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Bryophyte Flora in Alpine Grasslands of the Qinghai–Tibet Plateau Based on Plot Sampling

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Abstract: The species number of bryophytes is the second highest among land plants. Alpine grasslands on the Qinghai–Tibet Plateau (QTP) are the largest among global alpine biomes. However, bryophyte flora in alpine grasslands on the QTP remains poorly explored relative to its large geographic extent. A total of 347 plots were surveyed across the QTP, and 149 bryophyte taxa in 24 families and 49 genera were recorded in alpine grasslands. The largest family was Pottiaceae, followed by Bryaceae and Brachytheciaceae. The most species-rich genus was *Bryum*, followed by *Didymodon* and *Brachythecium*. The dominant species were *Didymodon tectorus*, *Didymodon fallax*, *Bryum caespiticium*, *Didymodon constrictus*, and *Didymodon ditrichoides*. The Jaccard similarity indexes of bryophyte compositions between alpine meadow and alpine steppe at the family, genus, and species levels were 0.375, 0.367, and 0.282, respectively. Turf was the most common life-form (75.2%), followed by weft (16.1%) and cushion (5.4%). Endemic species to China accounted for 8.05% of the total taxa. Bryophyte diversity in alpine grasslands on the QTP is exceptional and irreplaceable. The changes in species composition and life-forms between different grassland types reflect the adaptations of bryophytes to harsh environments.

Keywords: alpine meadow; alpine steppe; diversity; life-forms; Qinghai–Tibet plateau

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1. Introduction

Bryophytes, including mosses, liverworts, and hornworts, are the earliest lineages among land plants and are widely distributed from the equator to polar regions. Due to the lack of vascular tissues, they usually have a small size and are thus ignored in biodiversity surveys. In fact, the species number of bryophytes is the second highest among land plants [1]. The unique morphological structure and physiological characteristics of bryophytes enable them to survive in extremely arid and cold environments [2–4]. In alpine ecosystems, bryophytes play important roles in soil water retention [5,6], sand fixation [7], and frozen soil protection [8].

The Qinghai–Tibet Plateau (QTP), with a total area of approximately 2.5 million km^2 and an average elevation of ca. 4000 m, is the largest and highest plateau in the world. Thus, it is well known as the roof of the world. Diverse biomes, such as forests, grasslands, deserts, and tundra, are distributed across the QTP. Of these, alpine grasslands, covering 60% of the total plateau, are the largest [9,10], even among global alpine biomes [11]. Alpine grasslands of the QTP are mainly distributed in the Xizang Autonomous Region (Tibet) and Qinghai Province of China, and they have vast ecological and socioeconomic value, such as nutrient cycling regulation, fresh water provisioning, biodiversity, and pastoral production [11]. In particular, the two primary grassland types on the QTP, i.e., alpine meadow (AM) and alpine steppe (AS) [11], have been identified as two ecoregions of global biodiversity conservation priority [12].

For a long time, poor traffic conditions, severe climate, and complex topography, as well as the paucity of bryologists, have hampered the investigation of bryophyte flora in alpine grasslands on the QTP. In recent years, an increasing amount of research has focused on the Tibet Plateau (TP). Song et al. [13] conducted a bryological survey across the TP and reported 22 *Didymodon* spp. (Pottiaceae), including a new record to China in the alpine grasslands of Tibet. Several new species from genera, including *Bryoerythrophyllum* [14]**,** *Didymodon* [15–17], and *Encalypta* [18], are continuing to be described from TP grasslands. However, the bryophyte survey of the Qinghai Plateau has received little attention [19]. Therefore, bryophyte flora in alpine grasslands on the QTP remains poorly explored relative to its large geographic extent.

Biodiversity is multidimensional, including species richness, abundance, and evenness [20]. Plot sampling (PS) is one of the methods used to explore biodiversity and is especially common in community ecology and vegetation science. It is not only used to answer which and where species exist but also to quantify which species are dominant in plant communities of a certain area by a robust statistical analysis. Cheng et al. [21] carried out intensive fieldwork based on PS covering 11 vegetation types on the QTP to reveal the species richness of vascular plants. Unfortunately, to our knowledge, no studies thus far have attempted to estimate bryophyte biodiversity in the alpine ecosystem on a broad scale. The present study surveyed bryophytes in alpine grasslands across the QTP based on PS. The objectives were to elucidate species composition, life-forms, and endemism and to compare diversity between different grassland types. The results will improve our knowledge of bryophyte flora in alpine grasslands on the QTP and provide new insights into conservation strategies for bryophytes in alpine grasslands.

2. Materials and Methods

2.1. Study Area

The study area lies between 28°12′ and 38°47′ N and 79°27′ and 102°16′ E in Tibet and Qinghai Province of China on the QTP, with elevations ranging from 2185 to 5505 m (Figure 1). The QTP has an arid and semi-arid alpine climate. The uneven precipitation on the plateau forms the vegetation patterns of AM, AS, and alpine desert steppe (ADS) from east to west [22]. AM is characterized by a cold and wet climate, and the annual precipitation can reach up to 600 mm, and it is consequently dominated by *Kobresia* spp. [23–25]. Most AS is characterized by a cold and arid climate, and the annual precipitation varies from 600 mm in the east to below 60 mm in the west; therefore, it is dominated by *Stipa* spp. [23,25,26]. ADS is distributed in the west plateau and dominated by *Ceratoides compacta*, where it receives little precipitation (<50 mm yr^{-1}) and environmental conditions are extremely harsh with little or low vegetation coverage [23,25,26].

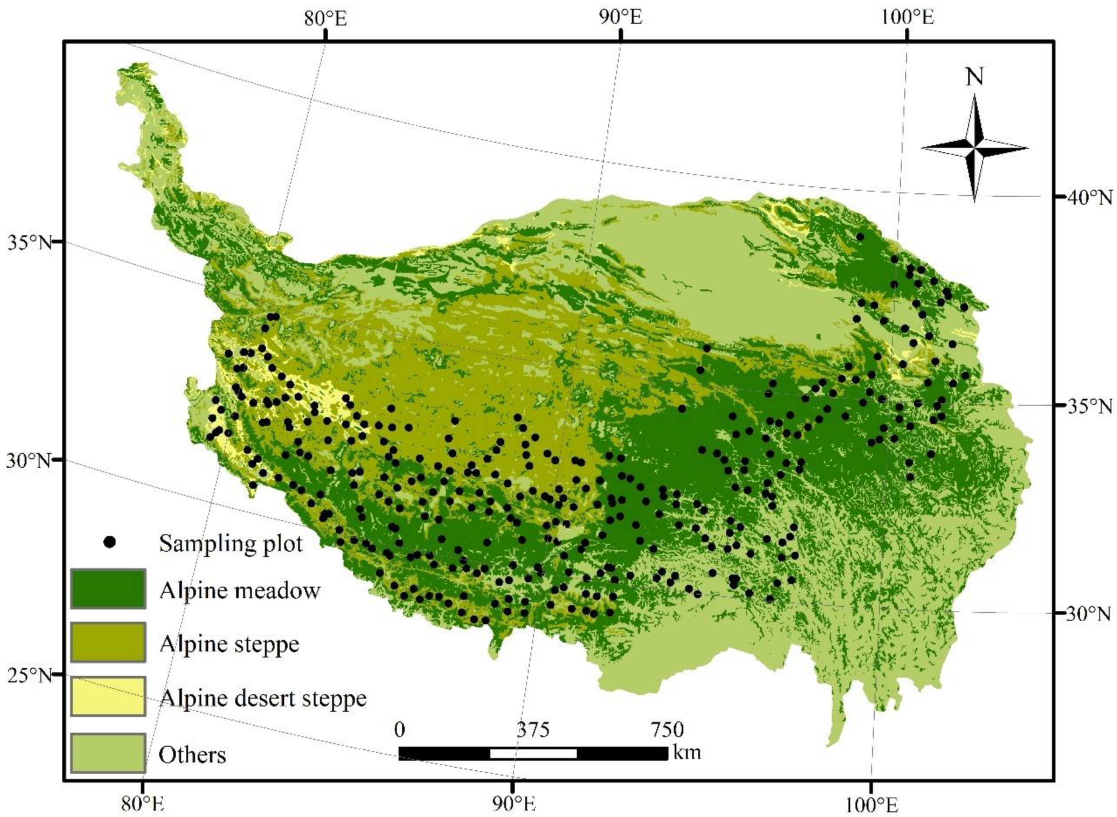

Figure 1. Sampling plots in alpine grasslands of the Qinghai−Tibet Plateau.

2.2. Plot Sampling

The PS of bryophyte flora in the alpine grasslands of the QTP was carried out from mid-July to late August 2019 and 2020. According to the Vegetation Map of China [22], plots were randomly selected at a scale of 0.5° × 0.5° grid cells. Based on the traffic accessibility, a total of 347 plots were selected, including 162 AS, 144 AM, and 41 ADS (Figure 1). A 20 m × 20 m plot was established, and its coordinates and elevation were recorded by a handheld GPS (Garmin, Beijing, China). A transparent plastic plate (20 cm × 20 cm) divided into 100 grids was used as the sampling quadrat. In each plot, 3–5 quadrats were randomly set. We collected all bryophytes and recorded the species cover in each quadrat. A total of 1454 quadrats were sampled. Since no bryophytes occurred in some harsh plots, 951 specimens were finally collected. They were taken back to the laboratory to identify the species level under a microscope and were stored in the Biological Herbarium of Chongqing Normal University (CTC). The nomenclature followed "Species 2000" (https://www.sp2000.org.cn/(accessed on 1 May 2023.).

2.3. Data Analysis

We used the importance value (IV), which was calculated as the average of the relative cover and relative frequency of a certain species in each plot, to identify the dominant species. Bryophyte life-forms followed those described by Bates [27] and Glime [28]. Since we unfortunately encountered any bryophytes in the sampling plots belonging to the ADS, we used the Jaccard similarity index (J) [29] to compare the floristic composition between AM and AS. It was calculated using the following formula: $J = c/(a + b - c)$, where a and b are the total number of families, genera, or species in AM and AS, respectively, and c is the number of families, genera, or species common to both grassland types.

3. Results

3.1. Species Composition and Dominant Species in Alpine Grasslands

Among the 347 investigated sampling plots, bryophytes were found in 199 of them, whereas none were found in the other plots, including 11 AM, 96 AS, and 41 ADS. In total, 149 bryophyte taxa in 24 families and 49 genera were recorded in the alpine grasslands of the QTP based on PS (Table 1). All of them were mosses. The largest family (i.e., species number > 10) was Pottiaceae (14 genera, 50 taxa), followed by Bryaceae (3, 26) and Brachytheciaceae (2, 12), accounting for 59.1% of the total number of taxa (Figure 2a). The most species-rich genus was *Bryum* (23 taxa), followed by *Didymodon* (14) and *Brachythecium* (11, Figure 2b). Details on the bryophyte families and genera are presented in Figure 2.

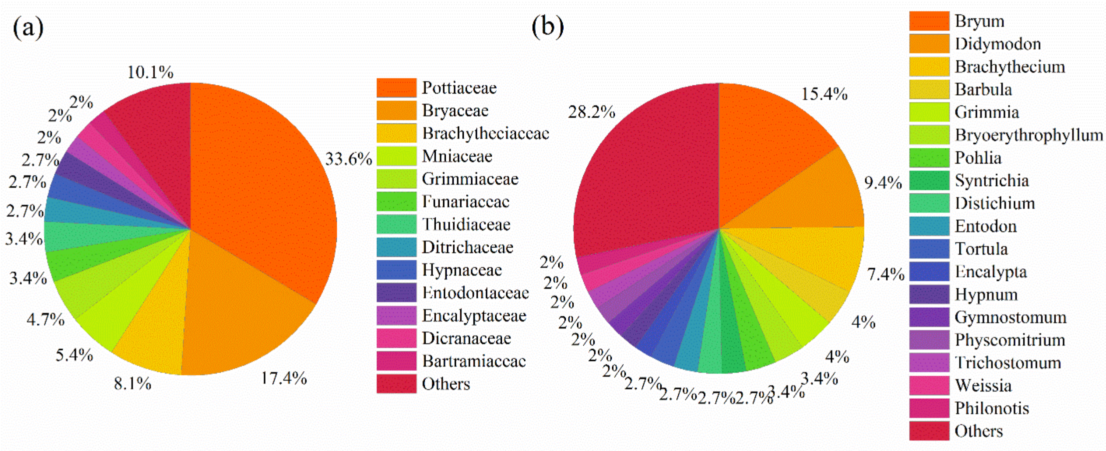

Figure 2. Composition of bryophyte families (**a**) and genera (**b**) in the alpine grasslands of the Qinghai—Tibet Plateau.

The top 10 dominant species in alpine grasslands were *Didymodon tectorus*, *Didymodon fallax*, *Bryum caespiticium*, *Didymodon constrictus*, *Didymodon ditrichoides*, *Bryum argenteum*, *Barbula gracilenta*, *Didymodon constrictus* var. *flexicuspis*, *Distichium brevisetum*, and *Didymodon michiganensis*. The rank of all bryophyte species based on IV is presented in Table 1.

Table 1. Bryophyte species, life-forms, cumulative importance value, and occurrence in grassland types in alpine grasslands of the Qinghai—Tibet Plateau. AM = alpine meadow; AS = alpine steppe.

No.	Family	Species	Life-Forms	Cumulative Importance Value	Grassland Types
1	Pottiaceae	*Didymodon tectorus*	Turf	25.255	AM, AS
2	Pottiaceae	*Didymodon fallax*	Turf	13.323	AM, AS
3	Bryaceae	*Bryum caespiticium*	Turf	11.866	AM, AS
4	Pottiaceae	*Didymodon constrictus*	Turf	10.044	AM, AS
5	Pottiaceae	*Didymodon ditrichoides*	Turf	10.019	AM, AS
6	Bryaceae	*Bryum argenteum*	Turf	6.873	AM, AS
7	Pottiaceae	*Barbula gracilenta*	Turf	6.110	AM, AS
8	Pottiaceae	*Didymodon constrictus var. flexicuspis*	Turf	5.567	AM, AS
9	Ditrichaceae	*Distichium brevisetum*	Turf	4.806	AM
10	Pottiaceae	*Didymodon michiganensis*	Turf	4.336	AM, AS
11	Bryaceae	*Bryum lonchocaulon*	Turf	4.029	AM, AS
12	Distichiaceae	*Distichium capillaceum*	Turf	3.031	AM, AS
13	Pottiaceae	*Didymodon asperifolius*	Turf	2.972	AM, AS
14	Pottiaceae	*Vinealobryum vineale*	Turf	2.958	AM, AS

15	Pottiaceae	*Didymodon rivicola*	Turf	2.813	AM, AS
16	Rhytidiaceae	*Rhytidium rugosum*	Weft	2.799	AM
17	Thuidiaceae	*Abietinella abietina*	Weft	2.761	AM
18	Thuidiaceae	*Haplocladium angustifolium*	Weft	2.735	AM
19	Bryaceae	*Bryum algovicum*	Turf	2.613	AM, AS
20	Entodontaceae	*Entodon challengeri*	Mat	2.260	AM
21	Pottiaceae	*Didymodon tophaceus*	Turf	2.256	AM, AS
22	Pottiaceae	*Aloina rigida*	Turf	2.242	AM, AS
23	Brachytheciaceae	*Brachythecium moriense*	Weft	2.217	AM
24	Brachytheciaceae	*Brachythecium populeum*	Weft	2.063	AM, AS
25	Pottiaceae	*Didymodon nigrescens*	Turf	2.003	AM, AS
26	Pottiaceae	*Gymnostomum calcareum*	Turf	1.961	AM, AS
27	Brachytheciaceae	*Brachythecium pulchellum*	Weft	1.873	AM, AS
28	Pottiaceae	*Weissia longifolia*	Turf	1.823	AM
29	Bryaceae	*Bryum alpinum*	Turf	1.732	AM, AS
30	Pottiaceae	*Didymodon vinealis var. vinealis*	Turf	1.731	AM, AS
31	Hypnaceae	*Hypnum revolutum*	Weft	1.676	AM
32	Brachytheciaceae	*Brachythecium coreanum*	Weft	1.498	AM
33	Pottiaceae	*Barbula yunnanensis*	Turf	1.476	AM, AS
34	Bryaceae	*Bryum uliginosum*	Turf	1.396	AM, AS
35	Pottiaceae	*Barbula unguiculata*	Turf	1.340	AM
36	Funariaceae	*Funaria hygrometrica*	Turf	1.327	AM, AS
37	Entodontaceae	*Entodon concinnus*	Mat	1.293	AM
38	Pottiaceae	*Barbula indica*	Turf	1.189	AM, AS
39	Pottiaceae	*Tortella tortuosa*	Turf	1.072	AM
40	Bryaceae	*Bryum pallescens*	Turf	1.017	AM, AS
41	Mniaceae	*Pohlia elongata*	Turf	1.017	AM
42	Pottiaceae	*Bryoerythrophyllum gymnostomum*	Turf	1.016	AM
43	Bryaceae	*Bryum paradoxum*	Turf	0.968	AM
44	Pottiaceae	*Weissia controversa*	Turf	0.904	AM
45	Pottiaceae	*Trichostomum crispulum*	Turf	0.851	AM, AS
46	Thuidiaceae	*Thuidium delicatulum*	Weft	0.794	AM
47	Pottiaceae	*Gymnostomum laxirete*	Turf	0.786	AM, AS
48	Bryaceae	*Anomobryum auratum*	Turf	0.775	AM, AS
49	Bryaceae	*Bryum cellulare*	Turf	0.768	AM, AS
50	Pottiaceae	*Syntrichia sinensis*	Turf	0.764	AM
51	Polytrichaceae	*Pogonatum perichaetiale*	Turf	0.734	AS
52	Bryaceae	*Bryum sauteri*	Turf	0.711	AM
53	Bryaceae	*Bryum pseudotriquetrum*	Turf	0.688	AM
54	Bryaceae	*Bryum arcticum*	Turf	0.671	AM, AS
55	Pottiaceae	*Tortella fragilis*	Turf	0.662	AM
56	Pottiaceae	*Bryoerythrophyllum brachystegium*	Turf	0.646	AM
57	Pottiaceae	*Gymnostomum calcareum*	Turf	0.639	AM, AS
58	Bryaceae	*Bryum dichotomum*	Turf	0.623	AM
59	Leucobryaceae	*Campylopus umbellatus*	Turf	0.605	AM
60	Ditrichaceae	*Distichium inclinatum*	Turf	0.589	AM
61	Pottiaceae	*Hymenostylium recurvirostrum*	Turf	0.585	AM
62	Hypnaceae	*Hypnum cupressiforme*	Weft	0.583	AM
63	Entodontaceae	*Entodon cladorrhizans*	Mat	0.573	AM
64	Bartramiaceae	*Philonotis thwaitesii*	Turf	0.547	AM
65	Hypnaceae	*Hypnum plumaeforme*	Weft	0.538	AM

66	Encalyptaceae	*Encalypta rhaptocarpa*	Turf	0.533	AM
67	Encalyptaceae	*Encalypta spathulata*	Turf	0.521	AM
68	Pottiaceae	*Syntrichia ruralis*	Turf	0.508	AM
69	Pottiaceae	*Barbula pseudo-ehrenbergii*	Turf	0.497	AM
70	Bartramiaceae	*Philonotis turneriana*	Turf	0.474	AM, AS
71	Pottiaceae	*Hymenostylium recurvirostrum var. insigne*	Turf	0.459	AM
72	Distichiaceae	*Distichium bryoxiphioidium*	Turf	0.450	AM
73	Funariaceae	*Funaria discelioides*	Turf	0.443	AM, AS
74	Pottiaceae	*Weissia longifolia*	Turf	0.442	AM, AS
75	Brachytheciaceae	*Brachythecium garovaglioides*	Weft	0.434	AM
76	Pottiaceae	*Didymodon ferrugineus*	Turf	0.429	AS
77	Pylaisiadelphaceae	*Isopterygium albescens*	Weft	0.415	AM
78	Pottiaceae	*Trichostomum tenuirostre*	Turf	0.404	AM
79	Brachytheciaceae	*Brachythecium plumosum*	Weft	0.399	AM
80	Dicranaceae	*Dicranum fragilifolium*	Turf	0.398	AM
81	Bryaceae	*Bryum capillare*	Turf	0.397	AM
82	Mniaceae	*Rhizomnium gracile*	Turf	0.395	AS
83	Bryaceae	*Bryum blindii*	Turf	0.386	AS
84	Brachytheciaceae	*Brachythecium reflexum*	Weft	0.378	AM
85	Dicranellaceae	*Dicranella divaricatula*	Turf	0.375	AM
86	Brachytheciaceae	*Brachythecium buchananii*	Weft	0.368	AM
87	Fissidentaceae	*Fissidens curvatus*	Turf	0.362	AM, AS
88	Pottiaceae	*Syntrichia princeps*	Turf	0.355	AM, AS
89	Grimmiaceae	*Grimmia montana*	Cushion	0.353	AM, AS
90	Thuidiaceae	*Haplocladium microphyllum*	Weft	0.339	AM
91	Bryaceae	*Bryum turbinatum*	Turf	0.318	AM, AS
92	Oncophoraceae	*Oncophorus virens*	Turf	0.311	AM
93	Dicranaceae	*Dicranum scoparium*	Turf	0.307	AM
94	Pottiaceae	*Bryoerythrophyllum recurvirostrum*	Turf	0.301	AM, AS
95	Funariaceae	*Physcomitrium coorgense*	Turf	0.300	AM
96	Brachytheciaceae	*Cirriphyllum cirrosum*	Weft	0.299	AM
97	Thuidiaceae	*Thuidium pristocalyx*	Weft	0.292	AM
98	Bartramiaceae	*Philonotis calomicra*	Turf	0.286	AM
99	Encalyptaceae	*Encalypta ciliata*	Turf	0.274	AM
100	Dicranaceae	*Paraleucobryum schwarzii*	Turf	0.257	AM
101	Mniaceae	*Pohlia timmioides*	Turf	0.254	AM
102	Pottiaceae	*Timmiella anomala*	Turf	0.253	AM
103	Bryaceae	*Bryum radiculosum*	Turf	0.252	AM
104	Pottiaceae	*Bryoerythrophyllum yunnanense*	Turf	0.250	AM
105	Pottiaceae	*Tortula leucostoma*	Turf	0.241	AM
106	Pottiaceae	*Barbula subcomosa*	Turf	0.217	AM
107	Pottiaceae	*Didymodon perobtusus*	Turf	0.216	AM
108	Orthotrichaceae	*Orthotrichum anomalum*	Cushion	0.201	AM
109	Pottiaceae	*Didymodon rufidulus*	Turf	0.201	AS
110	Grimmiaceae	*Grimmia pilifera*	Cushion	0.194	AM
111	Mniaceae	*Plagiomnium arbusculum*	Turf	0.189	AM
112	Fissidentaceae	*Fissidens exilis*	Turf	0.188	AM
113	Pottiaceae	*Trichostomum brachydontium*	Turf	0.188	AM
114	Brachytheciaceae	*Brachythecium kuroishicum*	Weft	0.183	AS
115	Mniaceae	*Pohlia minor*	Turf	0.174	AM
116	Bryaceae	*Bryum pallens*	Turf	0.173	AM

117	Entodontaceae	*Entodon obtusatus*	Mat	0.171	AM
118	Splachnaceae	*Tayloria lingulata*	Turf	0.154	AM
119	Grimmiaceae	*Grimmia elatior*	Cushion	0.146	AM
120	Mniaceae	*Plagiomnium drummondii*	Turf	0.146	AM
121	Mniaceae	*Pohlia nutans*	Turf	0.145	AM
122	Brachytheciaceae	*Brachythecium salebrosum*	Weft	0.141	AM
123	Pottiaceae	*Bryoerythrophyllum inaequalifolium*	Turf	0.131	AS
124	Bryaceae	*Bryum blandum subsp. handelii*	Turf	0.131	AM
125	Funariaceae	*Physcomitrium sphaericum*	Turf	0.126	AM
126	Bryaceae	*Bryum purpurascens*	Turf	0.115	AM
127	Pottiaceae	*Bellibarbula recurva*	Turf	0.113	AM
128	Brachytheciaceae	*Brachythecium piligerum*	Weft	0.108	AM
129	Pottiaceae	*Tortula planifolia*	Turf	0.101	AM
130	Bryaceae	*Brachymenium sinense*	Turf	0.100	AS
131	Pottiaceae	*Tortula muralis*	Turf	0.098	AM
132	Bryaceae	*Bryum thomsonii*	Turf	0.096	AM
133	Mniaceae	*Pohlia crudoides*	Turf	0.095	AM
134	Hypnaceae	*Ptilium crista-castrensis*	Weft	0.095	AM
135	Hylocomiaceae	*Rhytidiadelphus squarrosus*	Weft	0.095	AM
136	Funariaceae	*Physcomitrium eurystomum*	Turf	0.093	AM
137	Polytrichaceae	*Polytrichastrum papillatum*	Turf	0.092	AS
138	Grimmiaceae	*Grimmia anodon*	Cushion	0.092	AS
139	Grimmiaceae	*Grimmia elongata*	Cushion	0.089	AS
140	Splachnaceae	*Tayloria subglabra*	Turf	0.087	AM
141	Bryaceae	*Brachymenium nepalense*	Turf	0.085	AM
142	Bryaceae	*Bryum salakense*	Turf	0.073	AM
143	Pottiaceae	*Syntrichia caninervis*	Turf	0.064	AM
144	Leucobryaceae	*Campylopus flexuosus*	Turf	0.060	AM
145	Grimmiaceae	*Schistidium subconfertum*	Cushion	0.059	AM
146	Pottiaceae	*Tortula yuennanensis*	Turf	0.059	AM
147	Plagiotheciaceae	*Plagiothecium piliferum*	Mat	0.053	AM
148	Grimmiaceae	*Grimmia pulvinata*	Cushion	0.051	AM
149	Bryaceae	*Bryum rutilans*	Turf	0.040	AS

3.2. Comparing Species Composition between AM and AS

A total of 137 bryophyte taxa in 23 families and 46 genera were recorded in AM, while 54 taxa in 10 families and 21 genera were recorded in AS. Pottiaceae and Bryaceae were the most species-rich families in both AM and AS, cumulatively accounting for 51.1% and 74.0%, respectively (Figure 3a,c). *Bryum* and *Didymodon* were the most species-rich genera in both AM and AS. In particular, the proportions of *Didymodon* increased from 8.8% in AM to 24.1% in AS (Figure 3b,d).

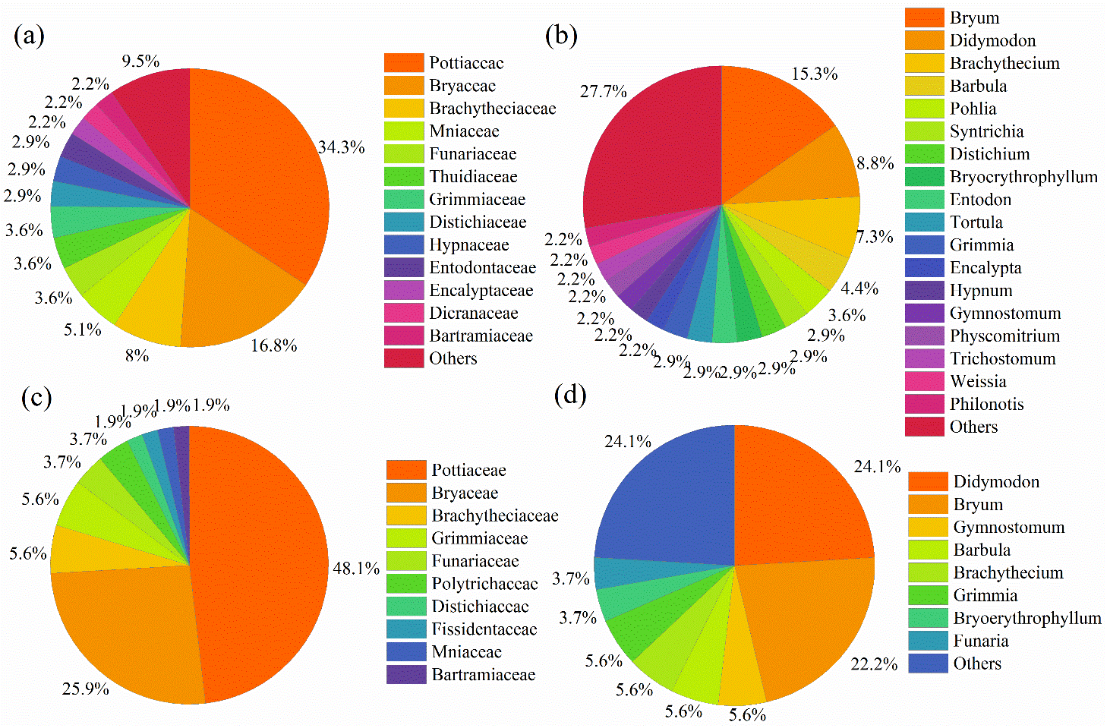

Figure 3. Bryophyte composition in two alpine grassland types of the Qinghai–Tibet Plateau: (**a**) families in alpine meadow; (**b**) genera in alpine meadow; (**c**) families in alpine steppe; and (**d**) genera in alpine steppe.

The Jaccard similarity indexes of bryophyte compositions between AM and AS at the family, genus, and species levels were 0.375, 0.367, and 0.282, respectively. AM and AS shared 42 taxa. A total of 95 taxa, including *Rhytidium rugosum*, *Abietinella abietina*, *Haplocladium angustifolium*, *Entodon challengeri*, *Brachythecium moriense*, *Brachythecium populeum*, and *Hypnum revolutum*, were only found in AM, while 12 taxa, including *Didymodon ferrugineus*, *Rhizomnium gracile*, *Bryum blindii*, and *Bryoerythrophyllum inaequalifolium*, only occurred in AS.

3.3. Bryophyte Life-Forms

Four types of bryophyte life-forms were observed in the alpine grasslands of the QTP (Figure 4). Turf was the most common (112 taxa, 75.2%), followed by weft (24, 16.1%) and cushion (8, 5.4%). The rank of life-forms was similar between AM and AS. Compared to AM, turfs increased by 13.7% in AS, while wefts sharply decreased (16.8% vs. 5.6%) and mats disappeared. Cushions (3, 5.6%) increased to as many as the wefts in AS.

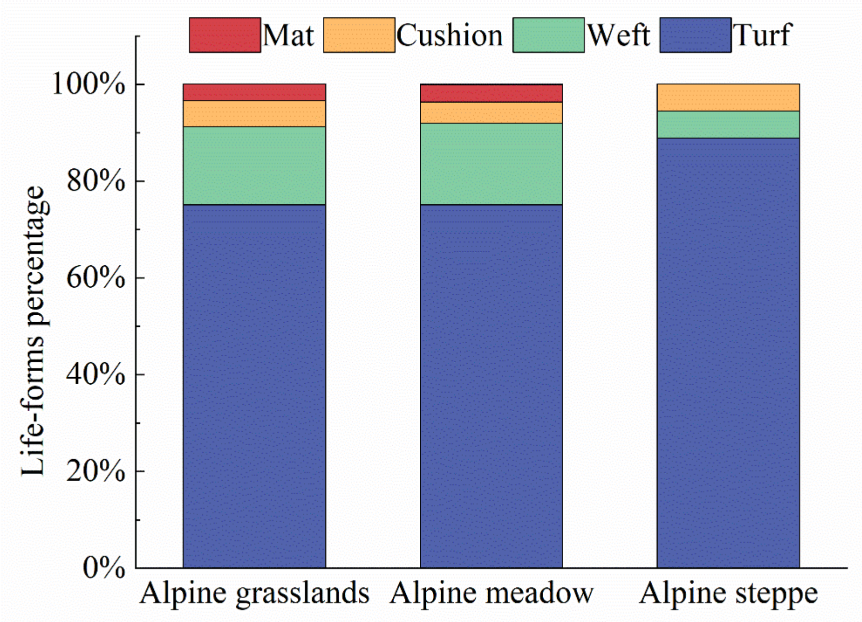

Figure 4. Bryophyte life-forms in alpine grasslands of the Qinghai–Tibet Plateau.

3.4. Endemism

Twelve species, namely *Barbula yunnanensis, Dicranella divaricatula, Distichium brevisetum, Didymodon constrictus var. flexicuspis, Didymodon rivicola, Didymodon rufidulus, Distichium bryoxiphioidium, Funaria discelioides, Gymnostomum laxirete, Pohlia timmioides, Tortula planifolia,* and *Tortula yuennanensis*, were endemic to China, accounting for 8.05% of the total taxa. Of which, five species occurred in both AM and AS; six and one species were only in AM and AS, respectively (Table 1).

4. Discussion

4.1. Sampling Methods for Estimating Biodiversity

Different sampling methods influence the detection of biodiversity [30–32]. Chen et al. [33] obtained the higher species richness of epiphytic bryophytes by using the PS method than by using the floristic habitat sampling (FHS) method. In contrast, Newmaster et al. [32] found that the FHS method was more efficient than the PS method in estimating bryophyte species in forest stands. Additionally, the diversity of forest floor bryophytes explored by microcoenose sampling was higher than that explored by random sampling [34]. Song et al. [13] collected some *Didymodon* species from the arid regions of southwestern Tibet, where no bryophytes occurred in our sampling plots. Moreover, we have not sampled any liverworts. This incomplete species pool is possibly due to the random sampling of the plots and quadrats, the unoptimized species–area relationship [35], and the uncovering of entire microhabitats [32]. Although PS may underestimate species diversity, we believe that the intensive sampling effort on a broad scale contributed the baseline information of bryophyte diversity to the QTP flora, even global alpine flora. More investigations incorporating the floristic sampling method are still needed to elucidate the overall bryophyte diversity in alpine grasslands on the QTP. In particular, the absence of bryophytes in sampling sites located in the ADS needs to be further tested to determine whether it results from sampling bias or growth limits in harsh environments.

4.2. Bryophyte Composition of Alpine Grasslands on the QTP

Pottiaceae and Bryaceae were dominant in both alpine grassland types, which are important components of the biological soil crusts in the dryland or desert [36–38]. The reasons for this predominance in the alpine grasslands of the QTP were not only because these two families were cosmopolitan and had abundant species but also because they possessed some morphological traits to resist drought stress. For instance, the laminal cells with papillae in most Pottiaceae species in Table 1 formed capillary spaces [39] and thus channeled water movement across the lamina [40,41]. The large proportions of hyaline basal laminal cells in such species as *Syntrichia* and *Bryoerythrophyllum* are associated with a higher speed of water conduction [40]. The leaf hair points of *Syntrichia* spp. and *Tortula* spp. aid in collecting water from the air [42] and therefore delay and reduce evaporation rates [43]. Overall, *Barbula*, *Bryoerythrophyllum*, *Didymodon*, *Syntrichia*, *Tortula*, and *Tortella* belonging to Pottiaceae and *Bryum* belonging to Bryaceae, which were identified in our inventory (Table 1), have been documented as desiccation-tolerant [44]. In particular, *Syntrichia* spp. [42,45,46] and *Bryum argenteum* [47,48] are emerging as important model organisms for desiccation tolerance in plants.

Although *Bryum* had the most abundant species in alpine grasslands on the QTP, 6 of the 10 dominant species belonged to the genus *Didymodon*, corroborating a previous study focused on arid and semi-arid areas of Tibet [13]. Furthermore, we noticed that the proportions of *Didymodon* increased nearly twofold from AM (8.8%, Figure 3b) to AS (24.1%, Figure 3d), providing additional evidence that *Didymodon* can be an indicator of climate change on the QTP [49].

Bryophyte diversity at the family, genus, and species levels in AM was much higher than that in AS, which was similar to the species richness pattern of vascular plants [21,50,51] along the decreased precipitation gradient from southeast to northwest on the QTP [52]. Moreover, mosses were rare in the AS of the QTP based on the PS performed by Miehe et al. [26], although they were not specific to bryophyte sampling. On the other hand, the similarities in bryophyte composition at different taxonomic levels between AM and AS were all very low, indicating the sensitivity of bryophytes to different environments. We speculated that one of the climatic drivers of the large differences may be attributed to precipitation. In addition, the simulations of Wen et al. [53] suggested that temperature seasonality and precipitation of the coldest quarter were the key climatic variables for bryophyte distribution on the QTP. Considering the limitations of the current analysis, the roles of various climatic variables in bryophyte composition need to be further examined.

4.3. Bryophyte Life-Forms and Indications for Climate Change

Bryophyte life-forms refer to the arrangements of the whole colony and interact with habitat conditions in terms of moisture availability and light intensity [27,28]. Turfs were predominant (72.5%) across alpine grasslands on the QTP, as previously described in natural grasslands [54], rupestrian grasslands [55], and the summits of Alps between the upper tree line and the nival belt [56]. Compared to AM, the 2/3 decreased proportion of wefts, the absence of mats, and the slightly increased cushions in AS occurred where bryophytes were subjected to stronger drought stress. These results support the general notion that turfs and cushions are common in arid and exposed habitats, whereas mats and wefts mostly occur in shady and humid habitats [27,28].

Turfs and cushions have advantages over wefts and mats to survive in harsh environments of alpine grasslands on the QTP, with strong solar radiation and drought stress. Their colonies are erect and compact, which are effective in retaining water within the capillary spaces between individuals, and thus protect against desiccation [39,57,58]. The dense colonies of turfs and cushions are also beneficial for receiving less light due to self-shading than those widely spaced, such as wefts and mats, and for providing photoprotection [27,59]. Therefore, the types of bryophyte life-forms in AM and AS reflect the adaptive strategies of species to severe environments.

Alpine grasslands on the QTP are among the most sensitive and fragile ecosystems to climate change [60]. The QTP is getting warmer and wetter. Its warming rate has been about twice the global mean in the last three decades [61], and precipitation has slightly increased [62]. In the context of climate change, AM is sharply decreasing, whereas AS is expanding [63]. Warming had different effects on plant productivity and composition in AM and AS [64]. Based on the observed changes in bryophyte life-forms between AM and AS, we suggest that bryophyte life-forms can be used to monitor vegetation dynamics in alpine grasslands of the QTP. Furthermore, they are easily and directly obtained in the field and have already been used to indicate land-use changes in tropical forests [65], in forest successions in Latvia [66], and among different land cover types in an alpine area of northern Italy [54].

4.4. Endemism

Species endemism is one of the most important metrics for evaluating biodiversity [67]. Our results showed that the proportion of endemic bryophytes to China in alpine grasslands on the QTP was 8.05%, which was lower than that of forests (21.8%) in the southeastern QTP [68]. The possible reasons for these are largely attributed to the differences in climate and habitat heterogeneity between the two vegetation types [69]. Mild climates with relatively higher temperatures and precipitation are undoubtedly favorable for supporting more bryophytes in the southeastern forests than in alpine grasslands on the QTP. Moreover, various substrates, such as soil, living trunk, rocks, and fallen logs, increase habitat heterogeneity in forests for bryophytes. In contrast, habitats in alpine grasslands are usually homogeneous. The differential climate of the two grassland types could also explain why more endemic bryophytes occurred in AM (11 species) than in AS (six species). Likewise, the decline of endemism from the southeastern (forests) to the northwestern (grassland) QTP has also been found in seed plants [69–71]. Additionally, compared with 38.2% endemic seed plants on the QTP [71], the lower level of bryophyte endemism is usually explained by the strong long-distance dispersal capacities and low diversification rates of bryophytes [72].

5. Conclusions

Our study is the first systematic description of bryophyte flora in alpine grasslands to an outstanding geographic extent based on PS. The bryophyte composition, richness, life-forms, and their changes in different alpine grassland types reflect the adaptations of bryophytes to harsh environments. Considering the conservation priority of AM and AS on the QTP for global biodiversity, bryophyte diversity in alpine grasslands on the QTP is exceptional and irreplaceable regardless of species richness, especially when these species are experiencing unusual ecological and evolutionary processes on a unique tectonic unit of the Earth. Therefore, the exploration of bryophyte flora and conservation should be strengthened in the future.

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