



SPECIAL FEATURE: VEGETATION SURVEY

## Alpine steppe plant communities of the Tibetan highlands

Georg Miehe, Kerstin Bach, Sabine Miehe, Jürgen Kluge, Yang Yongping, La Duo, Sonam Co & Karsten Wesche

### Keywords

Alpine desert; Endemics; Grazing; Plant functional types; Qinghai-Tibet Plateau; Steppe.

### Nomenclature:

Wu (1983–86), Liu (1992–99), Dickoré (1995) and the currently published volumes of Flora of China (Wu & Raven 1994).

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**Miehe, G.** (corresponding author, miehe@staff.uni-marburg.de); **Bach, K.** (bachk@staff.uni-marburg.de); **Miehe, S.** (Sabine.Miehe@gmx.net) & **Kluge, J.** (klugej@staff.uni-marburg.de): Faculty of Geography, University of Marburg, Deutschhausstraße 10, D-35032 Marburg, Germany  
**Yang Y.** (yangyp@itpcas.ac.cn): Kunming Institute of Botany, CAS, Heilongtan, Yunnan 650204, China  
**La Duo** (lhagdor2004@yahoo.com) & **Sonam Co** (Sonamtsco@hotmail.com): Department of Biology, Tibet University Lhasa, 36 Jiangso Road, Lhasa, A.R. Xizang 850000, China  
**Wesche, K.** (karsten.wesche@senckenberg.de): Senckenberg Museum of Natural History Görlitz, PO Box 300 154, 02806 Görlitz, Germany.

### Introduction

The Tibetan highlands host the highest and the least known steppe biome worldwide, namely the short-grass alpine steppe dominated by Poaceae, Cyperaceae and cushion plants. These alpine steppes comprise the largest biome of the Tibetan highlands, covering ca. 800 000 km<sup>2</sup>, mainly in the central and western highlands. *Kobresia pygmaea* pastures of the southeastern highlands cover ca.

### Abstract

**Aim:** To present a first description of plant communities of the Tibetan alpine steppes based on floristically complete vegetation records as a baseline reference for future ecological and palaeoecological studies. These constitute the world's largest alpine biome, but their vegetation is virtually unknown. Due to their vast extent, they are relevant for functioning of large-scale climatic systems. In turn, arid and alpine biomes are suspected to be highly sensitive to ongoing climate change, underwent climate-driven changes during the Last Glacial Maximum and have been subject to overgrazing and desertification.

**Location:** Northwestern Tibetan highlands (China: Xizang, Qinghai), 4200 to 5400 m a.s.l., total area ca. 800 000 km<sup>2</sup>.

**Methods:** Two hundred and fifty-three vegetation records with absolute percentage cover were classified based on expert knowledge and analysed by DCA; composition of plant functional types related to grazing resilience was also assessed.

**Results:** Ten communities of alpine steppe were distinguished. A set of 11 alpine steppe species is distributed throughout the highlands, with a precipitation gradient between 350 mm yr<sup>-1</sup> (southeast) and 20 to 50 mm yr<sup>-1</sup> (northwest). The elevational range of more than 80% of species is larger than 1000 m. The data set comprises 30% endemic species, with ten endemic genera.

**Conclusions:** The wide thermal and hygric range of many species and high rate of endemism do not support the idea of high sensitivity to climate change or occurrence of past climate-driven extinctions. The prevailing plant functional types are grazing resilient, and evidence for overgrazing is very limited. Cushion plants and dwarf shrubs, however, become increasingly rare around settlements, because they are uprooted for fuel. Hence, the world's largest arid alpine biome is apparently resilient to climatic changes and grazing. This contradicts common perceptions about arid and alpine ecosystems and therefore deserves intense multi-disciplinary research efforts.

450 000 km<sup>2</sup> (Miehe et al. 2008), while the high-alpine biome of gelifluction-adapted plant communities on the higher slopes of the mountain massifs cover ca. 400 000 km<sup>2</sup>. Cyperaceae swamps cover ca. 80 000 km<sup>2</sup> (Zhang et al. 1981; Atlas Tibet Plateau 1990; Miehe & Miehe 2000).

Due to the sheer size of the alpine steppes, radiation feedback effects are of undisputed relevance for future global change scenarios. They act as a high-elevation heat

source of importance to global circulation (Shi et al. 2001; Duan & Wu 2005). Knowledge of landscape surface properties is therefore of more than just regional interest. The biome falls into Diversity Zone 1, as one of the world's species-poorest areas (Barthlott et al. 1996). A number of floras cover the alpine steppes (Flora Xizangica, Wu 1983–86; Flora Qinghaiica, Liu 1992–99; Hoh Xil area, Wu & Feng 1996; Aksai Chin, Miehe et al. 2002). The most comprehensive current accounts of vegetation of the alpine steppe are those of Zhang (1988) and Wu & Feng (1996), both in Chinese, with vegetation maps (scale 1:1 to 1:3 Mio). Wang (1988) gives a description of the main plant communities with an enumeration of dominant species, and similar vegetation was also described for eastern Ladakh (Hartmann 1987, 1990, 1999; Klimeš 2003; Klimeš & Doležal 2010). However, given the vast area and unique structure of this region, surprisingly little is known about the plant communities.

Here, we give the first description of plant communities in alpine steppes of Tibet based on floristically complete vegetation records, providing for the first time data on elevational and hygric distribution ranges. Our floristic analyses allow determination of the abundance of endemic plants as a key proxy for palaeo-ecological *tabula rasa* scenarios (Kuhle 2001; Owen et al. 2005). Given that the alpine steppes have been used for centuries by nomads and their livestock (Rhode et al. 2007; Miehe et al. 2009), and before that by wild mammals, we also provide an analysis of grazing-related plant functional traits.

As arid as well as alpine biomes are thought to be highly susceptible to climatic and human impacts (Körner 1999; Kuper & Kröpelin 2006), our hypotheses are that (a) these alpine steppes are sensitive to climate changes, and thus (b) underwent wide extinction climatic impacts during the Last Glacial Maximum, and (c) are sensitive to grazing impacts.

## Methods

### Study area

The study area comprises the (semi-)arid parts of the Tibetan highlands with precipitation of  $< 350 \text{ mm yr}^{-1}$  (Fig. S1), comprising large parts of the Central Asian interior drainage system, but also the upper catchments of major rivers (Huang He, Yangtze, Yarlung Zangbo/Brahmaputra, Indus). The median elevation of our vegetation records is 4725 m, which reflects mean elevations of this biome. Summer precipitation prevails, with an increase of inter-annual variability towards the west. Even during periods of fair weather, thunderstorms occur regularly in the afternoon, producing hail that accumulates around taller plants. At elevations  $> 5000 \text{ m}$ , slush

is common in summer. Periodic heavy snowfall occurs, although snow cover-dependent plant communities are absent. Due to mass elevation effects, summer temperatures are relatively high (e.g. Gerze, 4415 m a.s.l., mean July temperature  $12^\circ\text{C}$ ; Fig. S2). Night frosts in spring cause needle-ice solifluction promoting the evolution of deflation pavements, particularly in the traverse river terraces in the rain shadow of the Himalaya. On summer nights, frosts are rare at elevations  $< 4500 \text{ m}$ . Higher up, frosts occur all year round. In the highlands north of ca.  $32^\circ\text{N}$ , the alpine steppes grow on continuous permafrost (Atlas Tibet Plateau 1990), creating a microrelief with numerous shallow ponds.

Most of the highlands are rolling hills of between 300 and 800 m within intra-montane basins of between 4500 and 4700 m a.s.l.; upper slopes are often covered with frost-shattered rock debris. The lower slopes and wide pediments bear a thin cover of loess (Kaiser 2004), whereas basins and larger valleys have gravel terraces and extended lake terraces. Salt swamps and dune fields occur around the – mostly saline – lakes. The prevailing soil types (Fig. S2) underline the aridity of the environment, with salt-crusts being common in the northwest (Fig. S3).

Most of the wild herbivore species are endemic to the Tibetan highlands (Schaller & Gu 1994), indicating the long-lasting impact of grazing. The Tibetan highlands are thus a low-productivity system with a long history of grazing on an evolutionary time scale (Cingolani et al. 2005). Starting from at least 8000 BP and possibly earlier (Miehe et al. 2009), human land use thus (at least partly) replaced a natural grazing system. Unpredictability of summer precipitation as the main driver of forage availability is moderate in Tibet, which is in contrast to the unpredictability of snowfall in winter. It seems that stock numbers are controlled by snowfall events, which trigger losses of 20 to 30% (Goldstein et al. 1990; Miller 2005). The winter pastures are bound to areas with low snowfall risk and direct access to the (then frozen) wetland vegetation (Goldstein et al. 1990; Miller 2005; Behrendes 2008). Currently, pastoral nomads are increasingly sedentarized (Long 2003; Næss et al. 2004; Behrendes 2008), and goats and sheep are the dominant stock in the alpine steppes (only 4% yak, Miller 2005).

### Vegetation sampling

Our database comprises 253 vegetation plots from the Central Tibetan highlands collected between 1992 and 2005 (by G. Miehe, S. Miehe, J. Nödling and J. Hanspach). Plots cover a longitudinal distance of 1200 km (Fig. S1). The elevation of the plots ranges from 4060 m in the east to 5360 m a.s.l. in the west, representing a proper alpine

belt. Traversing the alpine steppe regions along several routes, we collected a minimum of eight to ten plots of the main physiognomically different vegetation types. At a given location, selection of record sites, however, was deliberate, choosing homogeneous representative plots. Plots were always 10 × 10 m in size and geo-referenced using a Garmin 12 XL GPS. All vascular plant species were recorded with their absolute cover percentage, which seemed most feasible with respect to the rather open vegetation.

### Data analyses

The species by plot matrix was subjected to a detrended correspondence analysis (DCA, Hill & Gauch 1980), with log-transformed species cover values ( $\log(x+1)$ ) and detrending by 26 segments. The sequence of plots along the first axis was used to pre-order plots into groups. Further classification relied on manual phytosociological table analysis: in a basically iterative procedure, species and sample groups were successively re-arranged with the aim of devising groups characterized by more-or-less exclusive species (mainly presence/absence). Fidelity of characteristic species for the plant communities was additionally assessed using the  $\phi$  coefficients of association ( $\Phi$ ), with a threshold of 0.6 (based on equalized group size). Table analysis allowed us to devise clear classification rules that are presented as a dichotomous classification key (see Appendix S1). The key can be used for *a posteriori* assignment of further samples. Analyses were performed using PC-ORD 4.41 (MjM Software, Gleneden Beach, OR, USA) and JUICE 6.5 (Tichý 2002).

Plant species were grouped into functional types with special emphasis on grazing, largely following Grime (1977) and Díaz et al. (1992). Thus, the main criteria (see Fig. 1) were whether the bud is exposed to grazing or not, and whether plants are palatable or not (for classification, see legend to Fig. 1). Data on elevational distribution ranges are a combination of our records with notes in Flora Xizangica (Wu 1983–86).

## Results and Discussion

### Ecological range and diversity

The alpine steppe lacks closed vegetation cover. Total cover varies from a mean of 43% in the east to 14% in the northwest, corresponding to increasing aridity from 350 mm yr<sup>-1</sup> in the east to 20–50 mm yr<sup>-1</sup> in the west. Eighty per cent of the plants of the alpine steppe attain maximum cover of below 1%, and even for those with the highest frequency (e.g. *Stipa purpurea*, *Poa albertii* ssp. *albertii*), 75% of their records represent cover percentages of < 5%.

Alpine steppes host the most elevated vascular plant communities. The most widespread species (Table S1: alpine steppe species) have their upper distribution limit well above 5100 m a.s.l. Eighty-three per cent of all species have a vertical distribution range covering > 1000 m. Mean species numbers of communities 1 to 7 (alpine steppes) range between 20 (communities 4 and 6) and 28 (community 2, Table 1), while the range for alpine desert steppes (communities 8 to 10) is four to 13. Plot-level diversity and precipitation are highly correlated ( $R = -0.85$ ,  $P < 0.001$ ).

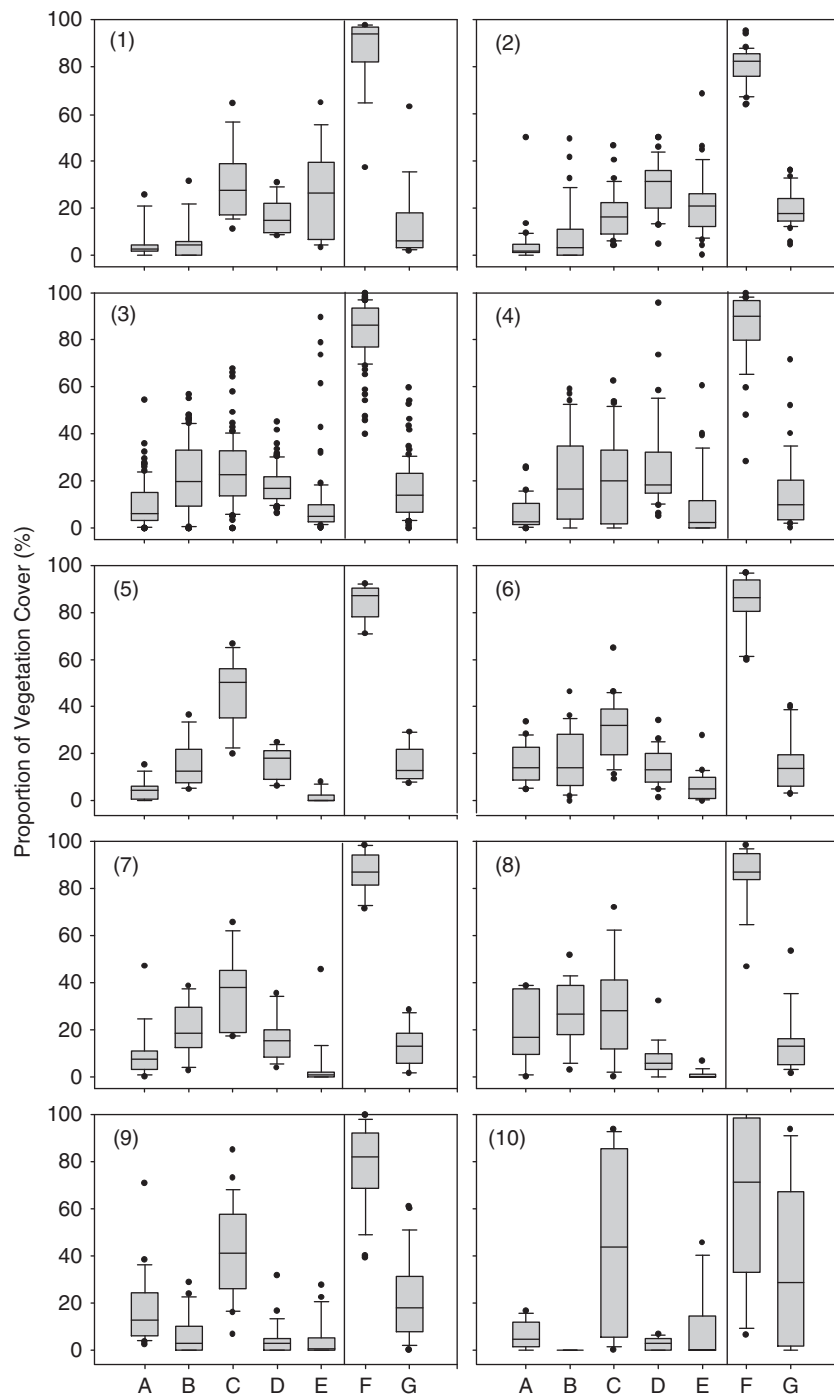
### Flora and plant functional types

We recorded 5145 occurrences of 288 flowering plant taxa (125 genera, 34 families). Mosses, mostly annual acrocarpous taxa, are rare (Pottiaceae, *Bryum*, Ditrichaceae, Funariaceae) and were not included in further analyses.

Asteraceae (18%), Poaceae (17%), Fabaceae (8%), Brassicaceae (7%) and Cyperaceae (6%) constitute 56% of all encountered species. The most diverse genera are *Saussurea* (17 species), *Poa* (13), *Artemisia* (13), *Kobresia* (11), *Astragalus* (10), *Oxytropis* (10) and *Potentilla* (9). The alpine steppe biome hosts 92 endemic taxa with ten endemic genera (Wu 1983–86; Liu 1992–99): *Littledalea*, *Kengyilia*, *Sinochasea*, *Stracheya*, *Milula*; the endemic *Cortella*, *Microula*, *Oreosolen*, *Przewalskia* and *Pomatosace* are common around settlements but their natural habitat is most probably on soil heaps in front of burrows of the endemic pika (*Ochotona curzoniae*, Yu et al. 2000) or open sites created by wallowing of wild herbivores (Tibetan wild ass, yak).

Alpine steppes are short-grass steppes with cushion plants (Fig. S4). Only a few plants exceed 15 cm in height, especially when grazed. A few taller species are poisonous and/or avoided by livestock (e.g. *Stellera chamaejasme*, *Cryptothladia kokonorica*, *Thermopsis* spp.); these are especially common at more productive sites with higher and reliable precipitation, where grazing impact is generally higher (Vetter 2005). However, the majority of plants is < 5-cm tall. Fifty per cent of the 288 species are plants forming rosettes, mats or cushions, constituting up to 46% of the total plant cover. Thirty-eight per cent of the cover is constituted by graminoids with buds close to the ground (e.g. *Stipa*) or rhizomes (e.g. *Carex moorcroftii*, *Kobresia stolonifera*). In total,  $83 \pm 15\%$  (mean  $\pm$  SD) of the vegetation cover is composed of grazing-tolerant species. However, it remains uncertain whether this reflects evolutionary adaptation to grazing or to cold and windy conditions (Körner 1999).

The most distinct plant life forms of the alpine steppes are plate-shaped cushions (Fig. S5), with a dense,



**Fig. 1.** Cover of main plant functional types (classified according to grazing tolerance) in communities 1 to 10. Each box plot is constructed from five values: the smallest value, the first quartile, the median, the third quartile, and the largest value. A=Plate-shaped cushions; B=Flat cushions (e.g. *Androsace tapete*); C=Buds close to the soil level (e.g. *Stipa purpurea*) or rhizomes (e.g. *Carex moorcroftii*); D=Rosettes (e.g. *Taraxacum sherriffii*); E=Poisonous (e.g. *Astragalus monbeigii*), spiny (e.g. *Cryptothladia*) or unpalatable at least during the growing season (e.g. *Artemisia* spp.); F=all grazing resilient plant functional types; G=non-grazing resilient plants (mostly graminoids, e.g. *Poa albertii*).

completely flat surface that does not protrude from the ground. The main genera are *Saussurea*, *Astragalus*, *Oxytropis*, *Potentilla* and *Sibbaldianthe*. This cushion type is

common in the arid South American Andes ('Tellerpolster' *sensu* Werdermann 1931; Rauh 1939). *Kobresia yadongensis*, *K. pygmaea*, *Carex sagaensis* or *Juncus trifidus* have

**Table 1.** Synoptic table for communities 1 to 10, listing all characteristic species and further remarkable species. Species having a higher fidelity value than 0.6 are marked in bold and with an asterisk within the corresponding community. Numbers in cells indicate frequency (%) of a species in a given community, overall frequency is given in the last column.

Community No.	1	2	3	4	5	6	7	8	9	10	Freq. (%)
No. of relevés	14	35	90	29	8	19	13	14	23	8	
No. of species/ 100 m <sup>2</sup>	21	28	22	20	22	21	22	13	9	4	
Mean altitude (m a.s.l.)	4734	4756	4693	4700	5129	4663	4553	5177	5158	5134	
Mean vegetation cover (%)	28	34	29	31	29	30	44	26	22	15	
Mean annual precipitation (mm)	209	320	321	319	265	245	210	61	60	53	
<b>Community 1</b>											
<i>Kobresia macrantha</i>	<b>79*</b>	3	–	–	13	–	–	–	–	–	5.1
<i>Artemisia pratensis</i>	<b>50*</b>	–	–	–	–	–	–	–	–	–	2.8
<i>Poa araratica</i> ssp. <i>psilolepis</i>	<b>43*</b>	–	–	–	–	–	–	–	–	–	2.4
<i>Anaphalis xylorhiza</i>	<b>43*</b>	–	–	–	–	–	–	–	–	–	2.4
<i>Swertia hispidicalyx</i>	<b>43*</b>	–	–	–	–	–	–	–	–	–	2.4
<i>Chamaerhodos sabulosa</i>	43	–	1	–	–	21	–	–	4	13	5.1
<i>Allium fasciculatum</i>	36	3	–	–	–	–	–	–	–	–	2.4
<i>Kobresia prairii</i>	36	–	–	–	–	–	–	–	–	–	2
<i>Pennisetum flaccidum</i>	29	6	–	–	–	–	–	–	–	–	2.4
<i>Androsace graminifolia</i>	21	–	–	–	–	–	–	–	–	–	1.2
<i>Onosma hookeri</i>	21	–	–	–	–	–	–	–	–	–	1.2
<i>Thermopsis lanceolata</i>	21	9	–	3	–	–	–	–	–	–	2.8
<i>Kobresia capillifolia</i>	14	6	–	–	–	–	–	–	–	–	1.6
<i>Stipa koelzii</i>	43	17	–	–	–	–	–	–	–	–	4.7
<i>Phlomis younghusbandii</i>	36	17	1	–	–	–	–	–	–	–	4.7
<b>Community 2</b>											
<i>Stellera chamaejasme</i>	14	<b>60*</b>	–	–	–	5	–	–	–	–	9.5
<i>Sedum perpusillum</i>	–	<b>69*</b>	3	7	–	–	–	–	–	–	11.5
<i>Saussurea leiocarpa</i>	–	<b>54*</b>	1	3	–	–	–	–	–	–	8.3
<i>Dracocephalum tanguticum</i>	21	43	–	–	–	–	–	–	–	–	7.1
<i>Stracheya tibetica</i>	–	37	–	–	–	–	–	–	–	–	5.1
<i>Anaphalis nubigena</i>	–	29	–	3	–	–	–	–	–	–	4.3
<i>Allium cyaneum</i>	–	29	8	–	–	5	–	–	–	–	7.1
<i>Silene caespitella</i>	14	20	7	–	–	–	–	–	4	–	6.3
<i>Astragalus monbeigii</i>	7	43	9	7	–	11	–	–	–	–	11.1
<i>Euphorbia stracheyi</i>	–	46	10	3	–	–	8	–	–	–	10.7
<i>Lomatogonium brachyantherum</i>	–	69	7	10	50	5	–	–	–	–	15
<b>Communities 1 to 4</b>											
<i>Incarvillea younghusbandii</i>	50	86	68	31	–	26	–	–	–	–	44.3
<i>Cryptothlasia kokonorica</i>	36	71	18	21	–	5	–	–	–	–	20.9

Table 1. Continued

<i>Rhodiola smithii</i>	64	34	16	3	—	16	—	—	—	—	—	15.4
<i>Chenopodium nepalense</i>	29	29	10	34	—	—	—	—	—	—	—	13
<i>Saussurea leontodontoides</i>	29	54	54	52	75	—	—	—	—	—	—	36.8
<i>Lasiocaryum munroi</i>	71	51	30	59	88	11	7	—	—	—	—	32.4
Community 3												
<i>Oreosolen wattii</i>	7	20	27	59	100	—	8	—	—	—	—	22.9
<i>Carex stenophylla</i>	—	74	76	52	—	—	—	—	—	—	—	43.1
<i>Gentiana hyalina</i>	—	63	50	38	—	—	—	—	—	—	—	30.8
<i>Viola kunawurensis</i>	7	49	37	14	—	11	—	—	—	—	—	22.5
<i>Koeleria litvinowii</i> ssp. <i>argentea</i>	—	17	36	55	—	—	15	—	—	—	—	22.1
<i>Comastoma pedunculatum</i>	—	17	32	17	—	—	—	—	—	—	—	15.8
<i>Polygonum sibiricum</i>	—	11	31	21	—	5	8	—	—	—	—	15.8
<i>Draba zongbeiensis</i>	—	6	26	17	—	11	23	—	—	—	—	13.8
<i>Artemisia tridactyla</i>	—	29	24	24	—	—	8	—	13	—	—	17
<i>Thalictrum elegans</i>	—	14	18	24	—	—	—	—	—	—	—	11.1
<i>Delphinium caeruleum</i>	7	20	17	7	—	—	—	—	—	—	—	9.9
<i>Gentiana pseudoaquadatica</i>	—	23	16	10	—	—	—	—	—	—	—	9.9
<i>Taraxacum sherriffii</i>	—	26	14	14	—	—	—	—	—	—	—	10.3
<i>Artemisia santolinifolia</i>	—	9	11	10	—	—	—	—	—	—	—	6.3
<i>Microula tangutica</i>	—	20	11	45	—	—	—	—	—	—	—	11.9
<i>Pleurospermum hedinii</i>	—	14	10	10	—	—	—	—	—	—	—	6.7
<i>Hypecaum leptocarpum</i>	—	11	4	28	—	5	—	—	—	—	—	6.7
Community 4												
<b><i>Axyris prostrata</i></b>	—	11	—	97*	13	—	—	—	—	—	—	13
<i>Hedinia tibetica</i>	—	—	6	21	13	—	—	—	—	—	—	4.7
<i>Galium exile</i>	—	—	1	17	—	—	8	—	—	—	—	2.8
<i>Lepidium capitatum</i>	—	—	—	14	—	5	—	—	—	—	—	2
<i>Artemisia hedinii</i>	—	—	—	7	—	—	—	—	—	—	—	0.8
Community 5												
<b><i>Kobresia yadongensis</i></b>	—	—	—	—	100*	—	—	—	—	—	—	3.2
<b><i>Gentiana vernayi</i></b>	—	—	—	—	88*	—	—	—	—	—	—	2.8
<b><i>Potentilla compacta</i></b>	7	—	—	—	88*	—	—	—	—	—	—	3.2
<b><i>Rheum globulosum</i></b>	—	—	—	—	75*	—	8	—	—	—	—	2.8
<b><i>Veronica ciliata</i></b>	—	11	1	3	75*	5	—	—	—	—	—	5.1
<b><i>Sinochasea trigyna</i></b>	21	—	1	—	75*	—	—	—	—	—	—	4
<b><i>Oxytropis williamsii</i></b>	14	—	—	—	75*	—	—	—	—	—	—	3.2
<b><i>Poa albertii</i> ssp. <i>poophagorum</i></b>	14	—	—	—	63*	—	—	—	—	—	—	3.2
<i>Trisetum spicatum</i> ssp. <i>spicatum</i>	—	—	—	—	38	11	—	7	—	—	—	2.4
<i>Cortella caespitosa</i>	14	—	7	14	88	21	54	—	4	—	—	11.9
Community 6												

<i>Saussurea andryaloides</i>	50	–	–	–	–	13	79	54	21	43	–	17
<i>Kobresia stolonifera</i>	36	3	3	3	–	–	58	15	–	–	–	9.1
<i>Oxytropis tatarica</i>	14	–	2	–	–	–	42	8	–	4	–	5.5
<i>Oxytropis microphylla</i>	29	–	–	–	–	–	37	8	–	–	–	4.7
<i>Alyssum canescens</i>	–	–	1	–	–	–	32	–	–	13	–	4
Community 6												
<i>Astragalus heydei</i>	21	–	10	3	–	–	32	15	–	–	–	8.3
<i>Pedicularis cheilanthisfolia</i>	–	37	3	–	–	–	26	31	7	–	–	10.3
<i>Astragalus golmunensis</i>	–	–	–	–	–	–	21	–	–	–	–	1.6
<i>Saussurea graminea</i> var. <i>ortholepis</i>	–	–	4	–	–	13	11	23	7	–	–	4.3
Community 7												
<b><i>Littledalea racemosa</i></b>	–	–	–	–	–	–	–	77*	7	–	–	4.3
<b><i>Astragalus densiflorus</i> var. <i>konlonicus</i></b>	–	–	–	–	–	–	–	62*	–	–	–	3.2
<b><i>Androsace tangulashanensis</i></b>	–	–	–	–	–	–	5	54*	7	–	–	3.6
<i>Aster flaccidus</i>	–	3	1	–	–	–	5	46	–	–	–	3.6
<i>Puccinella</i> spp. undetermined	–	–	–	–	–	–	11	38	7	–	–	3.2
<i>Oxytropis tianschanica</i>	–	–	–	–	–	–	5	31	–	–	–	2
<i>Potentilla sinonivea</i>	–	–	–	–	–	–	–	23	–	–	–	1.2
<i>Saussurea gnaphalodes</i>	–	–	–	–	–	–	–	23	21	4	–	2.8
<i>Saussurea tangutica</i>	–	–	–	–	–	–	–	15	7	–	–	1.2
High-Alpine Desert Steppe Community 8												
<i>Festuca tibetica</i>	–	–	–	–	–	50	21	15	86	4	–	9.1
<i>Astragalus strictus</i>	7	–	–	–	–	50	11	–	21	9	–	4.7
<b><i>Thylacospermum caespitosum</i></b>	–	–	–	–	–	–	–	8	79*	–	–	4.7
<b><i>Carex sagaensis</i></b>	–	–	–	–	–	–	–	8	71*	–	–	4.3
<b><i>Potentilla pamirica</i></b>	–	–	–	–	–	–	–	15	64*	13	–	5.5
<i>Stellaria decumbens</i>	–	–	–	–	–	–	5	15	43	17	–	5.1
<i>Braya rosea</i>	–	–	1	3	–	–	–	8	43	–	–	3.6
<i>Poa attenuata</i>	–	–	–	–	–	–	–	–	36	26	–	4.3
<i>Saussurea thomsonii</i>	–	–	–	–	–	–	–	–	21	–	–	1.2
<i>Soroseris glomerata</i>	–	–	–	–	–	–	–	–	14	4	–	1.2
<i>Saussurea subulata</i>	–	–	–	–	–	–	–	–	14	–	–	0.8
<i>Saussurea aster</i>	–	–	–	–	–	–	–	–	7	9	–	1.2
<i>Saussurea glacialis</i>	–	–	–	–	–	–	–	–	43	26	13	5.1
<i>Oxytropis densa</i>	–	–	–	–	–	–	–	8	79	74	50	13
Alpine Desert Steppe Communities 9 and 10												
<i>Krascheninikovia compacta</i>	–	–	–	–	–	–	5	15	7	57	63	8.7
<i>Stipa subsessiliflora</i>	7	–	–	–	–	–	11	–	7	52	50	7.9
<i>Astragalus hendersonii</i>	–	–	–	–	–	–	5	–	21	26	38	5.1
<i>Saussurea glanduligera</i>	–	–	–	–	–	–	–	–	14	22	38	4

Table 1. Continued

<i>Artemisia mihor</i>	7	–	7	7	–	11	–	21	17	25	7.9
Alpine Steppe											
<i>Carex moorcroftii</i>	14	20	16	24	63	26	46	50	78	63	30
<i>Oxytropis chiliophylla</i>	14	31	26	17		21	46	21	43	13	25.7
<i>Stipa roborovskii/purpurea</i>	79	100	93	79	13	95	62	–	39	–	74.7
<i>Leontopodium pusillum/nanum</i>	29	69	84	83	63	74	92	79	43	–	71.1
<i>Poa albertii</i> ssp. <i>albertii</i>	36	89	90	72	25	53	69	29	13	–	65.6
<i>Arenaria bryophylla/kansuensis</i>	43	23	54	24	100	58	92	71	48	–	48.2
<i>Dracocephalum heterophyllum</i>	29	43	60	38	38	47	15	14	30	–	42.3
<i>Elymus schrenkianus</i>	29	29	10	10	25	11	15	43	26	13	17.8
<i>Kobresia robusta</i>	21	29	52	31	75	58	38	7	52	–	41.1
<i>Astragalus arnoldii</i>	–	14	42	52		37	23	21	30	–	30.8
<i>Androsace tapete</i>	21	34	50	28	50	53	23	–	4	–	34
Alpine Steppe Communities 1 to 7											
<i>Potentilla bifurca</i> s.l.	36	46	66	90	25	79	31	–	9	–	51
<i>Pedicularis alaschanica</i>	29	57	58	34	13	21	8	–	–	–	36.4
<i>Artemisia stricta</i>	29	23	11	14	38	11		–	–	–	12.3
<i>Carex ivanovia/montis-everestii</i>	50	74	56	21	38	53	23	–	4	–	41.9
<i>Heteropappus semiprostratus/gouldii</i>	64	60	56	72	–	53	23	–	–	–	45.1
Alpine Steppe Communities 1 to 4, 6 and 7											
<i>Heracleum millefolium</i> var. <i>millefolium</i>	29	6	39	21	–	37	23	–	–	–	22.5
<i>Sibbaldianthe adpressa</i>	21	20	50	24	–	32	8	–	–	–	27.3
<i>Astragalus tribulifolius</i>	64	17	19	10	–	16	–	–	–	–	15
<i>Youngia simulatrix</i>	21	63	29	21	–	16	–	–	–	–	23.7
<i>Dontostemon glandulosus</i>	14	20	22	17	–		8	–	–	–	13.8
<i>Kengyilia thoroldiana</i> var. <i>thoroldiana</i>	7	43	31	17	38	32	38	–	–	–	24.9
Alpine Steppe Communities 2 to 4, 6 and 7											
<i>Callianthemum pimpinelloides</i>	–	57	30	14	–	32	23	–	–	–	23.7
<i>Oxytropis stracheyana</i>	–	43	39	28	–	37	15	–	–	–	26.5
<i>Potentilla exigua</i>	–	14	43	24	–	16	15	–	–	–	22.1
<i>Astragalus confertus</i>	–	31	72	72	–	37	38	–	4	–	43.5
<i>Festuca</i> cf. <i>valesiaca</i>	–	71	63	28	–	16		–	–	–	36.8
<i>Ajania tenuifolia</i>	–	26	49	28	–	32	23	–	–	–	27.7
<i>Iris potaninii</i> var. <i>potaninii</i>	–	26	26	28	–	32	23	–	–	–	19.4



a similar growth form but lack the taproot found in the above-mentioned genera (Miehe et al. 2002, 2008; Klimeš 2003, Fig. S6). In Tibet, plate-shaped cushion plants increase in species number and cover with increasing aridity, reaching their highest abundance in alpine desert steppes of the northwest highlands (Miehe et al. 2002).

Woody perennials are represented by only four species, which do not grow higher than the graminoids under the present grazing pressure. Cover is negligible, and only *Krascheninnikovia compacta* is a major component of communities in the arid northwest (Fig. S7). In contrast to other steppe biomes, like the mountain desert steppes of the southeastern Gobi Altai of Mongolia (Wesche et al. 2005), alpine steppe lacks dwarf shrubs growing on mounds or disturbed sites.

Annual plants (Chenopodiaceae, Brassicaceae, Boraginaceae) account for an unusually high fraction of the alpine species (Körner 1999), although similar values were recorded from high-altitude plant communities of Ladakh (Klimeš 2003). Among these species are a high number of endemics, today mainly growing in overgrazed pastures, at ruderal sites and on small mammal burrows.

## Plant communities

The 253 plots represent ten plant communities (Table 1). Ten common alpine species occur in all communities except for alpine desert steppe (community 10); another group of five characteristic species is shared by communities 1 to 7 (alpine steppe s. str.). A further group of five species are added to communities 1 to 4 at lower elevations of the southwest highlands (1), around Nam Co (2) and Zigetang Lake (3), and these comprise many disturbance indicators (4). These species do not occur in plots from the northern highlands. Another group of 14 species is not present in community 1 and in the northern highlands (communities 5 to 10). Communities 5 to 10 have only a few species in common but share their distribution range in the northern highlands, which are subject to permafrost and higher salinization. Communities 8, 9 and 10, which are characterized by a group of ten species, colonize the highest sites (mean 5160 m) and those with the strongest salinization.

Axis 1 of the DCA (Fig. S8) reflects a strong elevation–humidity gradient (*post-hoc* correlation  $R = -0.85$ ,  $P < 0.001$ ). Since elevation and precipitation gradients both follow an east–west direction, elevation is also highly correlated with axis 1 (*post-hoc* correlation  $R = 0.65$ ,  $P < 0.001$ ). The records with highest salinization (community 10, see Fig. S3) are found at the highest and most arid study sites. This is most probably in accordance with a salinity gradient responsible for the separation of

the vegetation types along axis 2. Floristic gradients along axis 1 correspond to slightly more than one complete species turnover (length of gradient: 5.6), which is relatively low with respect to the size of the area sampled and indicates that vast areas of Tibet host an essentially similar species set.

In the following, we provide a brief description of the ten communities, with special reference to climatic gradients and grazing regime.

### Community 1: *Kobresia macrantha* pasture

The records are mainly from the southern highlands and the Tangra Yumco area. They comprise several pasture types that have many species in common with degraded pastures of the montane belt (e.g. *Pennisetum flaccidum*, *Artemisia prattii*, *Stipa koelzii*, *Onosma hookeri*), while some grazing weeds are shared with community 2. Community 1 occurs on south-facing slopes with eroded loess cover or scree and sandy substrates. The mean cover (28%) and relatively low diversity (21 species) point to high grazing impact. The vegetation structure reflects the ecotonal character of these stands, because alpine cushion species (*Arenaria bryophylla*), and plate-shaped cushion species (e.g. *Oxytropis microphylla*) occur together with weeds of montane pastures, disturbance indicators and a set of species from degraded *Juniperus tibetica* woodlands (*Swertia hispidicalyx*, *Piptatherum laterale*, *Milula spicata*, *Androsace graminifolia*, *Pterocephalus hookeri*). Two plots (nos. 12 and 13; Fig. S9) conserve the rhizomull (Kaiser 2004) of a formerly closed *Kobresia pygmaea* lawn, with only a few small tufts remaining in a closed carpet of blackish Cyanophyceae. Structure and species set suggest that this is a replacement community that developed from woodlands or *Kobresia pygmaea* pastures.

### Community 2: *Stellera chamaejasme*–*Sedum perpusillum* pasture

The records represent southeastern alpine steppes occurring in the ecotone of *Kobresia pygmaea* pastures and *Juniperus* dwarf shrublands. Plots are in the northeastern Nam Co area, mostly on south-facing slopes of gently rolling hills and pediments. *Incarvillea younghusbandii* and *Youngia simulatrix* are species from southern Tibet and demarcate this community as a southern alpine steppe. The community contains many poisonous species (*Astragalus monbeigii*, *Stellera chamaejasme*, *Thermopsis lanceolata*) and also taller grazing weeds (*Cryptothladia kokonorica*, *Dracocephalum tanguticum*) at high frequencies. The combination of cover degree, high frequency and high cover of poisonous plants is a characteristic of degraded grazing systems (Vetter 2005), and such stands are indeed used as winter pasture (Behrendes 2008). The community shares

at least two species (*Ajuga lupulina*, *Corydalis hookeri*) with the *Juniperus pingii* var. *wilsonii* open dwarf shrublands. As the community occupies sites that are in the elevational range of the junipers and have the same slope aspect, it is highly probable that this community also at least partly replaces open dwarf juniper shrublands that have probably been eradicated for fuel use.

The structure is far more heterogeneous than in the other alpine steppe communities, due to the presence of tall poisonous plants and grazing weeds, reaching heights of 15 to 20 cm. Short grasses are abundant, as are rosette species such (*Saussurea leontodontoides*, *S. leiocarpa*, *Incarvillea younghusbandii*, *Lomatogonium brachyantherum*), while cushion plant forms are rare.

### Community 3: *Polygonum sibiricum* alpine steppe

The records for community 3 represent the species-poor, more humid, eastern alpine steppes defined by a lack of characteristic species. Plots were mainly sampled in the Zigetang Lake catchment or in lake basins south of Zigetang Lake. Grazing weeds are represented by some very small species (*Rhodiola smithii*, *Lasiocaryum munroi*) and the highest fidelity and frequency of *Polygonum sibiricum*, a widespread central Asian indicator of disturbance on slightly saline soils. *Incarvillea younghusbandii* and *Saussurea leontodontoides* confirm their affiliation to the southern highlands (common species for communities 1 to 4). Open sites on pediments and gravel terraces prevail; loess and sand, partly with open deflation pavements, are the most common substrates. Two cushion species (*Androsace tapete*, *Arenaria bryophylla*) have their highest frequencies here and the plate-shaped cushion plants *Astragalus confertus*, *Oxytropis stracheyana* and *Sibbaldianthe adpressa* are abundant. Dwarf graminoids also attain their highest cover degree.

### Community 4: *Axyris prostrata* wasteland

The records for community 4 can be classified as a variant of the previous community and also represent intensively used pastures, widely found in the eastern highlands in both the alpine steppe and *Kobresia pygmaea* biome. Our records are mostly from the lower part of the Zigetang area (all exposures). Due to a high organic matter content of the open sandy to silty soil, stands are known as 'black soil' (Ma et al. 1999). Many of the species have rhizomes and are obviously well adapted to the moving substrate (*Dracocephalum heterophyllum*, *Artemisia tridactyla*). Pika burrows provide nutrient-rich habitats colonized by *Urtica hyperborea*, the endemics *Oreosolen wattii* and *Przewalskia tangutica* also grow on the soil heaps at pika burrows. *Leontopodium nanum* has the highest frequency and cover here, fixing the open soil with its silvery mats, which are

of low grazing value ('Edelweiss semi-desert', Holzner & Kriechbaum 2000). The abundance of the widespread Central Asian taxa *Potentilla bifurca* and *Heteropappus* sp. also indicates heavy grazing. This community has the highest frequency of *Artemisia* (seven species, mainly very small and highly aromatic species, e.g. *A. hedinii*). In contrast to disturbance-adapted rhizomatous plants, cushion species with a taproot are rare. As in other disturbed sites, the vegetation structure is patchy.

### Community 5: *Kobresia yadongensis*–*Potentilla compacta* high-alpine steppe

The records for this community share occurrences at high elevations, low frequencies of typical alpine steppe species (Table 1) and absence of characteristic species of communities 1 to 6 with the desert steppe communities of the northwest. They do, however, lack the salt-tolerant species of communities 6, 8, 9 and 10. Species with alpine distribution ranges prevail, and we consider this community as a high-elevation variant of alpine steppe. The sites are located in watershed areas of the central Trans-Himalaya on sandy ground moraines and gravel terraces over permafrost; deflation pavements are formed by strong winter winds. Ten characteristic species, with fidelity values ranging from  $\phi = 0.48$  (*Trisetum spicatum* ssp. *spicatum*) to  $\phi = 1.0$  (*Kobresia yadongensis*), underline the unique position of this community. *Kobresia robusta*, *Rheum globulosum* and *Oxytropis williamsii* indicate sandy substrates, *Lasiocaryum munroi* and *Oreosolen wattii* benefit from the high abundance of pikas. *Kobresia yadongensis* forms plate-like turf patches in open soil (Fig. S6), colonized by grasses, rosette plants and cushion species. The successional status remains ambiguous because the sods of *Kobresia yadongensis* are partly decayed and colonized by rosette plants and grasses, which impede potential development towards closed turf cover.

### Community 6: *Saussurea andryaloides*–*Astragalus golmunensis* alpine steppe

The records represent alpine steppe of sandy flats of basins and plains, partly in an area of closed permafrost (Atlas Tibet Plateau 1990). The group of characteristic species is small and these only attain modest fidelity values. However, highest fidelity and frequency of the species in this group testify to the distinctness of the community. *Kobresia robusta*, *K. stolonifera* and *Astragalus heydei* are indicator plants for sandy soil, and plate-shaped cushions plants (especially *Astragalus/Oxytropis* species) reach 14% cover, higher than anywhere else except for the desert steppe of the northwestern highlands. Small feather grasses (*Stipa purpurea*) and taller bunch grasses (*Kobresia robusta*) are the second most abundant life form.

### Community 7: *Littledalea racemosa*–*Astragalus densiflorus* var. *konlonicus* alpine steppe

The records represent the alpine steppe of the north-eastern highlands at elevations between 4250 and 4870 m, which is above the potential treeline in northern parts of Tibet. Moreover, all sites are within the area of closed permafrost, as indicated by disturbance through frost heave formation and (on steeper slopes) gelifluction. *Saussurea gnaphalodes* and *Stellaria decumbens* are typical of alpine gelifluction sites; *Corydalis mucronifera*, *Lagotis brachystachya* and *Pomatosace filicula* grow on wet frost-moved substrates. *Carex sagaensis* and *Aster flaccidus* benefit from excess water at the permafrost sites, which are partly saline (*Puccinellia* spp.). Short grass clumps and a diverse range of cushion species are the most abundant life forms; annuals are very rare.

### Community 8: *Thylacospermum caespitosum* high-alpine desert steppe

The plots representing the high-alpine desert steppe contain the highest vascular plant communities known to date (Miehe et al. 2002), which can be seen as a high-altitude variant of community 9 below. They comprise salt-tolerant desert steppe species and drought-tolerant high-alpine species. Most records are from north-facing slopes with an inclination of 5° to 10°. Ice wedge polygons form over the closed permafrost (Fig. S10); needle ice formation and gelifluction are the main disturbance factors during the short growing season. The cushion-forming *Saussurea glanduligera* and *Thylacospermum caespitosum* dam the floating scree into terracettes, and the up to 30-cm wide compact hard cushions of *T. caespitosum* give community 8 its distinct physiognomy. Species numbers (mean 13) are on average one-third smaller than in alpine steppes (communities 1 to 7). The characteristic species (including many *Saussurea* spp. and Brassicaceae) are typical of arid high-alpine communities. Among Cyperaceae, only *Carex moorcroftii* from the desert steppe and *Carex sagaensis* from water surplus areas are reasonably common. *Stipa subsessiliflora* partly replaces *Stipa purpurea*. There are five plate-shaped cushion species, of which *Oxytropis densa* is most frequent. Typical grazing indicators are absent; only *Carex moorcroftii* (preferred forage of wild ass, Schaller & Gu 1994) and *Stipa subsessiliflora* (not grazed) are resilient to large herbivore grazing due to their life form.

### Community 9: *Krascheninnikovia compacta*–*Stipa subsessiliflora* alpine desert steppe

The records for communities 9 and 10 represent alpine desert steppe of the northwestern highlands. Community 10 is only distinguished by the absence of a set of common

alpine steppe species. Hence, fidelity and frequency is moderately similar in these two communities. They cover an area of ca. 400 000 km<sup>2</sup> (Wang 1988; Zhang 1988; Atlas Tibet Plateau 1990). The high frequency and cover degree of plate-shaped cushion species, the presence of a shrub layer (*Krascheninnikovia*) and crescent-shaped growth (*Stipa* spp., *Oxytropis chiliophylla*, *Saussurea glanduligera*) contrast with the other alpine steppe communities but are features shared with other arid mountains environments and the desert steppes of Central Asia (Werdermann 1931; Hilbig 1995; Wesche et al. 2005). The plots are located on gently inclined, mostly north-facing slopes and pediments. Surfaces are sealed with deflation pavements. All species seem to tolerate saline conditions, with the high number of *Saussurea* spp. (6), Poaceae spp. (9) and plate-shaped cushion plants (6) being conspicuous. The last group reaches higher cover here than anywhere else in Tibet and is widely harvested for fuel (Fig. S11: arrow). All sites are grazed by large herbivores and locally by smaller mammals, including marmot; the suffruticose *Krascheninnikovia compacta* is preferentially browsed and rarely allowed to grow taller than 5 cm.

### Community 10: *Carex moorcroftii* alpine desert

The records represent the highly distinct vegetation of alpine deserts on pediments and ancient lake terraces of the dry Aksai Chin plain (20–50 mm mean annual precipitation, Chang & Gauch 1986) at elevations between 4950 and 5280 m. Surfaces are covered by salts in layers up to 10-cm thick (Fig. S3); especially around the *Krascheninnikovia* shrubs growing at water surplus sites (Fig. S7). The upper 5 to 10 cm of soil was mostly free of roots and had a pH between 8.0 and 9.5, while the root horizon below 10 cm was completely closed, which is in stark contrast to the very open, above-ground vegetation surface plant cover (mean 15%). Ancient shorelines hint at the former presence of lakes (Atlas Tibet Plateau 1990; Miehe et al. 2002), when terrestrial plant life in the basins was extinguished due to high water levels; while in dry phases (as in the present phase), habitats become highly salinized. The species present have the highest salt tolerance in our data set (*Astragalus hendersonii*, *Krascheninnikovia compacta*, *Stipa subsessiliflora*). Species numbers range from eight to two, some species are shared with communities 8 and 9, while characteristic species of the alpine steppe are totally absent, except for *Carex moorcroftii*. The area is not used by nomads, and neither faeces nor tracks of wild herbivores were found.

## Conclusions

We analysed the vegetation of the alpine steppe of the Tibetan plateau in order to contribute to the three main

ecological research challenges of this biome: (a) high sensitivity to ongoing climate change, (b) climate-driven changes during the Last Glacial Maximum, and (c) risk of overgrazing and desertification.

(a) The elevational range of the species in our data set is more than 1000 m, which corresponds to a temperature range of 6 K (assuming a lapse rate of 0.6 K/100 m, Böhner 2006). Taking this vertical distribution range as a proxy for temperature tolerance, we conclude that this species set should be indifferent to temperature changes of a few degrees Kelvin. The 1200-km transect corresponds to a precipitation gradient from 350 mm to 20 mm  $\text{yr}^{-1}$ , where we find an essentially identical set of characteristic species. Thus, alpine steppes should also cope well with humidity changes.

(b) Of the 288 species of alpine steppe, 33% were endemic, including ten endemic genera. This corresponds well to the fraction of endemic taxa in the entire alpine flora of the Tibetan highlands (Chen et al. 2008). Endemism is a widely used proxy in biogeography to test whether biomes have suffered from extinction impact in the past (*tabula rasa* scenarios) or not (Hendrych 1982; Fjeldså & Lovett 1997). We conclude that this high percentage of endemic taxa contradicts any '*tabula rasa*' scenario.

(c) The alpine steppe vegetation is mainly built of species that are resilient to grazing (Fig. 1). The cover of tall graminoids, which can be destroyed by grazing because they lack bud protection against grazing (G), is only 2 to 4% in most communities. Cushion plant species are nearly absent under intense grazing at lower elevations (community 1), under more humid conditions (community 2) or in saline alpine deserts of the northwest (community 10). In contrast, unpalatable plants reach highest cover values only in communities 1 and 2. Grazing impact seems to be limited in all other communities (3 to 10), which seem to be driven by precipitation and its inter-annual variability (Vetter 2005) rather than grazing impact.

In spite of this obvious resilience of the forage resources to degradation, slow but lasting degradation is caused by the shortage of fuel. As yak droppings, which represent the main fuel resource of Tibetan nomads in the eastern highlands (Rhode et al. 2007), are not available in sufficient quantities in the arid northwest, dwarf shrubs and cushion species are uprooted for fuel (Fig. S11). The rate of fuel removal far exceeds the rates of regrowth, as evidenced by clear gradients of decreasing cushion plant cover towards settlements.

Taken together, the results of this first classification of plant communities and plant functional types of the alpine steppe of the Tibetan highlands lead us to suggest that the biomes are relatively tolerant to climatic changes,

have not suffered from extensive extinctions in the geological past, and are also likely to tolerate the present grazing influence, although harvesting of biomass for fuel purposes may present a problem.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Dichotomous key for identification of alpine steppe communities.

**Table S1.** Plant communities of the alpine steppe biome.

**Figure S1.** The Tibetan highlands with locations of vegetation plots (symbols indicate plant communities, and number of respective samples). Isohyets and the boundary of the interior drainage area are indicated (following the Atlas Tibet Plateau 1990; base map adapted from Miehe et al. 2001).

**Figure S2.** Soil types of the alpine steppe biome and climatic diagrams (amended from the Atlas Tibet Plateau 1990; climatic diagrams after data of the Meteorological Service China, as cited in Miehe et al. 2001).

**Figure S3.** Alpine deserts of the northwestern Tibetan highlands (Aksai Chin) with their salt-sealed surfaces and open gravel deflation pavement. The top layer consists of 10 cm of salt. Colonies of *Carex moorcroftii* (black arrow) are confined to water surplus sites. The area receives ca. 25 mm annual precipitation. 4970 m, 35°50'N/79°25'E, June 1992.

**Figure S4.** Alpine steppe of the central highlands with 25% plant cover. *Stipa purpurea*, *Poa albertii* and *Carex moorcroftii* attain 8 cm in height; two plate-shaped cushion species and *Leontopodium pusillum* cover 15%. The site is hardly grazed by livestock (4680 m, 31°23'N/90°40'E, Aug. 1993).

**Figure S5.** Plate-shaped cushion of *Saussurea graminea* var. *ortholepis* (1) and *Astragalus orotrefhes* (2) (4300 m, 28°21'N/86°05'E, Sept. 1984).

**Figure S6.** Alpine steppe of the Trans-Himalaya (community 5) in deflation pavements with scattered sods of *Kobresia yadongensis* (arrows, 5270 m, 29°49'N/86°47'E, Sept. 2003).

**Figure S7.** Alpine desert of the Aksai Chin. Water surplus depressions are overgrown by monotypic colonies of salt-covered *Krascheninnikovia compacta*, browsed down to the ground (4890 m, 35°43'N/79°25'E, June 1992).

**Figure S8.** Scatterplot of the DCA (total inertia = 15.084, eigenvalue of axis 1 = 0.619, eigenvalue of axis 2 = 0.445). Symbols indicate the ten plant communities; humidity and elevation were correlated (*post hoc*) with ordination axes ( $R = -0.85$  and  $R = 0.65$ , respectively).

**Figure S9.** Alpine steppe of southern Tibet (community 1, running no. 13, Table S1), probably in the transition from *Kobresia pygmaea* grazing lawns towards alpine steppe. The densely rooted loess is divided by polygonal cracks and the surface is largely sealed by Cyanophyceae. The tip of the ice axe is 1.5 cm long (inclination 20°, N-facing slope, 4620 m, 29°19'N/86°53'E, August 1993).

**Figure S10.** High alpine steppes of the northwestern highlands (community 8, running no. 215, Table S1), over closed permafrost (ice wedges) with 20% plant cover mainly of plate-shaped cushion plant species. 5120 m, 34°32'N/80°21'E, July 1992.

**Figure S11.** Sheep- and goat-keeping nomads in the western highlands collect cushion plant species (mainly *Arenaria bryophylla* and *Oxytropis chiliophylla*), which are uprooted with an antelope-horn (arrow) for fuel use as a supplement for yak dung (5100 m, 34°15'N/80°22'E, June 1992).

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