution and habitat preferences of Polytrichaceae (Bryophyta) in Tibet, China

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A R T I C L E I N F O

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A B S T R A C T

The Qinghai-Tibet Plateau stands as one of the most ecologically fragile and biodiversity-rich regions globally. Understanding the distribution of different taxa and their relationship with environmental factors is crucial for effective conservation and sustainable management. Polytrichaceae, a significant bryophyte family widely distributed in Tibet, displays distinct structural, morphological, and phylogenetic traits compared to other mosses. Despite its importance, the distribution of Polytrichaceae in Tibet and its correlation with environmental factors have yet to be explored. In this study, we used an optimized Maximum Entropy (MaxEnt) model to explore the potential suitable habitats of Polytrichaceae in Tibet, aiming to clarify their geographic distribution pattern as well as the key environmental influence factors. The model had high accuracy with an average Area Under the Curve (AUC) of 0.933 and True Skill Statistics (TSS) value of 0.789. The results showed that the potential suitability habitats of Polytrichaceae were mainly located in southeastern Tibet, and the low suitable, moderately suitable, and highly suitable habitats accounted for 12.53 %, 6.84 %, and 3.31 % of the total area of Tibet respectively. Unsuitable habitats were mainly located in northwestern Tibet, accounting for about 77.32 %. In Tibet, temperature factors (Mean Temperature of Coldest Quarter (Bio11) and Annual Mean Temperature (Bio1)) played a pivotal role in determining the potential suitable habitats for Polytrichaceae, and elevation, precipitation, and vegetation coverage also had an important influence. The family preferred warm, moist and densely vegetated habitats in Tibet. This study enriched our ecological understanding of bryophyte ecology in this region and provided data-driven support for biodiversity conservation and ecosystem management in Tibet.

List of Standard Abbreviations

Full Name	Abbreviation

(*continued on next page*)

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(*continued*)

Full Name	Abbreviation
Akaike Information Criterion Corrected	AICc
Annual Mean Temperature	Bio1
Annual Precipitation	Bio12
Area Under the Curve	AUC
Environmental niche models	ENMs
Feature classes	FC
Global Positioning System	GPS
Hinge	H
Isothermality	Bio3
Linear	L
Maximum Entropy	MaxEnt
Mean Diurnal Range	Bio2
Mean Temperature of Coldest Quarter	Bio11
Mean Temperature of Warmest Quarter	Bio10
Normalized Difference Vegetation Index	NDVI
Precipitation of Driest Quarter	Bio17
Precipitation of Wettest Quarter	Bio16
Precipitation Seasonality (Coefficient of Variation)	Bio15
Product	P
Quadratic	Q
Receiver Operating Characteristic	ROC
Regularization multipliers	β
Solar Radiation in January	Srad01
Solar Radiation in July	Srad07
Species distribution models	SDMs
Temperature Annual Range	Bio7
Threshold	T
True Skill Statistics	TSS

1. Introduction

Tibet, situated as the central region of the Qinghai-Tibet Plateau, harbors rich biodiversity, distinct climatic conditions, and varied landscapes, capturing the interest of numerous ecologists and conservationists [1]. However, owing to the delicate nature of Tibet's ecosystem, the tasks of ecological conservation and management are notably specialized and intricate [2]. Bryophytes represent the second largest group of land plants and thrive across diverse terrestrial habitats, spanning from tropical zones to the Arctic and Antarctic regions [3]. It is crucial to recognize that the distribution and habitat preferences of various moss taxa are frequently restricted by specific climatic and environmental ranges [4]. Bryophytes play multiple ecological roles in ecosystems, including soil conservation, water cycle regulation, climate regulation and biodiversity maintenance [5–7]. Therefore, acquiring a comprehensive understanding of the distribution of different bryophyte taxa and their environmental influencing factors is imperative for upholding the stability of Tibet's ecosystem and attaining sustainable management.

The Polytrichaceae family, the sole family in the order Polytrichales of the class Polytrichopsida, is characterized by its considerable diversity, comprising approximately 200 species across 19 genera [8–10]. Polytrichaceae exhibits a nearly worldwide distribution covering almost all climate zones except for lowland tropical areas [11,12]. The family includes numerous relatively large species that have good shade tolerance and are also well adapted to high-light environments, and can become the pioneer species in clear-cut habitats [13]. These species often serve as pioneer vegetation in freshly cleared habitats, playing crucial roles in ground cover within diverse ecosystems, including Northern Hemisphere forests, sub-arctic heathlands, alpine regions with snowbeds, and tundra landscapes [12,14–16]. Polytrichaceae species have been observed to be distinct from other mosses in terms of photosynthetic traits and capacities and light requirements [17]. While most mosses are ectohydric, relying primarily on external (whole plant surface) water transport [18], and are small in size and simple in structure, members of the Polytrichaceae are endohydric mosses with relatively large gametophytes and complex structures [11]. Polytrichaceae exhibit a well-developed internal water conduction system within their stem that enhances hydraulic conductivity and the ability to efficiently redistribute water, which is functionally similar to the vascular plants but relatively rare among mosses [19,20]. The presence of a "pseudo-mesophyll" layer on the lamina further supports the family's high photosynthetic rates in moist, well-illuminated environments [21,22]. Recent interest has surged in exploring the phylogenetic relationships, structure, and functions of various Polytrichaceae species, making them valuable subjects for comparative studies on vascular endohydry in bryophytes and tracheophytes, and exploring potential homologies between these groups [10,19,23,24]. Despite the growing research focus, the precise interplay between environmental conditions and the Polytrichaceae family remains somewhat elusive, necessitating further investigation.

Previous studies have focused on the high species richness of Polytrichaceae in Tibet, garnering significant attention from bryologists [25,26]. Currently, seven of the eight Polytrichaceae genera identified in China are also found in Tibet [27,28]. Recent studies have supported the status of the Himalayas as one of the global centers of diversity of this family [29]. Furthermore, species of this family have been identified as potentially valuable ecological indicators for assessing the impacts of forest harvesting on habitat and ecosystem restoration [13]. Therefore, Polytrichaceae plays a crucial role in ecosystem research and biodiversity conservation efforts. The extensive topographic and climatic diversity of Tibet provides a unique opportunity to investigate the habitat preferences and environmental determinants of Polytrichaceae.

Environmental niche models (ENMs) and species distribution models (SDMs) quantify statistical relationships between species observed and their environmental conditions, emerging as crucial tools for assessing ecological preferences or predicting potential species distribution of species [30,31]. The Maximum Entropy (MaxEnt) algorithm, based on the principle of maximum entropy [32], is known for its capacity to utilize species presence-only data and a set of environmental variables to make highly accurate predictions of potential distribution [33–35]. Building MaxEnt models has become a common approach for species distribution predictions and conservation [36–38]. In this paper, we built an optimized MaxEnt model based on species occurrence data from extensive field surveys in Tibet, predicted and analyzed the potentially suitable habitats of Polytrichaceae in Tibet, and identified the critical environmental factors affecting their distribution.

2. Materials and methods

2.1. Study area

The Tibet Autonomous Region, situated in the southwest of China between 26°50′-36°53′ N and 78°25′-99°06′ E, covers an area of approximately 1,202,800 km^2. Positioned in the southwestern region of the Qinghai-Tibetan Plateau, Tibet boasts an average elevation exceeding 4000 m. The climate of the area, influenced by topography, landforms, and atmospheric circulation, is complex and distinctive, displaying strong regional distribution patterns and significant seasonal variations in temperature and precipitation. The average annual temperature progressively decreases from southeast to northwest, along with substantial variations in annual precipitation, exceeding 800 mm in the southeast and dropping to less than 100 mm in the northwest. Summers are characterized by warm and humid conditions, while winters are cold and dry [39]. Consequently, Tibet's vegetation aligns with this climatic gradient, transitioning from forests in the southeast to central moist alpine meadows and steppe, and further to cold, arid desert steppe in the northwest [40].

2.2. Species occurrence records

We conducted field surveys in Tibet from July to August annually between 2015 and 2020, collecting bryophyte specimens and recording geographic coordinates using a handheld Global Positioning System (GPS). Our surveys encompassed seven subareas in Tibet—Lhasa, Shigatse, Chamdo, Ngari, Nagqu, Shannan, and Nyingchi—spanning significant elevational and environmental gradients from 721 m to 5325 m above sea level. We selected 696 sampling points under typical vegetation types along the main roads in Tibet based on geographic accessibility and made additional collections in the surrounding areas to cover as much bryophyte habitat as possible. These points were situated tens to hundreds of meters from the roads, representing diverse vegetation types including

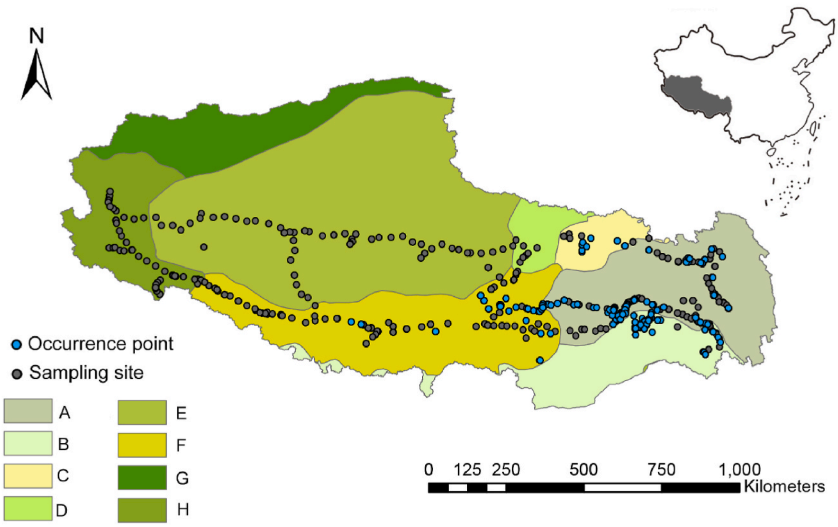

Fig. 1. Study area and sampling sites of Polytrichaceae in Tibet, China. Gray points indicate our field survey sampling sites, and blue points indicate the occurrence points of Polytrichaceae used in model running. A: subtropical mountain cold temperate coniferous forest zone; B: northern tropical seasonal forest, semi-evergreen rainforest zone; C: alpine shrubland and meadow zone; D: alpine meadow zone; E: alpine grassland zone; F: temperate grassland; G: alpine desert zone; H: temperate desert zone. Base map redrawn from the Resource and Environmental Sciences and Data Centre (https://www.resdc.cn/data.aspx?DATAID=133). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

subtropical mountain cold temperate coniferous forest, northern tropical seasonal forest, semi-evergreen rainforest, alpine shrubland and meadow, alpine meadow, alpine grassland, temperate grassland, and temperate desert zones (Fig. 1). In the identification and classification of the 1023 collected specimens from the Polytrichaceae family, we utilized classical taxonomic methods, referencing key literature such as the "Flora Bryophytorum Sinicorum" and the "Bryophyte Flora of Tibet". Each specimen was carefully examined and classified using a high-resolution microscope to ensure accurate identification. To support precise documentation and future referencing, each specimen was assigned a unique voucher number. These voucher specimens have been deposited in the China Agricultural University (BAU), where they have been authenticated by certified botanists specializing in bryophytes. For spatial thinning of species occurrence records, we used the R package "spThin" [41] in R v4.2.1 [42], generating datasets with minimum spatial intervals of 1 km, 2 km, 3 km, 4 km, 5 km, and 6 km between occurrence locations.

2.3. Environmental variables

In this study, 17 environmental variables were selected that are potentially relevant to the distribution for Polytrichaceae. These included elevation and ten bioclimatic variables: Annual Mean Temperature (Bio1), Mean Diurnal Range (Bio2), Isothermality (Bio3), Temperature Annual Range (Bio7), Mean Temperature of Warmest Quarter (Bio10), Mean Temperature of Coldest Quarter (Bio11), Annual Precipitation (Bio12), Precipitation Seasonality (Bio15), Precipitation of Wettest Quarter (Bio16), and Precipitation of Driest Quarter (Bio17); solar radiation (kJ m^{-2} day^{-1}) for June and December; elevation; and Vegetation Cover Index (NDVI) for the 2017 growing season (March–November). Additionally, three soil variables were considered: soil organic carbon ($\times$ 5 g/kg), soil water content (volumetric %) for 33 kPa, and soil pH at a depth of 0 m. The bioclimatic, solar radiation, and elevation data were sourced from the WorldClim dataset (http://www.worldclim.org) [43] with a spatial resolution of 30 s (ca. 1 km) recorded from 1950 to 2000. NDVI data with a 1 km spatial resolution, were obtained from the Resource and Environmental Sciences and Data Centre (https://www.resdc.cn). These data were resampled with a spatial resolution of 30 s. Soil data, initially at a resolution of 250 m, were retrieved from Zenodo (https://zenodo.org) and then resampled to match the 30-s spatial resolution for consistency.

2.4. Establishment, optimization and evaluation of model

In this study, we optimized the MaxEnt model by carefully selecting the most appropriate occurrence dataset and fine-tuning the parameters. Initially, we developed seven models using MaxEnt 3.4.1 software, each based on different thinning levels of species occurrence data. The first model was built using the 'Remove duplicate presence records' setting in MaxEnt [44], eliminating multiple records of Polytrichaceae within the same grid cell (30 s). Subsequent models were built based on six spatially thinning levels as described in 2.2. 75 % of data were selected for model training, the rest 25 % for model testing [32], and the other parameters were at default settings. We compared the AUC (Area Under the Curve) [44] and TSS (True Skill Statistics) [45] values of these models to determine the optimal thinning level. TSS was calculated based on MaxEnt model output using the formula (TSS = Sensitivity + Specificity - 1) according to Allouche et al. [45]. Further, the ENMeval package was used to evaluate different combinations of regularization multipliers (β) and feature classes (FC) to optimize the model parameters [46]. β and FC are two significant parameters that affect the performance of the Maxent model [32,47]. In the default parameters setting, β value is 1 and the selection of FC is related to the number of species distribution points [48]. By default, MaxEnt uses the presence count to determine which feature categories to use. The higher the presence count, the more feature categories are used; if the presence count is greater than 80, all feature categories are used. Furthermore, there is an option to manually specify feature categories [34]. Using the default auto-configuration may not be appropriate for all taxa, so it is important to evaluate and optimize the model parameters [34,49]. We collected 10,000 background points from study areas, dividing occurrences with the checkerboard1 method to reduce spatial-autocorrelation between points. We tested different combinations of 8 β (viz. 0.5, 1.0, 1.5, 2.0, 2.5, 3.0, 3.5, 4.0) and 6 FC: 'L', 'H', 'LQ', 'LQH', 'LQHP', 'LQHPT' (L = linear; Q = quadratic; H = hinge; P = product; T = threshold). The performance of 48 models was evaluated using the Akaike Information Criterion corrected (AICc), with the model exhibiting the smallest AICc value (delta AICc = 0) being considered the best. Finally, using the optimal spatial thinning level of occurrence datasets and the optimized model parameters, we built the final MaxEnt model. This model was trained for ten repetitions using cross-validation and the final result was the average of the ten repetitions. The final model 's performance was evaluated using AUC and TSS values [44]. The AUC value ranges from 0 to 1 and the accuracy of the model modeling results is proportional to the AUC value. TSS value ranges from −1 to +1, where +1 indicates perfect agreement and values of 0 or less indicate a performance no better than random [44]. The model generated habitat suitability values (*p*) ranging from

Table 1
Comparison of the Maximum Entropy (MaxEnt) model performance of different spatial thinning levels of species occurrence.

Spatial thinning level	Number of occurrences	Training AUC	Test AUC	True Skill Statistics (TSS)
30 s	202	0.966	0.936	0.819
1 km	165	0.961	0.944	0.776
2 km	141	0.965	0.919	0.817
3 km	128	0.964	0.918	0.732
4 km	117	0.954	0.959	0.716
5 km	112	0.951	0.942	0.846
6 km	100	0.966	0.936	0.840

Note: "30 s" represents a spatial thinning interval of 30-arcsecond, about 1km at the Equator.

0 to 1, where 0 is the least suitable and 1 is the most suitable [50,51]. We used ArcGIS to convert the ASC file output by MaxEnt into a raster file and applied Jenks' natural breaks method [52,53] to reclassify habitat suitability into four classes: unsuitable area ($p \leq 0.10$), low suitable area ($0.10 < p \leq 0.31$), moderately suitable area ($0.31 < p \leq 0.60$), highly suitable area ($0.60 < p$).

3. Results

3.1. Model optimization and accuracy evaluation

In this study, we developed seven initial models based on species occurrence datasets of different spatial thinning levels. The results showed that AUC values varied minimally among the models, with both training AUC and testing AUC surpassing 0.9 (Table 1). Notably, the highest TSS value was observed at the 5 km thinning level (TSS = 0.846), indicating that this level provided the best balance between sensitivity and specificity for prediction. Therefore, we selected the 5 km level for building the final model. Optimization of the model parameters showed that only one model met our selection criteria of the delta AICc = 0 with the β = 0.5 and FC = LQ (Fig. 2). The final model's mean AUC of 10 repeated runs was 0.933, with a standard deviation of 0.017 (Fig. 3) and a mean TSS of 0.789 (Table 2). The model demonstrated strong performance and high predictive accuracy, effectively forecasting potential suitable habitats for Polytrichaceae in Tibet.

3.2. Potential suitable habitats distribution

In this study, we identified 31 species (including two varieties) in seven genera of Polytrichaceae from Tibet (Table 3). According to the MaxEnt model prediction, the potential suitable distribution area of Polytrichaceae in Tibe was shown in Fig. 4. The prediction was aligned with the actual distribution observed during our field surveys. The distribution of the Polytrichaceae across Tibet was notably uneven, with suitable habitats primarily found in the southeastern region. Highly suitable areas were predominantly along major rivers, such as the Yarlung Tsangpo, Lancang, and Nujiang Rivers. In contrast, much of the entire northwestern region was characterized as unsuitable habitat for Polytrichaceae. Specifically, the areas of low, moderately, and highly suitable habitats were about 150,711 km^2, 82,272 km^2, and 39,813 km^2 respectively, accounting for 12.53 %, 6.84 % and 3.31 % of the total area of Tibet. In stark contrast, the unsuitable habitat covered approximately 930,005 km^2, accounting for 77.32 % of Tibet's total land area.

3.3. Environmental variable contributions

The jackknife test results illuminated the impact of various environmental variables on the development of the MaxEnt model (Fig. 5). Key variables that influenced the model's performance included Bio11, Bio1, elevation, and NDVI, all of which exhibited significant gains when assessed in isolation, underscoring their substantial independent predictive contributions. Additionally, Bio7, Bio10, Bio12 and Bio16 also made notable contributions. Notably, the environmental variable with the highest gain when used in isolation was Bio11, which, therefore, appeared to have the most useful information in itself. The environmental variable that decreased the gain the most when it was omitted was Bio17, which, therefore, appeared to have the most information that wasn't present in the other variables.

3.4. Response to key environmental variables

Response curves depicted the relationships between key environmental variables and the probability of Polytrichaceae presence in Tibet (Fig. 6). Each curve was generated by using solely the corresponding variable. The results showed that with the increase of the values of environmental variables, the probability of occurrence of prediction increased first, reached the peak, and then decreased as the values of environmental variables continued to increase. When the Tau value was greater than 0.63, it corresponded to what MaxEnt considered to be "typical" location environmental conditions for Polytrichaceae in Tibet [54]. The designated ranges for these

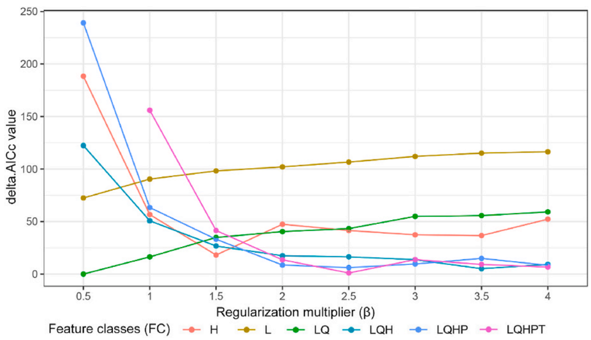

Fig. 2. Evaluation metrics of Maximum Entropy (MaxEnt) model generated by ENMeval. The x-axis represents 8 different Regularization multipliers (β), while the y-axis corresponds to the delta AlCc values.

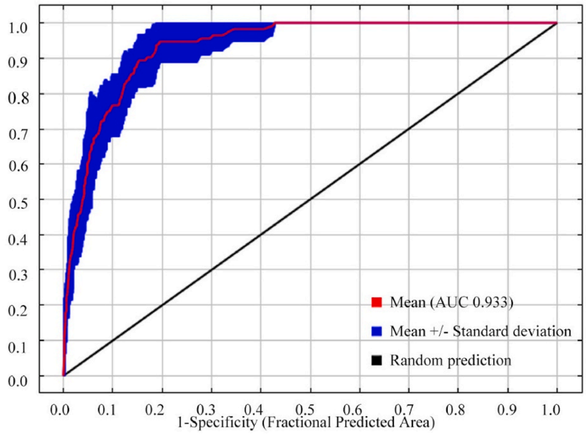

Fig. 3. Receiver Operating Characteristic (ROC) curve and Area Under the Curve (AUC) values of the Maxent model. The red curve indicates training data, the blue curve indicates test data, and the black line indicates random prediction. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 2
Average TSS value from ten iterations of the MaxEnt model.

Models	TSS
Polytrichaceae_0	0.656
Polytrichaceae_1	0.818
Polytrichaceae_2	0.839
Polytrichaceae_3	0.783
Polytrichaceae_4	0.862
Polytrichaceae_5	0.726
Polytrichaceae_6	0.718
Polytrichaceae_7	0.823
Polytrichaceae_8	0.816
Polytrichaceae_9	0.853
	Mean = 0.789

key environmental variables were Bio1 (3.2–18.4 °C, Fig. 6a), Bio7 (23.1–31.0 °C, Fig. 6b), Bio10 (11.0–25.9 °C, Fig. 6c), Bio11 (−5.2 to 11.0 °C, Fig. 6d), Bio12 (623–2050 mm, Fig. 6e), Bio16 (364–1141 mm, Fig. 6f), NDVI values (0.6–1, Fig. 6g), and elevation (897–3966 m, Fig. 6h).

4. Discussion

In this study, we employed an optimized MaxEnt model to estimate the potential suitable habitats for Polytrichaceae in Tibet and obtained reliable results. The species occurrence data we collected were obtained through relatively extensive field surveys, with GPS used to locate species distribution points accurately, rather than relying on literature or database information, thereby enhancing the reliability of the model. A large number of species occurrence points allowed us to explore the effect of different spatial thinning levels on modeling accuracy in our study area. Conducted across a significant environmental gradient, our research and field further improving the model's explanatory or predictive capacity [55,56]. Our findings closely aligned with the previous preliminary findings of Xu et al. [26] and corresponded well with our field observations. In particular, the model predicted that Yadong County in southern Tibet as a suitable distribution area for Polytrichaceae. Although our field survey did not cover this area, previously reported distribution records of this family (e.g. *Pogonatum microstomum* (R. Br. ex Schwägr.) Brid.) [57], substantiate our model's high accuracy. It's important to acknowledge that due to terrain and transportation constraints, our surveys did not cover the low-altitude areas of Tibet, particularly those below 700 m. Given the distinct natural geographic conditions of these regions compared to the rest of Tibet, our results might not fully reflect the distribution patterns of Polytrichaceae in these low-elevation areas. Furthermore, anthropogenic land-use changes could influence actual plant distribution patterns, underscoring the need to consider these limitations fully when interpreting our findings.

We observed that the distribution of Polytrichaceae in Tibet was uneven, with their potential suitable habitats primarily located in the southeast (Fig. 4). Bryophytes are a highly diverse group of plants on the Qinghai-Tibetan Plateau and exhibit a wide distribution range [58]. However, different taxa may show different distribution patterns [59]. For instance, genera such as *Bryoerythrophyllum* and *Didymodon* belonging to the Pottiaceae family were found to have extensive potential suitable habitats in Tibet, particularly in central

Table 3
List of species of Polytrichaceae from the field survey in this study.

Genus	Species
Atrichum	*Atrichum crispulum* Schimp. ex Besch.
	Atrichum rhystophyllum (Müll. Hal.) Paris
	Atrichum subserratum (Hook.) Mitt.
	Atrichum yakushimense (Horik.) Mizut.
	Atrichum undulatum var. *gracilisetum* Besch.
Delongia	*Delongia glacialis* (C.C. Towns.) N.E. Bell, Kariyawasam, Hedd. & Hyvönen
Lyellia	*Lyellia crispa* R. Br.
	Lyellia platycarpa Cardot & Thér.
Oligotrichum	*Oligotrichum aligerum* Mitt.
	Oligotrichum crossidioides P. C. Chen & T. L. Wan ex W. X. Xu & R. L. Xiong
	Oligotrichum falcatum Steere
	Oligotrichum obtusatum Broth.
Pogonatum	*Pogonatum cirratum* (Sw.) Brid.
	Pogonatum contortum (Brid.) Lesq.
	Pogonatum fastigiatum Mitt.
	Pogonatum inflexum (Lindb.) Sande Lac.
	Pogonatum microstomum (R. Br. ex Schwägr.) Brid.
	Pogonatum neesii (Müll. Hal.) Dozy
	Pogonatum nudiusculum Mitt.
	Pogonatum perichaetiale (Mont.) A. Jaeger
	Pogonatum perichaetiale var. *thomsonii* (Mitt.) Hyvönen
	Pogonatum proliferum (Griff.) Mitt.
	Pogonatum subfuscatum Broth.
	Pogonatum urnigerum (Hedw.) P. Beauv.
Polytrichastrum	*Polytrichastrum alpinum* (Hedw.) G. L. Sm.
	Polytrichastrum emodi G. Sm.
	Polytrichastrum formosum G. L. Sm.
	Polytrichastrum ohioense (Renauld & Cardot) G. L. Sm.
	Polytrichastrum papillatum G. L. Sm.
	Polytrichastrum xanthopilum (Wilson ex Mitt.) G. L. Sm.
Polytrichum	*Polytrichum juniperinum* Hedw.
	Polytrichum piliferum Schrad. ex Hedw.

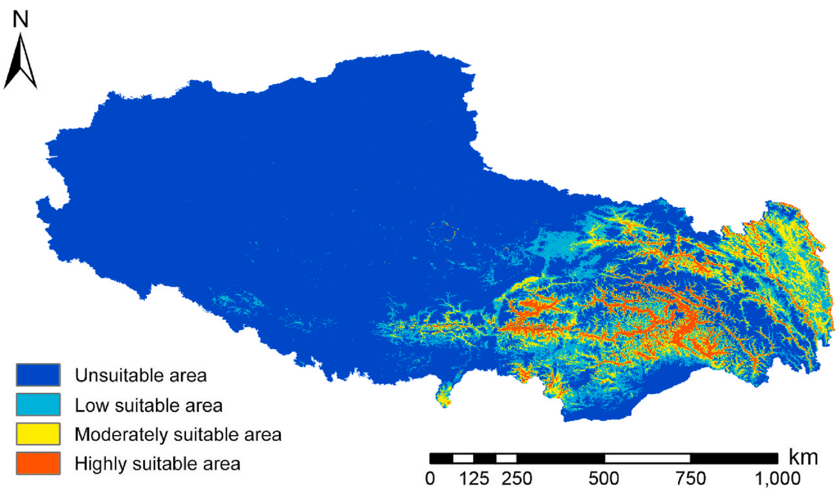

Fig. 4. Potential suitable distribution of Polytrichaceae in Tibet.

areas [60]. This difference in distribution pattern led us to consider the underlying driving factors. Significant differences in gametophyte size, leaf shape and structure, and cellular morphology between Polytrichaceae species and those of *Bryoerythrophyllum* and *Didymodon* contribute to diverse water-use strategies and photosynthetic mechanisms. These morphological and functional differences likely serve as key drivers of their different distribution patterns in Tibet [61]. Moreover, bryophyte distribution patterns might also be influenced by their evolutionary history [62]. Future research into the origins, evolution, and migration processes of different taxa could enhance our understanding of bryophyte distribution patterns on the Tibetan Plateau and the mechanisms of diversity formation.

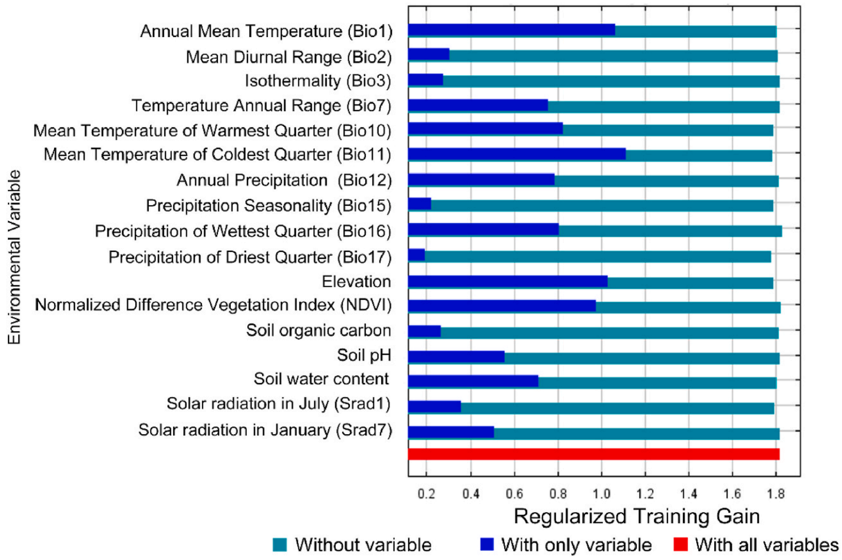

Fig. 5. Variable importance based on Jackknife tests. The vertical axis represents the screened environmental variables, and the horizontal axis represents the score of each environmental variable. The dark blue column represents the model score with only this environmental factor existing, the light blue column represents the sum of the scores of other variables except for this variable, and the red represents the sum of all variable's scores. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Our research findings demonstrated the collective impact of bioclimate, elevation, and vegetation factors on the distribution of Polytrichaceae in Tibet (Fig. 5). Specifically, low temperatures restricted the distribution of this family to higher elevations and colder conditions, and they preferred relatively warmer habitats (Fig. 6a–d), which might be related to their high photosynthetic optimum temperature [63]. Recent studies found that Polytrichaceae species were highly sensitive to humidity, necessitating relatively humid environmental conditions for their photosynthetic processes [19]. This observation is consistent with our results, indicating that suitable habitats for Polytrichaceae were predominantly concentrated along the river valleys in southeastern Tibet (Fig. 4). The presence of major rivers in this region aids in the transportation of significant amounts of water vapor, creating favorable conditions for the growth of Polytrichaceae [64,65]. Conversely, the limited water vapor transfer in the interior northwestern areas of Tibet renders this vast area unsuitable for the family. Thus, ample precipitation plays a pivotal role in determining the distribution of Polytrichaceae in Tibet.

Vegetation significantly influenced the distribution of Polytrichaceae, with increased vegetation cover enhancing the habitat suitability (Figs. 5 and 6). Notably, specific bryophyte taxa exhibit rapid responses to environmental changes through their presence or absence in the ecosystem [66]. Previous research has demonstrated that the distribution of a species of Polytrichaceae was closely related to vegetation coverage, and forest logging on the eastern Tibetan Plateau could significantly promote the invasion, establishment, and development of this population in cutover areas [13]. Due to its large size, Polytrichaceae is easily monitored compared to other taxa, and its distinctive morphology allows for straightforward identification, making it practical for forest managers with limited expertise in mosses. As a prevalent and widely distributed pioneer moss in boreal and temperate coniferous forests, Polytrichaceae has the potential to serve as an effective bioindicator for monitoring forest dynamics on the Qinghai-Tibet Plateau. This could be particularly valuable for assessing the impacts of anthropogenic environmental changes [13,67–69].

As a special group of vegetation, bryophytes have attracted significant attention for their adaptive capacity and ecological roles in extreme environments. They play a crucial role in maintaining ecosystem stability and biodiversity on the Qinghai-Tibetan Plateau. Environmental factors such as altitude, temperature, precipitation, and vegetation cover exert a substantial influence on bryophyte distribution [70–72], resulting in complex distribution patterns on the Qinghai-Tibet Plateau. However, the extensive and intricate topography of the Qinghai-Tibetan Plateau presents challenges for data collection and monitoring of ecosystem changes. The applications of modelling techniques have provided new research paths, especially for the rare or hard-to-observe species and inaccessible areas. The use of models not only accurately predicts the distribution of species, but also identifies biodiversity hotspots and provides support for determining priority areas for management and conservation actions [73–75]. It is noteworthy that model predictions necessitate consideration of the influence of data quality and parameter settings [32,76]. Consequently, integrating modelling techniques with field surveys and expert knowledge is essential to develop the most effective management strategies. Future research should prioritize the exploration of ecological attributes among different bryophyte taxa, integrating field observations to establish a comprehensive scientific foundation for conservation and management purposes.

5. Conclusion

Our study identified the suitable habitats for Polytrichaceae in Tibet and assessed the impact of environmental factors on its

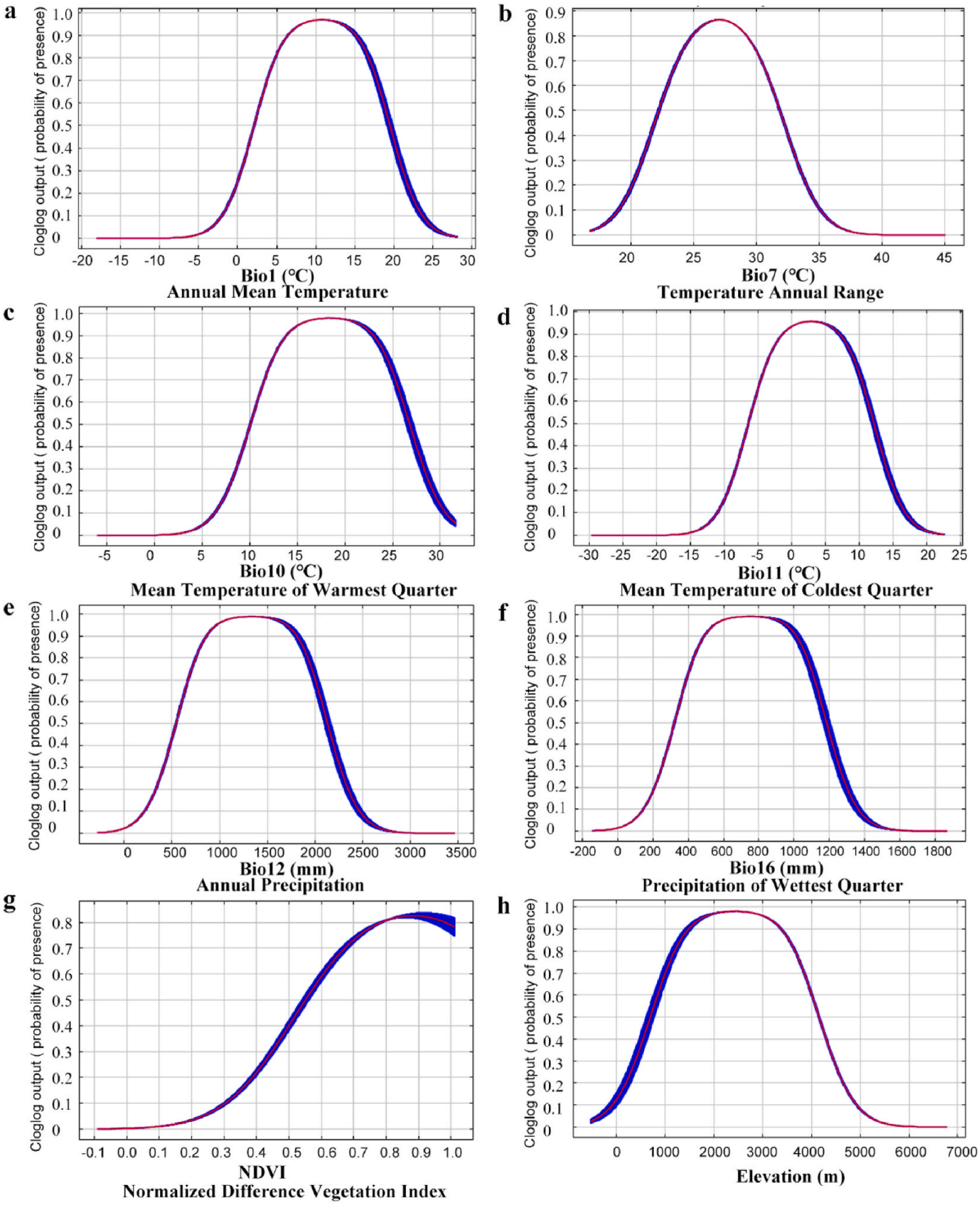

Fig. 6. Response curves of environmental variables to distribution probability of Polytrichaceae in Tibet. The curves show the mean response of the 10 replicate MaxEnt runs (red) and the mean ± standard deviation (blue, two shades for categorical variables). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

distribution. The distribution of Polytrichaceae in Tibet was found to be uneven, with the highly suitable habitats mainly concentrated in southeastern Tibet, particularly along the river valleys. Temperature was identified as a key factor influencing the habitat suitability of this family, with elevation, precipitation, and vegetation coverage also playing significant roles in their distribution. Polytrichaceae exhibited a preference for warm, moist, and densely vegetated habitats in Tibet. These findings offer valuable insights into the distribution patterns of bryophytes on the Qinghai-Tibet Plateau, serving as a valuable reference for future research and conservation initiatives.

Supporting information

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Data availability statement

Data will be made available on request.

CRediT authorship contribution statement

Xiaotong Song: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Jiqi Gu:** Writing – review & editing, Visualization, Software, Methodology, Investigation, Formal analysis. **Ling Liu:** Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Yujia Liao:** Validation, Software, Methodology, Investigation, Conceptualization. **Heping Ma:** Resources, Methodology, Investigation, Data curation. **Ruihong Wang:** Validation, Resources, Investigation, Data curation. **Yanhui Ye:** Validation, Supervision, Resources, Investigation, Formal analysis, Data curation. **Ji Li:** Supervision. **Xiaoming Shao:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of competing 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.

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