J. Resour. Ecol. 2018 9(5) 526-537
DOI: 10.5814/j.issn.1674-764x.2018.05.010
www.jorae.cn

Vegetation Pattern in Northern Tibet in Relation to Environmental and Geo-spatial Factors

TIAN Li[1,3], ZHANG Yangjian[1,2], Claus HOLZAPFEL[4], HUANG Ke[1], CHEN Ning[1], TAO Jian[1], ZHU Juntao[1,*]

1. Lhasa Plateau Ecosystem Research Station, Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China;
2. Chinese Academy of Sciences Center for Excellence in Tibetan Plateau Earth Sciences, Beijing 100101, China;
3. Qianyanzhou Ecological Research Station, Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China;
4. Department of Biological Sciences, Rutgers, The State University of New Jersey, 195 University Avenue, Newark NJ 07102, USA

Abstract: Environmental and Geo-spatial factors have long been considered as crucial determinants of species composition and distributions. However, quantifying the relative contributions of these factors for the alpine ecosystems is lacking. The Tibetan Plateau has a unique ecological environment and vegetation types. Our objectives are to quantify the spatial distributions of plant communities on the Northern Tibetan Alpine grasslands and to explore the relationships between vegetation composition, Geo-spatial factors and environmental factors. We established 63 field plots along a 1200-km gradient on the Northern Tibetan Plateau Alpine Grassland and employed the two-way indicator species analysis (TWINSPAN) and the detrended canonical correspondence analysis (DCCA). Fourteen communities of alpine grassland were identifiable along the transect and consisted of three vegetation types: Alpine meadow, Alpine steppe, and desert steppe. Vegetation composition and spatial distribution appeared to be largely determined by mean annual precipitation and less influenced by temperature. A large fraction (73.5%) of the variation in vegetation distribution was explained by environmental variables along this transect, somewhat less by Geo-spatial factors (56.3%). The environmental and Geo-spatial factors explained 29.6% and 12.3% of the total variation, respectively, while their interaction explained 43.9%. Our findings provide strong empirical evidence for explaining biological and environmental synergetic relationships in Northern Tibet.

Key words: alpine grasslands; environmental interpretation; spatial pattern; Tibetan Plateau; vegetation composition

1 Introduction

The Tibetan Plateau, has been called the third Pole of the Earth, and it has fundamental regional and global ecological significance by providing the source of major rivers and affecting large-scale climate patterns (Li, 2000). The grasslands of Northern Tibet, at the core of the Tibetan Plateau, cover an area of 0.48×10^6 km^2, and are the critical biome determining the ecological functions of the Tibetan Plateau (Cincotta *et al*., 1991). They provide basic food resources for the livestock of Tibetan herders (Gao *et al*., 2010a) and harbor vast numbers of wild ungulates. Within the region, the Tibetan alpine grassland is one of the most sensitive ecosystems that is vulnerable to climate change (Xu *et al*., 2010). In recent years, climate change and long-term overgrazing have resulted in grassland degradation, accompanied by reduced productivity, poisonous weed invasion and

Received: 2018-01-12 **Accepted:** 2018-04-20
Foundation: National Key Technology Research and Development Program of China (2016YFC0501802, 2017YFA0604802); National Natural Science Foundation of China (41571195, 41501103); Youth Innovation Team Project of Key Laboratory of Ecosystem Network Observation and Modeling (LENOM2016Q0002).
***Corresponding author:** ZHU Juntao, E-mail: zhujt@igsnrr.ac.cn

Citation: TIAN Li, ZHANG Yangjian, Claus HOLZAPFEL, *et al*. 2018. Vegetation Pattern in Northern Tibet in Relation to Environmental and Geo-spatial Factors. *Journal of Resources and Ecology*, 9(5): 526–537.

desertification (Li and Liu, 2005; Yu *et al*., 2012). These critical issues have attracted mounting attention from a wide range of research fields such as rangeland ecology (Duan *et al*., 2010; Gao *et al*., 2010a), climate change effects (Gao *et al*., 2010b; Zhong *et al*., 2010; Chen *et al*., 2014), and ecosystem function (Xiong *et al*., 2014; Wu *et al*., 2013, 2014a, 2014b).

Knowledge about the spatial pattern of species composition forms the basis for environmental and biological conservation. In this respect, previous studies have described spatial patterns of the main plant communities in the alpine steppes of the Tibet Plateau (Wang, 1988; Miehe *et al*., 2011), and similar studies have also been conducted for eastern Ladakh (Hartmann, 1999; Klimeš, 2003; Klimeš and Doležal, 2010). Despite these studies, only limited attention has focused on the form and shape plant communities of the Northern Tibet grassland system. Spatial patterns of vegetation distribution are the collective result of many factors, including environmental factors (such as temperature and precipitation), Geo-spatial factors (spatial location), and other undetermined factors (including interference and interspecific interactions; Legendre and Fortin, 1989). Environmental interpretations of vegetation patterns have been often reported for complex and high diversity vegetation systems such as subtropical forest, temperate forest and temperate grassland and such interpretations vary with complexity (Shen and Zhang, 2000; Zhang *et al*., 2004; Song *et al*., 2010; Li *et al*., 2011; Zhang *et al*., 2012). The Northern Tibetan biome belongs to the "Diversity Zone 1", one of the world's most species-poor areas (Barthlott *et al*., 1996). The alpine climate of the Northern Tibetan Plateau represents extreme conditions in respect to low temperatures and aridity. Studies on environmental interpretations that explain vegetation patterns of simple, species–poor systems under extreme environmental conditions such as the Tibetan Plateau grasslands are still lacking. The current study therefore aims to complement our knowledge on the regulating role of environmental and Geo-spatial factors on the species composition at the extreme end of the global environmental gradient and contributes to our understanding of global species composition and its spatial patterns.

We here document the composition of the vegetation in Northern Tibet along an east-to-west aridity gradient, and we quantify the relative roles of environmental and spatial variables in explaining its distribution pattern. First, we summarized the variation in species composition of 63 study plots by cluster analysis using the TWINSPAN algorithm. Second, we investigated the effects of environmental and Geo-spatial factors, together with their intersection, on vegetation pattern by using the DCCA. Specifically, our objectives were to: 1) reveal the spatial pattern of plant communities of the Northern Tibetan alpine grassland; and 2) identify the main drivers of vegetation composition and spatial pattern. We hypothesize that the relatively simple community of the alpine grasslands on the Tibetan plateau allows stronger environmental interpretation than more complex vegetation types. The information learned in this study can guide biome conservation, wildlife habitat management and ecological rehabilitation in Northern Tibet.

2 Materials and methods

2.1 Study area

We established an approximately 1200-km southeast–northwest transect in the high altitude grassland (the Northern Tibetan Plateau Alpine Grassland Transect, NTPAGT) in May 2009. The NTPAGT covers longitude from 79°42'36"E to 92°01'48"E and latitude from 30°30'00"N to 33°27'00"N (Fig. 1). From east to west along the transect, the mean annual temperature (*MAT*) is between –2.32 and 1.19°C, the

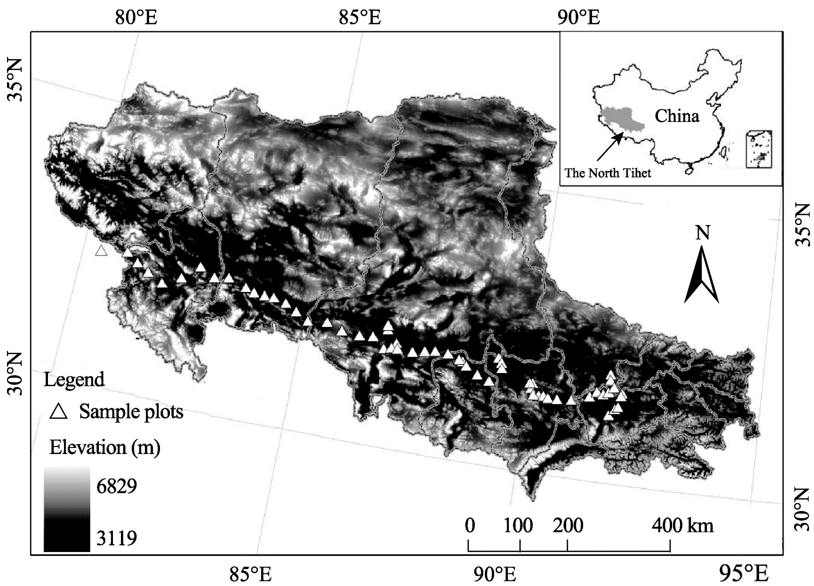

Fig.1 Locations of the 63 study sites along the Northern Tibetan Plateau Alpine Grassland Transect (NTPAGT)

mean annual precipitation (*MAP*) is between 242 mm and 550 mm, and the elevation of the sample sites ranges from 4374 to 4953 m.

The NTPAGT traverses three main natural vegetation types (Photo 1): alpine meadow (AM, dominated by *Kobresia pygmaea*), alpine steppe (AS, dominated by *Stipa purpurea*) and alpine desert steppe (ADS), and alpine meadow dominated by *Stipa subsessiliflora* (Li *et al.*, 2011). Alpine steppe dominated by *S. purpurea* is the most widely distributed vegetation type on the Northern Tibetan Plateau (Chang, 1981, Chinese Academy of Sciences, Integrative Expedition Team to Qinghai-Tibet Plateau, 1988), and the desert steppe dominated by *Stipa subsessiliflora* along the east-west gradient in Northern Tibet.

2.2 Data collection

Field surveys were conducted every 20 km along the west-east transect during late July to early August in 2011 and 2012. In total, 63 fixed sites were selected away from roads, with similar slope aspects, and fenced to prevent grazing (Photo 1). Within each site, ten 1 m×1 m quadrats were selected randomly within a 100 m×100 m area and all vascular plant species were identified and their cover and height were recorded. Species cover and height at each site was averaged across the ten quadrats. We recorded geographical coordinates, elevation, and vegetation type for each site. At the center of each plot, soil bulk density at 10 soil depths (0–5, 5–10, 10–20, 20–30, 30–50 cm) was measured by using a cylindrical sampler (50.46 mm diameter, and 50 mm length). Three replicates were taken at each soil depth.

Climate data was obtained from the China Meteorological Administration (CMA). We selected daily mean temperature and daily total precipitation records from 1985 to 2010 and aggregated them to a half-month average. The aggregated climate data were interpolated to achieve spatial

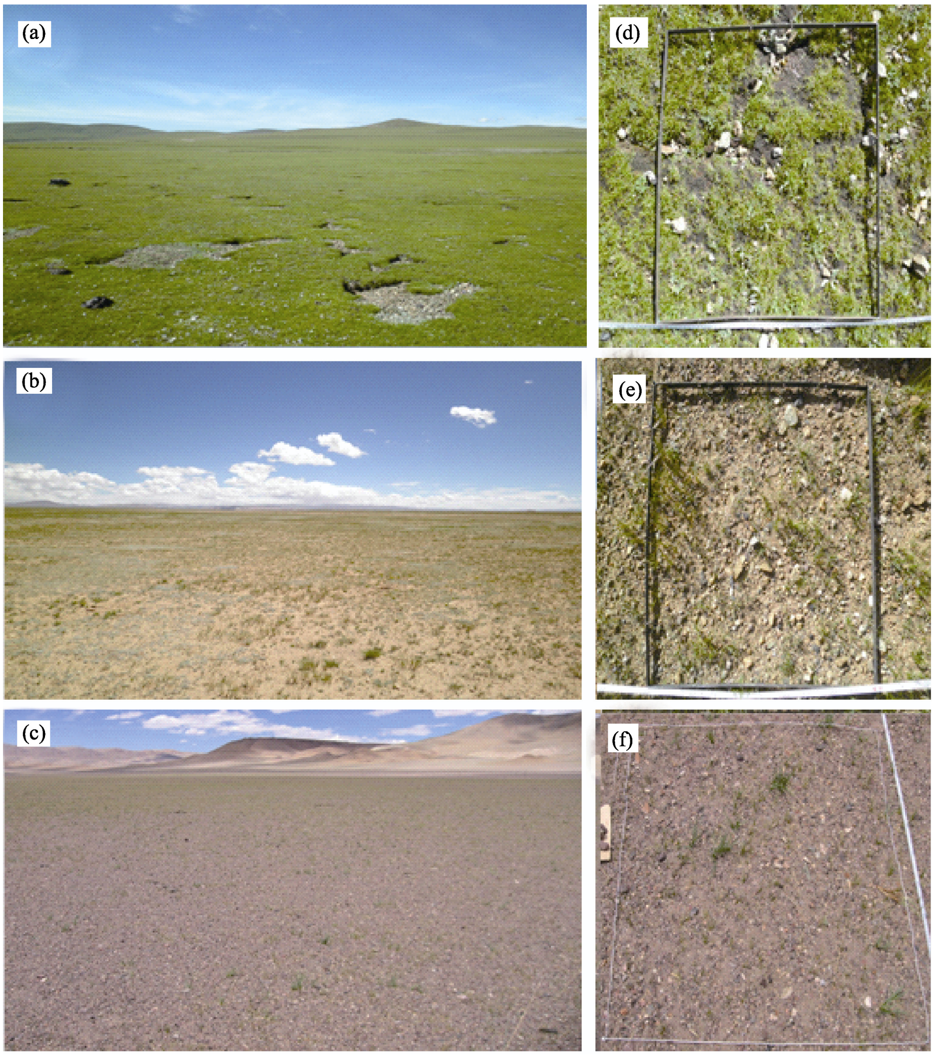

Photo 1 Landscape/vegetation aspects of the three major grassland types

Note: (a)(d): alpine meadow (characterized by *Kobresia pygmaea*), (b)(e): alpine steppe (characterized by *Stipa purpurea*), (c)(f): desert steppe (characterized by *Stipa subsessiliflora*) along the east-west gradient in Northern Tibet. (d), (e) and (f) represent plant quadrat method.

continuity and then re-aggregated to mean annual precipitation (*MAP*) and mean annual temperature (*MAT*) with an 8 km × 8 km spatial resolution. The *MAP* and *MAT* for each site were extracted using a Geographic Information System (GIS)-based multiple regression method developed by Ninyerola et al. (2000) in ArcGIS 9.2 (ESRI, Redlands, CA, USA).

2.3 Data analysis

The importance value (*IV*) of each species was calculated and used in multivariate analysis of the communities. The importance value was calculated by the formula (Zhang 1995, 2004, Meng et al. 2012):

$$IV = \frac{(\text{Relative coverage} + \text{Relative height})}{200}$$

Relative coverage/height refers to the proportion of one species accounting for the sum calculated for each plot individually. The plot associated environmental variables included *MAP*, *MAT* and soil bulk density (*SBD*) and spatial variables consisted of longitude (*LNG*), latitude (*LAT*) and elevation (*ELE*). We generated a data matrix of plots and species (63 × 106), one for environmental variables (63 × 3), and another one for spatial variables (63 × 3).

The quantitative classification and ordination, a type of multivariate analysis technique, has been widely used for exploring the linkage between vegetation composition, spatial pattern and environmental factors in vegetation ecology (Mucina, 1997; Lepš and Šmilauer, 2003). To identify the most important indicator species within each vegetation group, a hierarchical divisive vegetation group analysis was performed using the WinTWINS (Version 2.3) (Hill and Šmilauer 2005) (Fig. 2). Diagnostic species of plant associations were identified using a fidelity calculation (Tichy and Chytry, 2006). The Phi coefficient of association (Φ) was used as a measure of fidelity. Before the Phi coefficient calculation, each group of plots was virtually equalized to 5% of the total data. The species with Phi values higher than 0.2 and Fisher's exact test significance lower than 0.05 were treated as diagnostic. The DCCA ordination analysis and Monte Carlo test was performed using CANOCO (Version 4.5) (Braak and Šmilauer, 2002).

Graphical model of partitioning of the variation of a response matrix ***Y*** into environmental (matrix ***X***) and Geo-spatial (matrix ***W***) explanatory variables. The rectangle represents 100% of the variation in *Y*, which is divided into four parts labeled [a] to [d]: [a], pure environmental variation; [b], environment + Geo-spatial intersection; [c], pure spatial variation; and [d], unexplained variation. The calculations were based upon three canonical analyses (*Y-X*; *Y-W*; *Y-X*, *W*) (Borcard *et al.* 1992; Legendre 2008).

3 Results and discussion

3.1 Flora and plant communities

We recorded 106 species along the transect in total (57 genera, 26 families) (Table S1). The most diverse genera are Potentilla (7), Kobresia (5), Astragalus (5), Oxytropis (5), Carex (4), Artemisia (4), Arenaria (4), Stipa (3), Saussurea (3), Poa (3), Gentiana (3), Festuca (3), and Gentiana (3). The results of the TWINSPAN classification separated 14 plant communities grouped into four plant associations (Table 1 and Table 2). In areas with precipitation over 500 mm, plant communities are characterized by the dominant grass *Kobresia pygmaea* and the forb *Potentilla bifurca* (Association Ⅰ). In areas with decreased precipitation first the grasses *Stipa purpurea* and *Kobresia humilis* are characteristic for (Association Ⅱ) and then the grass *Stipa purpurea* and the forb *Leontopodium nanum* are typical for Association Ⅲ. In areas with precipitation lower than 300 mm, the plant community is dominated by the grass *Stipa subsessiliflora* and the cushion plant *Ptilotrichum wageri* (Association Ⅳ) (Table 2 and Fig. 3).

The 14 plant communities can be grouped into three

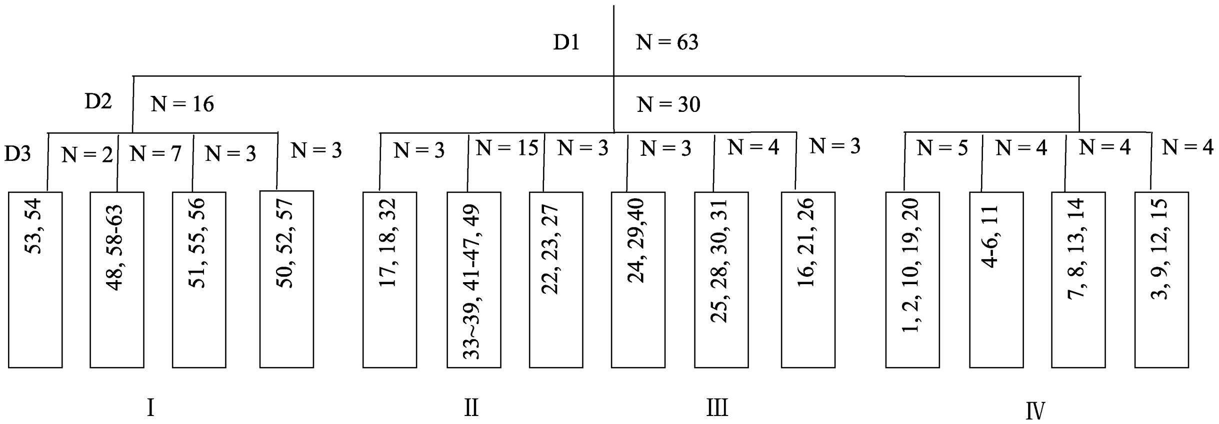

Fig.2 Dendrogram of the TWINSPAN classifications of the 63 vegetation sampling sites (630 quadrats) in Northern Tibet

Note: *D* represents the level of division. *N* represents the number of plots.1-63 represents plot numbers. I, II, III and IV represents the four plant associations.

Table 1 Synoptic table showing percentages of diagnostic species occurrence (bold values) in Northern Tibetan alpine grassland system identified by cluster analysis

Grassland vegetation types	Alpine meadow				Alpine steppe						Desert steppe			
Plant associations	[I]				(II)			(III)			{IV}			
Community types	[1]	[2]	[3]	[4]	(5)	(6)	(7)	(8)	(9)	(10)	{11}	{12}	{13}	{14}
Number of plots	2	7	3	3	3	15	3	3	4	3	5	4	4	4
Kobresia pygmaea	**70**	**80**	**73**	**60**	0	1	0	0	0	0	0	0	0	0
Potentilla bifurca	0	**20**	**20**	0	0	7	20	0	**20**	0	12	0	5	5
Youngia simulatrix	10	**20**	13	20	0	5	0	0	5	0	0	0	0	0
Potentilla cuneata	10	17	7	**20**	0	0	13	0	**20**	13	0	0	0	0
Kobresia tibetica	10	0	0	**20**	0	0	0	0	0	0	0	0	0	0
Potentilla saundersiana	**20**	**20**	**20**	20	0	0	0	0	0	0	0	0	0	0
Saussurea alpina	10	**20**	13	20	0	0	0	0	0	0	0	0	0	0
Potentilla multifida	10	0	13	0	0	4	0	0	0	0	0	0	0	0
Taraxacum Tibeticum	**20**	0	0	0	0	0	0	20	0	0	0	0	0	0
Kobresia macrantha	10	0	0	0	0	0	0	**20**	0	0	0	0	0	0
Lagotis brachystachya	**20**	0	7	0	0	4	0	0	10	0	0	0	0	0
Potentilla fruticosa	0	0	0	**20**	7	0	0	0	0	0	0	0	0	0
Carex ivanoviae	20	11	7	0	0	**20**	0	0	0	0	0	0	0	0
Leontopodium nanum	**20**	11	13	0	**33**	8	7	0	0	0	4	0	0	5
Androsace tapete	**20**	0	0	0	0	7	13	0	10	0	0	0	0	0
Lancea tibetica	0	0	13	0	0	0	0	0	0	0	0	0	0	0
Poa crymophila	10	9	0	20	13	17	13	0	15	0	0	0	0	0
Leontopodium ochroleucum	0	3	7	0	0	**23**	0	0	0	0	0	0	0	0
Stipa purpurea	0	9	**20**	20	**40**	**31**	**40**	**20**	**60**	**60**	**76**	**20**	0	8
Kobresia humilis	0	0	0	0	**20**	**21**	**20**	**40**	**25**	**20**	0	0	0	0
Astragalus polycladus	10	3	7	0	7	9	**27**	0	15	13	8	0	0	0
Oxytropis stracheyana	0	0	0	0	0	3	13	0	0	13	0	0	0	0
Pedicularis alaschanica	0	0	0	0	0	0	0	**20**	5	7	0	0	0	0
Astragalus hendersonii	0	0	0	0	13	1	0	**20**	0	7	0	0	0	0
Elymus dahuricus	0	0	0	0	0	1	0	0	0	7	8	0	0	10
Astragalus acaulis	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euphorbia tibetica	0	0	0	0	0	3	0	0	5	0	0	0	0	0
Deyeuxia pulchella	0	0	0	0	0	0	0	20	0	0	0	0	0	0
Poa parvissima	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arenaria serpyllifolia	0	0	0	0	7	4	0	**20**	5	0	0	0	0	0
Viola kunawarensis	0	0	0	0	0	9	0	0	0	0	0	0	0	0
Carex moorcroftii	10	3	7	0	7	3	0	0	0	0	0	**80**	0	5
Oxytropis glacialis	0	0	0	0	0	0	0	0	0	**20**	4	0	0	0
Artemisia duthreuil-de-rhinsi	0	0	0	0	0	0	0	0	0	0	0	0	15	**45**
Swertia tetraptera	0	0	0	0	0	1	0	0	0	**20**	16	0	10	0
Ptilotrichum wageri	0	0	0	0	0	1	**20**	0	5	**20**	**24**	**20**	**20**	15
Polygonum thomsonii	0	0	0	0	7	0	0	0	0	0	0	**20**	0	0
Oxytropis microphylla	0	0	0	0	0	0	0	0	10	13	0	0	5	15
Stipa subsessiliflora	0	0	0	0	0	0	0	0	0	0	0	0	**75**	**70**
Ranunculus banguoensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heteropappus semiprostratus	0	0	0	0	0	5	13	20	**20**	0	0	0	0	0

Continued

Grassland vegetation types	Alpine meadow				Alpine steppe						Desert steppe			
Plant associations	[I]				(II)		(III)				{IV}			
Community types	[1]	[2]	[3]	[4]	(5)	(6)	(7)	(8)	(9)	(10)	{11}	{12}	{13}	{14}
Number of plots	2	7	3	3	3	15	3	3	4	3	5	4	4	4
Thalictrum alpinum	20	0	0	20	0	0	0	0	0	0	0	0	0	0
Astragalus pulvinatus	0	3	0	20	0	0	0	0	0	0	0	0	0	0
Festuca coelestis	0	0	0	0	0	15	0	0	0	0	0	0	0	0
Salsola nepalensis	0	0	0	0	0	0	0	20	0	0	4	0	0	0
Leymus secalinus	0	0	0	0	0	0	0	20	0	0	0	0	0	0
Heracleum millefolium	0	0	0	0	0	0	0	20	0	0	0	0	0	0
Festuca wallichanica	0	0	0	0	0	0	0	20	0	0	0	0	0	0
Potentilla fragarioides	0	0	0	0	0	0	7	0	0	0	0	0	0	0
Myricaria prostrata	0	0	0	0	0	0	0	20	0	0	0	0	0	0
Artemisia stracheyi	0	0	0	0	0	0	0	20	0	0	0	0	0	0
Glaux maritima	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Dracocephalum tanguticum	0	0	0	0	0	0	0	20	0	0	0	0	0	0
Eritrichium sinomicrocarpum	0	0	7	0	0	13	0	0	5	0	0	0	0	0
Chenopodium tibeticum	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Saussurea graminea	10	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxytropis chiliophylla	10	0	0	0	0	0	0	0	0	0	0	0	0	0
Morina kokonorica	0	0	0	0	0	0	0	0	0	7	0	0	0	0
Torularia parvua	0	0	0	0	7	0	0	0	0	0	0	0	0	10
Rhodiola sangpo-tibetana	0	0	0	0	0	4	7	0	10	0	0	0	0	0

Note: Light grey shading indicates fidelity $\Phi > 0.20$ and Fisher's exact test significance < 0.05. Only species with the percentage consistently greater than 10% are listed. The community names, their plot composition and environmental characteristics are presented in Table 2. Different parentheses indicate which community types are grouped into the four plant associations: [], Alpine meadow; (), Alpine steppe; {}, Desert steppe.

Table 2 The results of TWINSPAN classification of 63 plots and environmental characteristics of 14 community types along a precipitation gradient

No.	Community name	Plant plots	*MAP*(mm)	*MAT*(°C)	*ALT*(m)
1	*Kobresia pygmaea+Potentilla saundersiana+Taraxacum Tibeticum+Lagotis brachystachya+Leontopodium nanum+Androsace tapete*	53,54	528±55	−1.6±0.5	4725±59
2	*Kobresia pygmaea+Potentilla bifurca+Youngia simulatrix+Potentilla saundersiana+Saussurea alpine*	48,58-63	533±58	−0.8±0.3	4603±52
3	*Kobresia pygmaea+Potentilla bifurca+Potentilla saundersiana+Stipa purpurea*	51,55,56	542±60	−0.6±0.3	4563±47
4	*Kobresia pygmaea+Potentilla cuneata+Kobresia tibetica+Potentilla fruticosa*	50,52,57	543±54	−0.8±0.2	4577±45
5	*Stipa purpurea+Leontopodium nanum+Kobresia humilis*	17,18,32	364±41	−1.0±0.4	4800±55
6	*Stipa purpurea+Leontopodium ochroleucum+ Kobresia humilis+ Carex ivanoviae*	33-39,41-47,49	440±47	−0.6±0.2	4644±50
7	*Stipa purpurea+Astragalus polycladus+ Kobresia humilis+Ptilotrichum wageri*	22,23,27	351±40	−0.2±0.08	4597±45
8	*Kobresia humilis+Kobresia macrantha+Arenaria serpyllifolia+Pedicularis alas-chanica+Astragalus hendersonii+Stipa purpurea*	24,29,40	389±45	−0.4±0.1	4570±48
9	*Stipa purpurea+Kobresia humilis+Potentilla bifurca+Potentilla cuneata+Heteropappus semiprostratus*	25,28,30,31	366±35	−0.8±0.3	4650±46
10	*Stipa purpurea+Kobresia humilis+Oxytropis glacialis+Swertia tetraptera+Ptilotrichum wageri*	16,21,26	328±36	−0.2±0.06	4581±43
11	*Stipa purpurea+Ptilotrichum wageri*	1,2,10,19,20	294±32	−0.2±0.06	4577±50
12	*Carex moorcroftii+Stipa purpurea+Ptilotrichum wageri+Polygonum thomsonii*	4-6,11	283±35	−0.7±0.2	4814±57
13	*Stipa subsessiliflora+Ptilotrichum wageri*	7,8,13,14	274±24	0.6±0.2	4466±48
14	*Stipa subsessiliflora +Artemisia duthreuil-de-rhinsi*	3,9,12,15	273±28	0.6±0.2	4478±41

Note: *MAP* means annual precipitation; *MAT* means annual temperature; *ALT* means altitude.

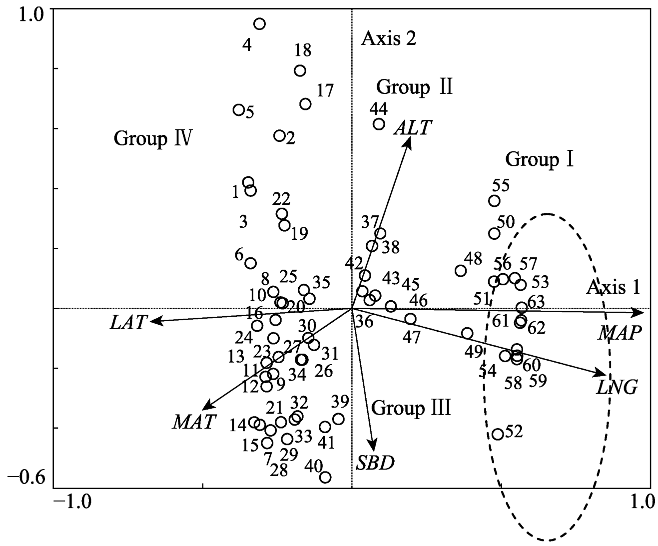

Fig.3 Detrended canonical correspondence analysis (DCCA) ordination diagram of the 63 sampling sites in Northern Tibet

Note: *MAP* means annual precipitation; *MAT* means annual temperature; *SBD* means soil bulk density; *LNG* means longitude; *LAT* means latitude; *ALT* means altitude. The dotted line represents precipitation line. Group I-IV represent plant association.

distinct grassland types: alpine meadow Association I), alpine steppe (Association II and III) and desert steppe (Association IV). The Alpine meadow is dominated mainly by *K. pygmaea*; other less common but frequently observed species include *K. humilis*, *Potentilla saundersiana*, *Leontopodium ochroleucum*, *Lancea tibetica*, *Youngia simulatrix* and *Festuca ovina*. The Alpine steppe is dominated by *S. purpurea*, accompanied by *Poa annua*, *Leontopodium nanum*, *Carex moorcroftii*, *Festuca ovina* and *Oxytropis microphylla*. The desert steppe is dominated by *S. subsessiliflora* with low diversity, and frequently observed species include *Ptilotricum canescens*, *Elymus dahuricus* and *Artemisia duthreuil-de-rhinsi*. The species composition within each grassland type corresponds well with previous related studies in the region (Yang *et al*., 2004; Li *et al*., 2011).

3.2 Relationships between vegetation composition, Geo-spatial factors and environmental factors

Plant community distribution is correlated strongly with the first two ordination axes, with coefficient values of 0.962 and 0.743, respectively (Fig. 3 and Fig. 4). The first two axes alone explained 78.5% of the community distribution variation (Table 3). Monte Carlo test runs (with 499 cycles) showed that there is an extremely significant correlation between community distribution and environment in the first axis (F = 5.105, p = 0.002, n = 499) (Table 3). Precipitation

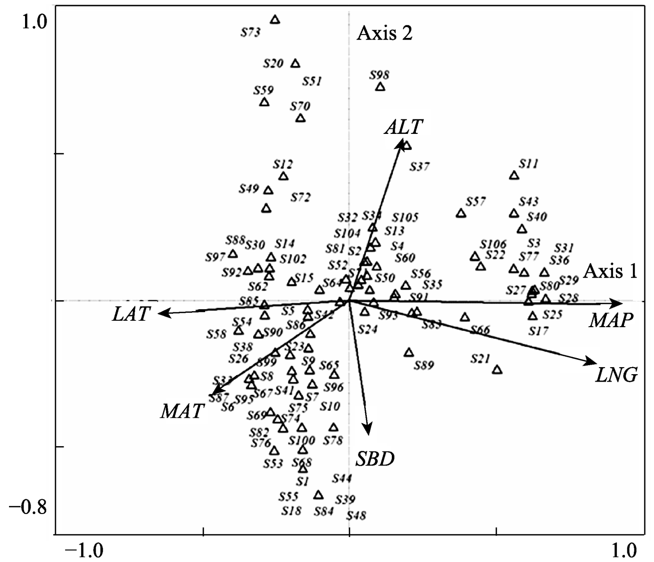

Fig.4 Detrended canonical correspondence analysis (DCCA) ordination diagram of the main plant species in Northern Tibet.

Note: The letter S and numbers indicate the dominant species as listed in Table S1. *MAP*: mean annual precipitation; *MAT*: mean annual temperature; *SBD*: soil bulk density; *LNG*: longitude; *LAT*: latitude; *ALT*: altitude.

Table 3 The correlation coefficients of the first and second axes of the DCCA for the six factors (mean annual precipitation, mean annual temperature, soil bulk density, longitude, latitude, altitude)

Item	*SPEC AX1*	*SPEC AX2*	*ENVI AX1*	*ENVI AX2*	*MAP*	*MAT*	*SBD*	*LNG*	*LAT*	*ALT*
SPEC AX1	1.000									
SPEC AX2	0.026	1.000								
ENVI AX1	0.962**	0.000	1.000							
ENVI AX2	0.000	0.743**	0.000	1.000						
MAP	0.911**	–0.011	0.946**	–0.014	1.000					
MAT	–0.459**	–0.240*	–0.476**	–0.323**	–0.553**	1.000				
SBD	0.069	–0.354**	0.071	–0.477**	0.110	0.095	1.000			
LNG	0.816**	–0.160	0.848**	–0.216*	0.959**	–0.528**	0.145	1.000		
LAT	–0.621**	–0.031	–0.646**	–0.042	–0.845**	0.390**	–0.100	–0.873**	1.000	
ALT	0.178*	0.411**	0.185*	0.553**	0.311**	–0.877**	–0.143	0.275*	–0.314**	1.000

Note: ** means p < 0.01, * means p < 0.05. *MAP* means annual precipitation; *MAT* means annual temperature; *SBD* means soil bulk density; *LNG* means longitude; *LAT* means latitude; *ALT* means altitude; SPEC AX1 means species axis 1; SPEC AX2 means species axis 2; ENVI AX1 means environmental factors axis 1; ENVI AX2 means environmental factors axis 2.

(*MAP*) is strongly correlated with the first axis, and altitude (*ALT*) with the second axis, which indicates that these two factors played a major role in determining community distribution in Northern Tibet (Fig. 3). The dispersion of these species in the ordination space (Fig. 4) corresponds closely with their grouping into plant associations. For example, the sites assigned to Group Ⅰ, with the three dominant species (S28, S17, S40, see Table 1 for species names) are all distributed on the right portion of the ordination space (Fig. 4). Along the first axis, precipitation (*MAP*) increases from left to right, and a number of dominant species (S97, S95, S92, S62, S90, S102, S86, S42, S24, S93, S40, S17, S28) appeared along the gradient with increasing *MAP* (Fig. 4).

The ranges of temperature and altitude are relatively narrow in this study (Table 2). *MAP* played a more important role than other variables in determining community distribution, a fact that can be attributed to the comparatively larger range of this factor. Our results are consistent with previous studies that also show that precipitation patterns significantly affected community structure and species diversity in Northern Tibetan Plateau (Yang *et al.*, 2004, Wu *et al*., 2012). A similar aridity gradient effect on the zonation of vegetation types in Tibetan Plateau has been described by Chang (1981). But some special species such as the grass *S. purpurea* was present in 12 different plant communities and spanned three grassland types. This indicates that *S. purpurea* is able to inhabit a wide range of ecological conditions. Hu *et al.* (2012) suggested that *S. purpurea* might be able to maintain stable physiological function by changing leaf density and thickness when exposed to cold or drought conditions. Another species found in a wide range of ecological conditions was *Stipa* species, which contributes significantly to the abundance of the Tibetan Plateau grasslands and largely determines the value of these grasslands as forage for wild and domestic ungulates (Schaller, 1998).

3.3 Environmental interpretation and variation partitioning

The DCCA ordination analysis indicated that the total variation within the species abundance matrix was 8.55. The sum of canonical eigenvalues for environment factors was 6.28, for Geo-spatial factors, 2.53 for pure environment factors (when Geo-spatial factors are removed), and 1.05 for pure Geo-spatial factors (when environmental factors are removed). Most (73.5%) of the community distribution variation was explained by environmental variables and somewhat less (56.2%) by Geo-spatial factors, such as latitude and longitude. Environmental factors alone explained (29.6%) and Geo-spatial factors alone explained 12.3% of the total variation while 43.9% of the total variation was explained by their shared intersection. Only a small fraction (14.2%) remained unexplained, most likely due to interspecific interactions, degradation caused by grazing and other random factors (Borcard *et al*., 1992). This indicates that environmental variables strongly control community distribution in alpine grasslands, at least in comparison to more mosaic and complex systems.

The influence of environmental factors on the vegetation spatial pattern includes both pure environmental factors and their intersection with spatial variables. Their intersection plays a dominant role (43.9%), which implies that environmental conditions and community distribution have a fairly similar spatial structuring (Borcard *et al*., 1992, Song *et al*., 2010) and that the spatial pattern of the alpine Tibetan grassland is the result of mutual development between plants and environment.

The environmental interpretation of the vegetation pattern varies with vegetation complexity. In the alpine grasslands studied here, 73.5% of the total variation of community distribution was explained by environmental variables. This high explanation rate further supports our hypothesis - that the explanatory power of environmental factors on community distribution increases with a declining vegetation complexity and with abiotic stress such as low temperature and aridity (from subtropical evergreen broad-leaved forest, temperate typical steppe to alpine grassland).

4 Conclusions

In our field survey, only 14 communities are identified in the 1200-km long, (almost) linear transect. The vegetation composition and its spatial pattern is mainly driven by mean annual precipitation on the Northern Tibetan plateau. For the communities found, most distribution variation is explained by environmental variables, and this is higher than for other lowland communities. The presented data from the extremely cold and arid Alpine grasslands of Tibet, complements our knowledge on species composition distribution and its driving factors.

References

Barthlott W, Lauer W, Placke A. 1996. Global distributions of species diversity in vascular plants. Towards a world map of phytodiversity. *Erdkunde*, 50: 317–328.

Borcard D. 1992. Partialling out the spatial component of ecological variation. *Ecology*, 73(3): 1045–1055.

Chang H S. 1981. The vegetation zonation of the Tibetan Plateau. *Mountain Research and Development*, 1(1): 29–48.

Chen B X, Zhang X Z, Tao J *et al*. 2014. The impact of climate change and anthropogenic activities on alpine grassland over the Qinghai-Tibet Plateau. *Agricultural and Forest Meteorology*, 189: 11–18.

Chinese Academy of Sciences, Integrative Expedition Team to Qinghai-Tibet Plateau, 1988. The Vegetation of Xizang (Tibet). Beijing: Science Press. (in Chinese)

Cincotta R P, Soest P J V, Robertson J B, *et al*. 1991. Foraging ecology of livestock on the Tibetan Changtang: A comparison of three adjacent grazing areas. *Arctic Antarctic and Alpine Research*, 23: 149–161.

Duan M, Gao Q Z, Wan Y F, *et al*. 2010. Effects of grazing on community characteristics and species diversity of Stipa purpurea alpine grassland in Northern Tibet. *Acta Ecologica Sinica,* 30(14): 3892–3900. (in Chinese)

Gao Q Z, Wan Y F, Li Y, *et al*. 2010a. Spatial and temporal pattern of alpine grassland condition and its response to human activities in Northern Tibet, China. *Rangeland Journal*, 32: 165–173.

Gao Q Z, Wan Y F, Xu H M, *et al*. 2010b. Alpine grassland degradation index and its response to recent climate variability in Northern Tibet, China. *Quaternary International*, 226(2): 143–150.

Hartmann H, 1999. Studien zur Flora und Vegetation im östlichen Transhimalaya von Ladakh (Indien). *Candollea*, 54: 171–230.

Hill P S. 2005: TWINSPAN for Windows version 2.3. Centre for Ecology & Hydrology and University of South Bohemia, Huntingdon & České Budějovice.

Hu M Y, Lin Z, Luo T X, *et al.* 2012. Variations in leaf functional traits of Stipa purpurea along a rainfall gradient in Xizang, China. *Chinese Journal of Plant Ecology*, 36(2): 136–143. (in Chinese)

Klimeš L. 2003. Life-forms and clonality of vascular plants along an altitudinal gradient in E Ladakh (NW Himalayas). *Basic and Applied Ecology*, 4(4): 317–328.

Klimeš L, Doležal J. 2010. An experimental assessment of the upper elevational limit of flowering plants in the western Himalaya. *Ecography*, 33(3): 590–596.

Legendre P. 2008. Studying beta diversity: ecological variation partitioning by multiple regression and canonical analysis. *Journal of Plant Ecology*, 1(1): 3–8.

Legendre P, Fortin M J.1989. Spatial pattern and ecological analysis. *Plant Ecology*, 80(2): 107–138.

Lepš J, and Šmilauer P. 2003. Multivariate Analysis of Ecological Data Using CANOCO. Cambridge, Cambridge University Press.

Li H X, Liu S Z. 2005. Systematic analysis on the driving force of grassland degradation in North Tibet. *Research of Soil and Water Conservation*, 12(6): 215–217. (in Chinese)

Li M S. 2000. Rational exploitation of grassland resources in the Northern Xizang Plateau. *Journal of Natural Resources*, 15(4): 335–339. (in Chinese)

Li S Q, Wang D M, Wang T, *et al*. 2011. Spatial pattern analysis of herbaceous community for dominant species and communities in Changzhi wetland, Shanxi. *Acta Prataculturae Sinica*, 20(3): 43–50. (in Chinese)

Li X J, Zhang X Z, Wu J S, *et al*. 2011. Root biomass distribution in alpine ecosystems of the northern Tibetan Plateau. *Environmental Earth Sciences*, 64(7): 1911–1919.

Meng D, Zhang J T, Li M. 2012. Diversity of woodland communities and plant species along an altitudinal gradient in the Guancen Mountains, China. *Scientific World Journal*, (2): 1-7. doi:10.1100/2012/398765.

Miehe G, Bach K, Miehe S, *et al*. 2011. Alpine steppe plant communities of the Tibetan highlands. *Applied Vegetation Science*, 14(4): 547–560.

Mucina L. 1997. Classification of vegetation: past, present and future. *Journal of Vegetation Science*, 8(6): 751–760.

Ninyerola M, Pons X, Roure J M. 2000. A methodological approach of climatological modelling of air temperature and precipitation through GIS techniques. *International Journal of Climatology*, 20(14): 1823–1841.

Schaller G B. 1998. Feeding ecology of ungulates. In Wildlife of the Tibetan steppe. The University of Chicago Press.

Braak C J F, Smilauer P. 2002. CANOCO reference manual and user's guide to Canoco for Windows: Software for Canonical Community Ordination (version 4.5). Microcomputer Power, Ithaca, NY, US

Tichy´ L, Chytry´ M. 2006. Statistical determination of diagnostic species for site groups of unequal size. *Journal of Vegetation Science*, 17(6): 809–818.

Wang J T. 1988. The steppes and deserts of Xizang plateau (Tibet). *Plant Ecology*, 75: 135–142.

Wu J S, Shen Z X, Zhang X Z. 2014a. Precipitation and species composition primarily determine the diversity-productivity relationship of alpine grasslands on the Northern Tibetan Plateau. *Alpine Botany*, 124(1):13–25.

Wu J S, Shen Z X, Shi P L, *et al*. 2014b. Effects of grazing exclusion on plant functional group diversity alpine grasslands along a precipitation gradient on the Northern Tibetan Plateau. *Arctic Antarctic and Alpine Research*, 46(2): 419–429.

Wu J S, Zhang X Z, Shen Z X, *et al*. 2013. Grazing-exclusion effects on aboveground biomass and water-use efficiency of alpine grasslands on the Northern Tibetan Plateau. *Rangeland Ecology and Management*, 66(4): 454–461.

Xiong D P, Shi P L, Sun Y L *et al*. 2014. Effects of grazing exclusion on plant productivity and soil carbon, nitrogen storage in alpine meadows in northern Tibet, China. *Chinese Geographical Science*, 24(4): 488–498.

Xu G P, Chao Z G, Wang S P, *et al*. 2010. Temperature sensitivity of nutrient release from dung along elevation gradient on the Qinghai-Tibetan Plateau. *Nutrient Cycling in Agroecosystems*, 87(1): 49–57.

Yang Y H, Rao S, Hu H F, *et al*. 2004. Plant species richness of alpine grasslands in relation to environmental factors and biomass on the Tibetan Plateau. *Chinese Biodiversity*, 12(1): 200–205. (in Chinese)

Yu C Q, Zhang Y J, Claus H *et al*. 2012. Ecological and environmental issues faced by a developing Tibet. *Environmental Science and Technology*, 46(4): 1979–1980.

Zhang J T. 1995. Methods in Quantitative Vegetation Ecology. Beijing: Science Technology Press. (in Chinese)

Zhang J T. 2004. Quantitative Ecology. Beijing: Science Press. (in Chinese)

Zhong L, Ma Y, Salama M S, *et a*l. 2010. Assessment of vegetation dynamics and their response to variations in precipitation and temperature in the Tibetan Plateau. *Climatic Change*, 103: 519–535.

Zhou X M, Wang Z B, Du Q. 1987. The Vegetation of Qinghai. Xining: Qinghai People’s Press. (in Chinese)

藏北高原植被的分布与环境和空间因素的关系分析

田 莉[1,3]，张扬建[1,2]，Claus HOLZAPFEL[4]，黄 珂[1]，陈 宁[1]，陶 建[1]，朱军涛[1]

1. 中国科学院地理科学与资源研究所生态系统网络观测与模拟重点实验室拉萨生态实验站，北京 100101;
2. 中国科学院地理科学与资源研究所生态系统网络观测与模拟重点实验室高原生态研究中心，北京 100101;
3. 中国科学院地理科学与资源研究所生态系统网络观测与模拟重点实验室千烟洲生态实验站，北京 100101;
4. 美国罗格斯大学新泽西州立纽瓦克分校生物科学系，纽瓦克 NJ 07102，美国

摘 要：环境和空间因素长期以来被视为决定物种组成和分布的关键因素。然而，这些因素对高原植被的影响研究较少。青藏高原拥有一个独特的生态系统和全球环境梯度极端值。我们的目标是量化藏北高寒草地群落的空间分布，揭示植被的物种组成、空间因素和环境因素。在藏北高寒草地分布区，我们沿着 1200 公里长的梯度建立了 63 个采样点，采用双向指示种分析（TWINSPAN）和去趋势典范对应分析（DCCA）。调查发现沿横断面可识别的三种类型（高山草甸，高山草原，沙漠草原）中有 14 个高寒草地种群。分析发现高寒草地的植被组成和空间分布主要由年平均降雨量影响，受温度影响较小。沿着该断面，73.5%植被分布的变化能够被环境变量解释，56.3% 被空间因素解释。环境和空间因素分别解释了总变异的 29.6%和 12.3%，而他们交互作用解释了 43.9%。我们的研究结果为藏北高寒草地的生物和环境保护提供强有力的实证依据。

关键词：高寒草地；环境解说；空间格局；青藏高原；植被组成

Table S1 List of species distributed along the Northern Tibet transect

No.	Species	Family name	No.	Species	Family name
S1	*Pedicularis alaschanica*	Scrophulariaceae	S28	*Kobresia pygmaea*	Cyperaceae
S2	*Leontopodium nanum*	Compositae	S29	*Thalictrum alpinum*	Ranunculaceae
S3	*Kobresia tibetica*	Cyperaceae	S30	*Glaux maritima*	Primulaceae
S4	*Festuca coelestis*	Gramineae	S31	*Saussurea graminea*	Compositae
S5	*Dracocephalum heterophyllum*	Labiatae	S32	*Elymus atratus*	Gramineae
S6	*Ranunculus banguoensis*	Ranunculaceae	S33	*Dracocephalum tanguticum*	Labiatae
S7	*Heteropappus semiprostratus*	Compositae	S34	*Blysmussinocompressus*	Cyperaceae
S8	*Oxytropis glacialis*	Leguminosae	S35	*Leontopodium ochroleucum*	Compositae
S9	*Incarvillea younghusbandii*	Bignoniaceae	S36	*Oxytropis chiliophylla*	Leguminosae
S10	*Rhodiola sangpo-tibetana*	Crassulaceae	S37	*Potentilla fruticosa*	Rosaceae
S11	*Stracheya tibetica*	Leguminosae	S38	*Potentilla anserina*	Rosaceae
S12	*Astragalus hendersonii*	Leguminosae	S39	*Leymus secalinus*	Gramineae
S13	*Kobresia robusta*	Cyperaceae	S40	*Lancea tibetica*	Scrophulariaceae
S14	*Kobresia macrantha*	Cyperaceae	S41	*Stellera chamaejasme*	Thymelaeaceae
S15	*Androsacetapete*	Primulaceae	S42	*Poa crymophila*	Gramineae
S16	*Arenaria pulvinata*	Caryophyllaceae	S43	*Chenopodium tibeticum*	Chenopodiaceae
S17	*Potentilla saundersiana*	Rosaceae	S44	*Heracleum millefolium*	Umbelliferae
S18	*Artemisia stracheyi*	Compositae	S45	*Gentiana leucomelaena*	Gentianaceae
S19	*Oxytropis biflora*	Leguminosae	S46	*Gentiana algida*	Gentianaceae
S20	*Lamiophlomis rotata*	Labiatae	S47	*Taraxacum eriopodum*	Compositae
S21	*Lagotis brachystachya*	Scrophulariaceae	S48	*Festuca wallichanica*	Gramineae
S22	*Potentilla multifida*	Rosaceae	S49	*Potentilla fragarioides*	Rosaceae
S23	*Astragalus polycladus*	Leguminosae	S50	*Anaphalis xylorhiza*	Compositae
S24	*Potentilla bifurca*	Rosaceae	S51	*Corydalis hendersonii*	Papaveraceae
S25	*Trigonotis rockii*	Boraginaceae	S52	*Poanimuana*	Gramineae
S26	*Arenaria gerzeensis*	Caryophyllaceae	S53	*Astragalus tribulifolius*	Leguminosae
S27	*Saussureaalpina*	Compositae	S54	*Elymusdahuricus*	Gramineae

Continued

No.	Species	Family name	No.	Species	Family name
S55	*Myricaria prostrata*	Tamaricaceae	S81	*Eritrichium sinomicrocarpum*	Boraginaceae
S56	*Taraxacum tibeticum*	Compositae	S82	*Artemisia minor*	Compositae
S57	*Koeleria cristata*	Gramineae	S83	*Sedum fischeri*	Crassulaceae
S58	*Artemisia duthreuil-de-rhinsi*	Compositae	S84	*Deyeuxia pulchella*	Gramineae
S59	*Carex moorcroftii*	Cyperaceae	S85	*Torularia parvua*	Cruciferae
S60	*Morina kokonorica*	Dipsacaceae	S86	*Kobresia humilis*	Cyperaceae
S61	*Pleurospermum pulszkyi*	Umbelliferae	S87	*Oxytropis mi crophylla*	Leguminosae
S62	*Swertia tetraptera*	Gentianaceae	S88	*Poa parvissima*	Gramineae
S63	*Pedicularis cheilanthifolia*	Scrophulariaceae	S89	*Potentilla cuneata*	Rosaceae
S64	*Roegneria thoroldiana*	Gramineae	S90	*Festuca ovina*	Gramineae
S65	*Thalictrum foetidum*	Ranunculaceae	S91	*Allium fistulosum*	Alliaceae
S66	*Youngia simulatrix*	Compositae	S92	*Erigeron annuus*	Compositae
S67	*Astragalus acaulis*	Leguminosae	S93	*Carex ivanoviae*	Cyperaceae
S68	*Arenaria serpyllifolia*	Caryophyllaceae	S94	*Silene fortunei*	Caryophyllaceae
S69	*Euphorbia tibetica*	Euphorbiaceae	S95	*Stipa subsessiliflora*	Gramineae
S70	*Saussurea tibetica*	Compositae	S96	*Gentiana crenulato-truncata*	Gentianaceae
S71	*Viola kunawarensis*	Violaceae	S97	*Ptilotrichum canescens*	Brassicaceae
S72	*Pleurospermum thomsonii*	Umbelliferae	S98	*Carex moorcroftii*	Cyperaceae
S73	*Polygonum thomsonii*	Polygonaceae	S99	*Oxytropis stracheyana*	Leguminosae
S74	*Silenegracilicaulis*	Caryophyllaceae	S100	*Salsola nepalensis*	Chenopodiaceae
S75	*Artemisia demissa*	Compositae	S101	*Trigonotispeduncularis*	Boraginaceae
S76	*Arenaria bryophylla*	Caryophyllaceae	S102	*Stipa purpurea*	Gramineae
S77	*Amaranthus viridis*	Amaranthaceae	S103	*Eritrichium hemisphaericum*	Boraginaceae
S78	*Dimorphostemon pinnatus*	Cruciferae	S104	*Carex dolichostachya*	Cyperaceae
S79	*Dimorphostemon glandulosus*	Cruciferae	S105	*Androsace graminifolia*	Primulaceae
S80	*Astragalus pulvinatus*	Leguminosae	S106	*Stipa capillata*	Gramineae

Table S2 The number of species, vegetation coverage and environmental variables in each study site

Study site	Species number	Vegetation coverage (%)	*MAP* (mm)	*MAT* (°C)	*ALT* (m)
P1	2	4	242	0.62	4522
P2	2	2	255	−0.10	4505
P3	3	2	252	0.58	4544
P4	4	21	283	−0.88	4814
P5	3	18	268	0.60	4609
P6	5	19	256	1.19	4420
P7	3	8	254	0.86	4406
P8	2	8	265	0.67	4470
P9	5	13	265	0.67	4456
P10	3	4	277	0.35	4427
P11	5	27	272	0.99	4374
P12	3	6	282	0.46	4475
P13	3	25	289	0.15	4524
P14	3	6	288	0.56	4463
P15	3	11	293	0.70	4435
P16	7	17	314	0.01	4590
P17	6	31	357	−2.32	4877
P18	4	18	364	−2.17	4953

Continued

Study site	Species number	Vegetation coverage (%)	*MAP* (mm)	*MAT* (℃)	*ALT* (m)
P19	2	21	349	−1.09	4755
P20	4	17	345	−0.75	4678
P21	6	18	334	0.39	4494
P22	10	21	350	−0.26	4622
P23	10	18	349	−0.19	4589
P24	5	18	351	−0.26	4636
P25	6	22	352	−1.53	4814
P26	6	33	335	−0.85	4660
P27	6	35	353	−0.10	4579
P28	10	29	353	−0.04	4546
P29	8	26	354	−0.07	4533
P30	6	32	373	−0.90	4666
P31	7	29	384	−0.84	4572
P32	6	17	370	−0.22	4571
P33	10	20	377	−0.09	4549
P34	9	31	394	-0.25	4596
P35	9	22	401	−0.03	4608
P36	8	48	444	−0.72	4617
P37	10	55	456	−1.59	4803
P38	8	39	450	−1.44	4793
P39	10	38	391	−0.97	4647
P40	6	25	389	−0.41	4570
P41	9	29	395	−0.35	4574
P42	8	37	455	−0.48	4650
P43	11	29	459	−0.41	4632
P44	9	43	465	−1.17	4788
P45	9	46	463	−0.24	4605
P46	6	39	473	−0.29	4590
P47	12	57	481	0.00	4548
P48	8	57	510	−0.85	4654
P49	8	54	502	−0.50	4568
P50	8	48	520	−0.89	4622
P51	9	75	536	−1.51	4566
P52	10	71	502	−1.26	4631
P53	10	72	531	−2.09	4788
P54	12	69	525	−1.13	4661
P55	7	60	551	−0.31	4586
P56	9	49	539	0.04	4537
P57	10	75	543	−0.13	4577
P58	7	82	535	−0.77	4595
P59	10	76	535	−0.77	4589
P60	6	77	535	−0.77	4596
P61	8	83	535	−0.77	4585
P62	7	66	536	−0.75	4591
P63	9	71	543	−0.93	4602

Note: *MAP* means annual precipitation; *MAT* means annual temperature.