

Chapter 6

RESILIENCE OR VULNERABILITY? VEGETATION PATTERNS OF A CENTRAL TIBETAN PASTORAL ECOTONE

***Georg Miehe,^{1,*} Sabine Miehe,¹ Kerstin Bach,¹
Karsten Wesche,² Elke Seeber,³ Lena Behrendes,¹ Knut Kaiser,⁴
Christoph Reudenbach,¹ Jasmin Nölling,¹ Jan Hanspach,⁵
Mark Herrmann,⁶ Ma Yaoming⁷ and Volker Mosbrugger⁶***

¹Faculty of Geography, University of Marburg, Marburg, Germany

²Senckenberg Museum of Natural History Görlitz, Goerlitz, Germany, Germany

³Faculty of Biology – Geobotanik und Botanischer Garten,
University of Halle-Wittenberg, Halle (Saale), Germany

⁴Acatech - German Academy of Science and Engineering, Berlin, Germany

⁵Helmholtz Zentrum für Umweltforschung UFZ, Leipzig, Germany

⁶Forschungsinstitut und Naturmuseum der Senckenbergischen
Naturforschenden Gesellschaft, Frankfurt, Germany

⁷Institute of Tibet Plateau Research, Chinese
Academy of Sciences, P.R. China

ABSTRACT

The question of the resilience or vulnerability of Tibetan highland pastures is not only of regional importance but also of global relevance for the Earth's energy budget and atmospheric circulation. A climate and grazing driven environmental change of the Tibetan highland albedo could induce feedback effects within an ecotone of approximately 200 km between Cyperaceae-dominated grazing-lawns and alpine steppes stretching over 2000 km between the Qilian Shan (38°N) and the Himalaya (28°N). Understanding the vegetation structure of this region would enable accurate modeling approaches for global change scenarios.

* Corresponding author: Georg Miehe. Faculty of Geography, University of Marburg, Deutschhausstraße 10, D-35032 Marburg, Germany. E-mail: miehe@geo.uni-marburg.de.

We analyzed the Central Tibetan pasture vegetation in the wider Nam Co area using phytosociological vegetation surveys and remote sensing techniques (ASTER, SRTM). The survey described in this chapter recorded a total of 105 vegetation relevés, with a total of 233 species. The species-based approach using DCA and phytosociological classification distinguishes six plant communities including juniper woodlands and juniper open dwarf shrublands, alpine steppe communities, *Kobresia pygmaea* communities and transitional mosaics with fragments of *Kobresia* turf and alpine steppe. The most common community was the transitional mosaic of *Kobresia pygmaea* mats and alpine steppe. Except for the phanerophytic communities and the grazing lawns of *Kobresia pygmaea*, plant communities are characterized by low overall plant cover with two thirds of species showing values lower than 1%. An analysis of plant functional types shows that most species are adapted to intense grazing regimes. The prevalence of dwarf growth forms, rhizomes and repellent characteristics shows that the pastures are grazing resilient. By contrast, the fragmented turf cover is vulnerable and endangered by intense grazing, digging by small mammals, turf removal and periglacial weathering.

Keywords: Alpine steppe, grazing, *Kobresia pygmaea*, plant functional types, Qinghai-Tibet Plateau, remote sensing

INTRODUCTION

The central Tibetan highlands are a sensitive ecotone between the closed, golf course-like pastures of a tiny endemic sedge, *Kobresia pygmaea*, in the south-eastern plateau and the semi-arid alpine steppe in the north-western plateau. This ecotone occupies a diagonal area of more than 2000 km long and around 200 km wide. It is located between the Qilian Shan in the north-east and the Inner Valleys of the Himalayas in the south-west (Figure 1). The radiation feedback effects of the Tibetan highlands have a crucial impact on the monsoon regime. Any potential changes in the Tibetan surface properties may have consequences for the global climate. Thus, the vulnerability and resilience of the Tibetan pastures are not only of regional but also of global importance. Both, resilience and vulnerability are related approaches in life sciences and the social sciences. Here we understand resilience and vulnerability as complementary concepts (see review of Miller et al., 2010) referring to resilience as the (plant) communities' resistance to disturbance, whereas vulnerability is understood as the condition encompassing characteristics of exposure susceptibility. Specifically, a shift from a closed plant cover to a degraded surface with bare soil would have detrimental effects on evapotranspiration, albedo and surface roughness. It is in this sense understood as vulnerable, whereas its regenerative capacity would be understood as resilience.

The knowledge of the impact of humans on the Tibetan highlands is limited and controversial. Climate-driven shifts of Holocene vegetation have been reconstructed based on lake sediment cores (Co Ngion, 31°24'N/91°28'E, Shen et al., 2008; Nam Co, Zhu et al., 2008; Herrmann et al., 2009).

However, like nearly all climate-sensitive ecotones of the world, this area has also been shaped by humans and their livestock. Nevertheless, some scientists still regard the vegetation of the Tibetan highlands as natural (e.g. Ni, 2000; Song et al., 2004; Yu et al., 2001; Herzschuh et al., 2006).

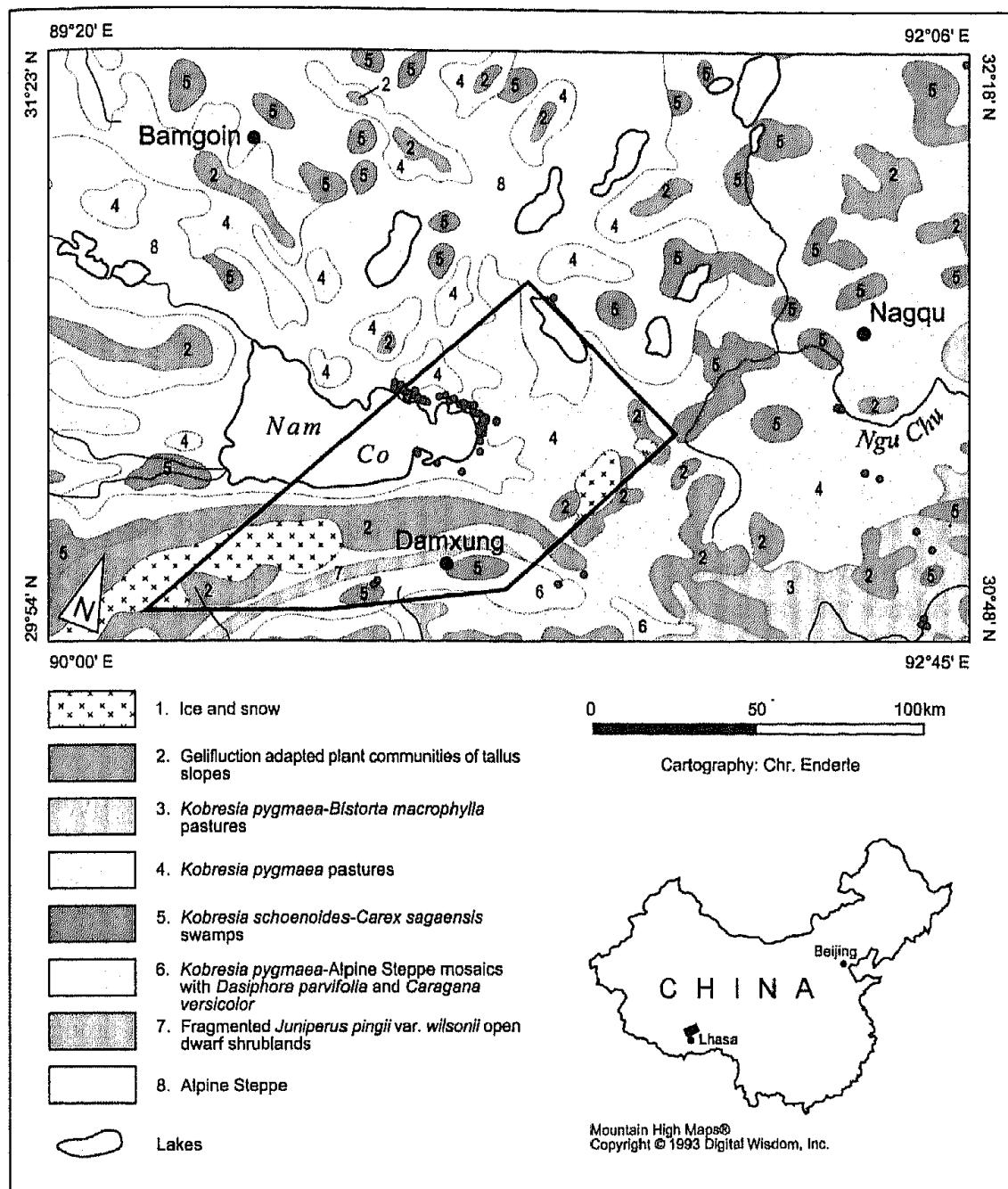


Figure 1. The vegetation of the study area (according to Zhang 1988, changed) with locations of vegetation records (red dots). The black frame indicates the position of the land cover map in Figure 916.

It is remarkable that many modeling approaches of past or future scenarios ignore the possibility of any human impact. Such attempts could generate scenarios that are no better than the starting assumption (cp. Song et al., 2005).

In fact, there is plenty of experimental and palaeoecological evidence that the biomes of at least the humid south-eastern half of the highlands are a human-made plagioclimax that replaced natural tall grassland, forests, and woodlands (Miehe et al., 2008a, b, 2009).

The earliest archaeological records of humans on the Tibetan plateau correspond to undated, probably epipalaeolithic artifacts.

The archaeological exploration of Tibet (Aldenderfer, 2007; Brantingham et al., 2007; Bellezza, 2008) has revealed some evidence that ecosystems were shaped by foragers and herders since the Late Pleistocene.

These groups were certainly capable of using fire, and evidence for fires may serve as a proxy of human impact. Fires might also have occurred naturally after lightning events. However, lightning occurs exclusively during the rainy season and is usually associated with torrential rains which would have prevented any spread of fires. Moreover, the Tibetan flora does not have any fire-adapted plants. Charcoal particles have been found in two palaeo-ecological analyses, even at the base of the respective cores (Damxung: 13 ka cal BP, Miehe et al., 2009; Nam Co: 8 ka cal BP, Herrmann et al., 2009; Adamczyk, 2010). These findings indicate that humans have been present at least since the Late Glacial in this region.

It is unknown when livestock grazing began in Tibet. It is similarly unknown when one of the most important livestock species, the yak, was domesticated (Olsen, 1990; Guo et al., 2006; Rhode et al., 2007), and when sheep and goats were introduced from the Middle East (Flad et al., 2007; Miehe et al., 2009). The palynological record is so far the only source of information to provide proxies wherewith the onset of animal husbandry in the area can be reconstructed. Palynological data (Kaiser et al., 2008; Miehe et al., 2009; Herrmann et al., 2009) both for the valley south of the Nyenquentangla Shan and the Nam Co basin provide the first evidence of grazing weeds during the mid-Holocene climatic optimum. These estimations are ambiguous, however, because all grazing weeds of Tibet are endemic to the highland, and because wild mammals could potentially have had an impact similar to that of livestock. A comparison of vegetation patterns and climate between the more humid south-eastern and the drier north-western Tibetan plateau may shed light on the effects of land use in this region. Theory predicts that in equilibrium systems, like in the south-eastern highlands, livestock grazing should be detrimental to ecosystem stability. Here, precipitation is higher and fodder availability for livestock husbandry much more reliable. Under these conditions, relatively large herds can be maintained but high livestock numbers can lead to ecosystem degradation. By contrast, the non-equilibrium conditions in the drier north-west are highly variable (coefficients of variation in the annual precipitation are greater than 30%). Here, herds are likely to experience non-equilibrium dynamics, with high mortality in drought years but relatively low mortality on average. As a consequence, degradation in these plant communities should be low (Ellis and Swift, 1988; Vetter, 2005). Moreover, vegetation in this region could remain stable even under permanent, intense grazing, if key species possess functional traits adapted to high grazing pressure (Diaz et al., 2001).

To what extent current livestock grazing pressure might exceed the natural grazing impact of wild herbivores is not known. It is possible that grazing induced a long-lasting selection process, in which unpalatable and dwarf plants were favoured over palatable forage plants. Surprisingly, the grazing impact of large wild herbivores in Tibet is rarely mentioned in the literature. This effect can hardly be studied as wildlife has been displaced to the marginal parts of the alpine steppe, in the north-western highlands (Schaller, 1998). Today, the most important remaining wild mammal across Tibet is the endemic plateau pika (*Ochotona curzoniae*), a territorial, winter-active lagomorph of 150 to 200 g (Smith and Foggin, 1999; Pech et al., 2007). Pikas inhabit *Kobresia* pastures in large numbers, especially in the most heavily degraded pastures around settlements ("black soil", Ma et al., 1999). Their role in the destruction of *Kobresia* turfs has not yet been investigated but it is striking that their main distribution area coincides with the distribution of *Kobresia* pastures.

The overall aim of this work is to investigate current and past vegetation patterns in the Tibetan highlands that could serve as reference for future modeling of environmental changes at a regional and global scale.

In this chapter, we use vegetation records and remote sensing techniques to classify and analyze the plant communities of Nam Co, in Tibet. We also conducted interviews with local herders in order to describe the past and present rangeland management system in this area. Our hypotheses are:

Both the grazer-driven equilibrium system of the humid *Kobresia pygmaea* pastures and the rain-driven non-equilibrium system of the arid alpine steppes are both resilient to degradation due to a high proportion of grazing-tolerant plants.

By contrast, the felty turf-cover of the *Kobresia pygmaea* pastures—alpine steppe ecotone is fragmented due to superimposed abiotic, biotic and cultural impacts, which is an indication of its vulnerability.

METHODS

Study Area

The study area is located in the vicinity of Tibet's second largest lake, the Nam Co, in China (1920 km², Zhu et al., 2008; Figure 1). This region occupies the watershed areas among the upper catchment of the northern Kyi Chu river tributaries (Lhasa River, Yarlung Zhangbo/Brahmaputra drainage), the northern tributaries of the Salween (Nu Jiang), and the interior drainage systems of the central Tibetan highlands, the “Changtang” (i.e. northern plain), behind the mountain range of the Nyenquentangla Shan. Climate in this region is a transition between the humid conditions favoured by the drainage system in the south and the dry conditions generated in the endorheic basins in the north. In the south, river gravel beds are located at 4200 m, the valleys of the upper Salween tributaries at 4500 m, and the Nam Co basin at 4700 m altitude. The area belongs to the Damxung county, Lhasa prefecture, and the Nagqu county, Nagqu prefecture.

Climate and Weather

Precipitation is highest from May to September during the Asian summer monsoon, which delivers humid air-masses from the south-east. In winter, climate is controlled by the dry and cold westerlies (Böhner, 1996). Mean annual temperature in the study area is slightly below 0 °C. Minimum and maximum monthly temperatures at the Bamgoin climate station range from -11.8 °C in January to +9.4° C in July, and at the Nagqu station from -10.2° C in January to +9° C in July (Figure 2). Annual precipitation is low and variable (around 300 mm, Figure 3). The difference in precipitation between the two stations reflects the influence of the monsoon system. The mean precipitation is lower and more variable at Bamgoin, in the north-west (mean: 320, SD: ±133 mm) than in Nagqu, in the south-east (450 ± 112 mm), especially in the growing season (JJA; 206 ± 109 mm vs. 267 ± 87 mm).

Recent studies suggest increasing precipitation totals (Morrill, 2004; Xu et al., 2007); but totals may be less important than the seasonal distribution. Winter precipitation has clearly increased over the last 40 years; i.e. snowfall has significantly increased while summer precipitation has remained more or less stable (Figure 3). The higher frequency of snowfall events has an indirect impact on both the vegetation and rangeland quality, because snowfall may cause loss of livestock and reduced grazing pressure.

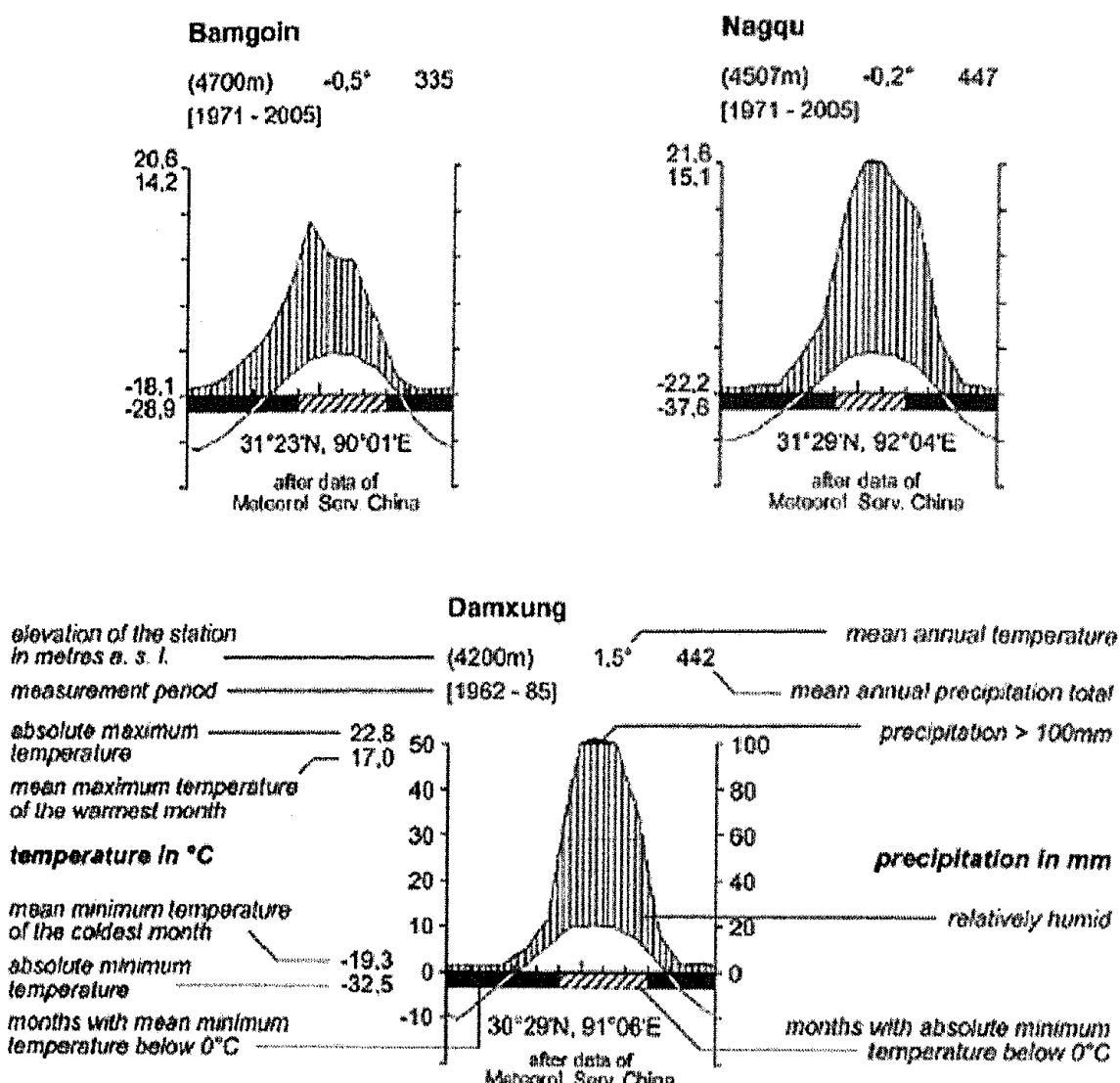


Figure 2. Climatic diagrams from the study area. Data source: Meteorological Services of China (processed by C. Reudenbach, design by C. Enderle).

Geology, Landforms and Soils

The study area is divided by the Nyenquentangla Shan. Its granites and slates are shaped by glacial erosion and periglacial processes. Lower slopes are covered by large side moraines of different age and by talus accumulations. The rolling hills north-east and north of the Nyenquentangla consist of Cretaceous limestone and Jurassic clay rich sandstone. The loess cover on the ridges has been widely eroded and has accumulated as colluvium at their bases. The intramontane basins are characterized by loess-covered pediments and gravel terraces. Valley floors and depressions have stagnant water with Cyperaceae turfs growing in rhizohydromors.

Slope deposits, developed from schist, are the dominant substrate on slope ridges (see transect in Figure 4.) Foothills are mainly covered by moraine sediments. Lacustrine pebbles, gravels and sands occur up to nearly 30 m above the present lake level. The highest shoreline has formed a marked cliff into the moraines of mid-Pleistocene age. Numerous lake terraces and shorelines indicate that the lake shrank during the Holocene (Zhu et al., 2008). Palaeosoils in and below the widespread, thin loess cover are evidence of increasing aridity during the mid- and late Holocene.

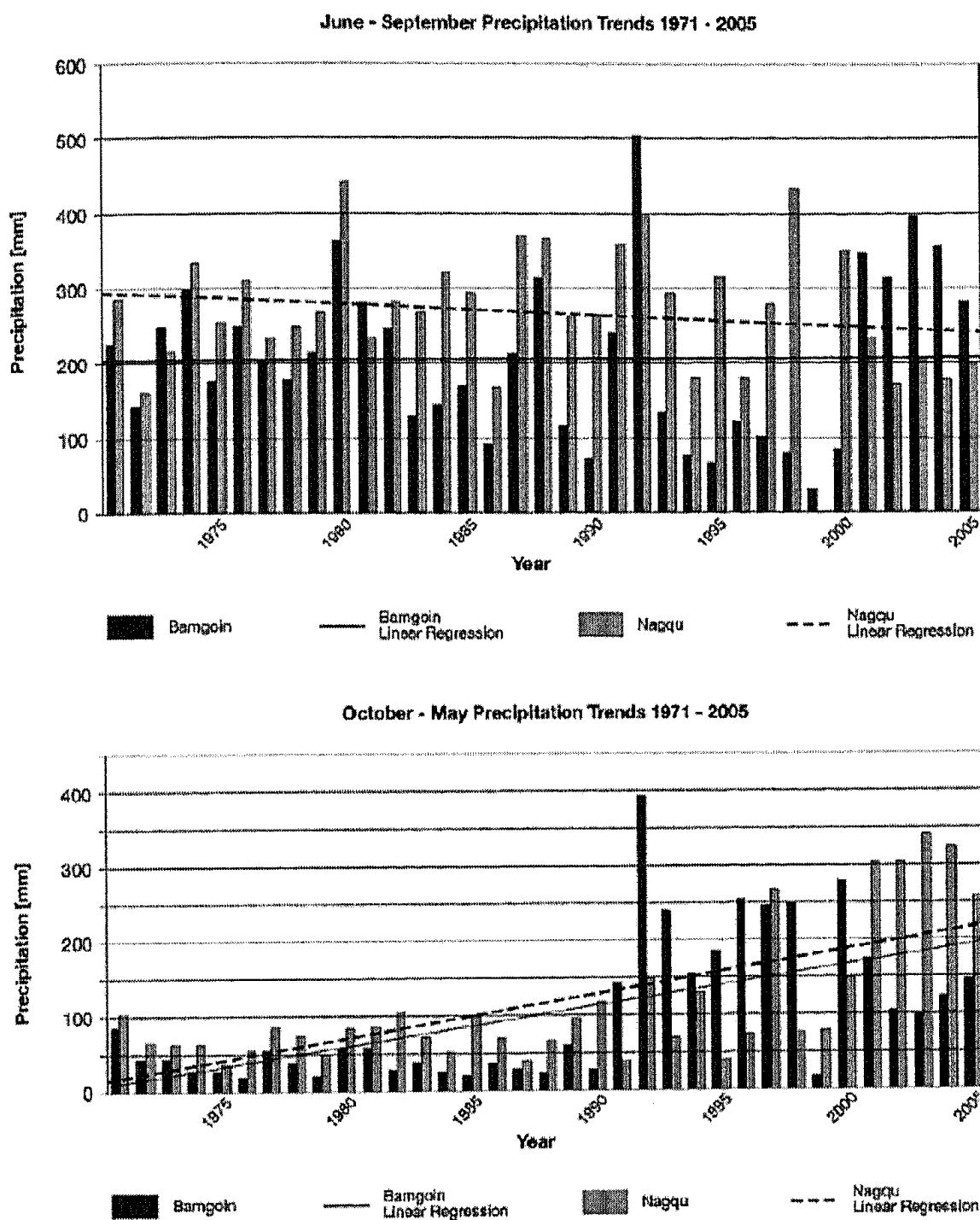


Figure 3. Seasonal precipitation trends for Bamgoin and Nagqu for the period 1971-2005, for the growing season of June - Sept. (a) and Oct. - May (b). Data are based on CWS 2008 (own calculation). The dashed lines are trends predicted by linear regression analysis.

A stagnic cambisol occurs near the ridge. Its stagnic properties might be related to the underlying permafrost. The slopes below the ridges are dominated by weakly developed cambisols that are at least partly covered by a layer of *Kobresia pygmaea* roots and rhizomes (Rhizomull, "Afe"). Moist to wet alluvial fans have gleysols. Thick lacustrine deposits are overlain by loess covers (up to 50 cm thickness) with well developed cambisols. As a rule, the deeper the lacustrine sediments, the thinner the loess cover.

Finally, a sequence of beach ridges next to the lake shore is characterised by arenosols and gleysols.

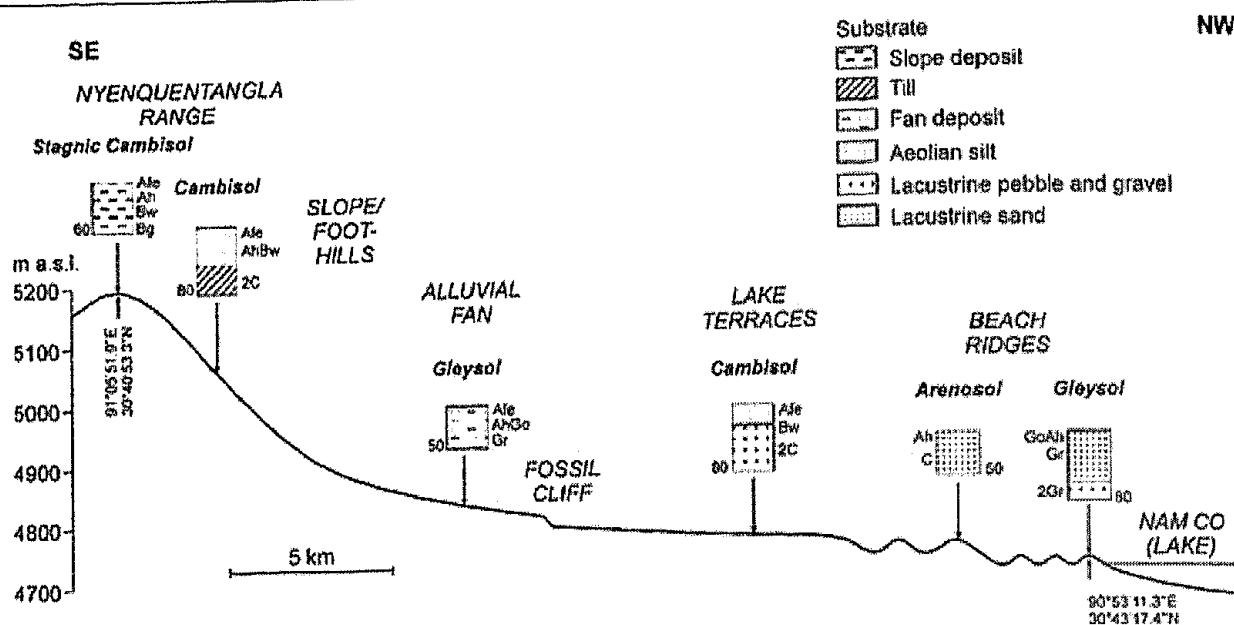


Figure 4. Soil transect from the Nyenquentangla Pass to the Nam Co (after Kaiser 2004, changed).

Past and Present Rangeland Management

Little is known about past rangeland management in the study area. Presumably, a wide range of diverse rangeland management systems have existed. Literature surveys and our own fieldwork surveys suggest that land use systems were variable and locally adapted. In the recent past, they have undergone a major transformation under the Chinese administration.

Herdsmen developed a mobile grazing system in response to the low and highly variable summer precipitation, periodic high snowfalls and different vegetation patterns. Herdsmen used to live in black tents to assure a high degree of daily and seasonal mobility. To exploit further resources, each household had an extra tent (gur) which enabled herdsmen to split the herd and establish a further starting point for daily movements. Since the 1960s, the national rangeland policy aimed to increase production (Goldstein et al., 1990). This policy led to a destruction of traditional trading systems, sedentarization, changes in herd composition, and a reduction of herd size (Sheehy et al., 2006). Today, most herdsmen have a permanent house at least in winter. With the onset of privatization and large scale fencing of pastures, mobility has been further restricted. In some regions, keeping livestock has been given up entirely (Sheehy et al., 2006; own data).

In the eastern catchment of the Nam Co (Figure 5), livestock is still the only source of income. Herds are mainly made up of sheep, yak (17-30 % of the herds), and a few goats and horses. People live in traditional black tents for most of the year. It is only during the winter months that they move into their houses, near the *Kobresia schoenoides* swamps north of the lake. The herdsmen live here from October to either February or March and await snowmelt in the spring and summer pastures. Once spring has arrived, people and livestock move to the eastern edge of the lake where they stay for one or two months. In early summer, they relocate to the southern shore of the lake. By mid-July, when all snow in the northern valleys of the Nyenquentangla Shan has melted, herds move northwards and reach altitudes of 5100 m. In September, herds are driven to the eastern shore, before they return to their winter places. Every year and every season, each household returns to the same place. Approximately 150 to 200 households follow this lifestyle (herders' direct communications and data based on counted summer tents and winter houses).

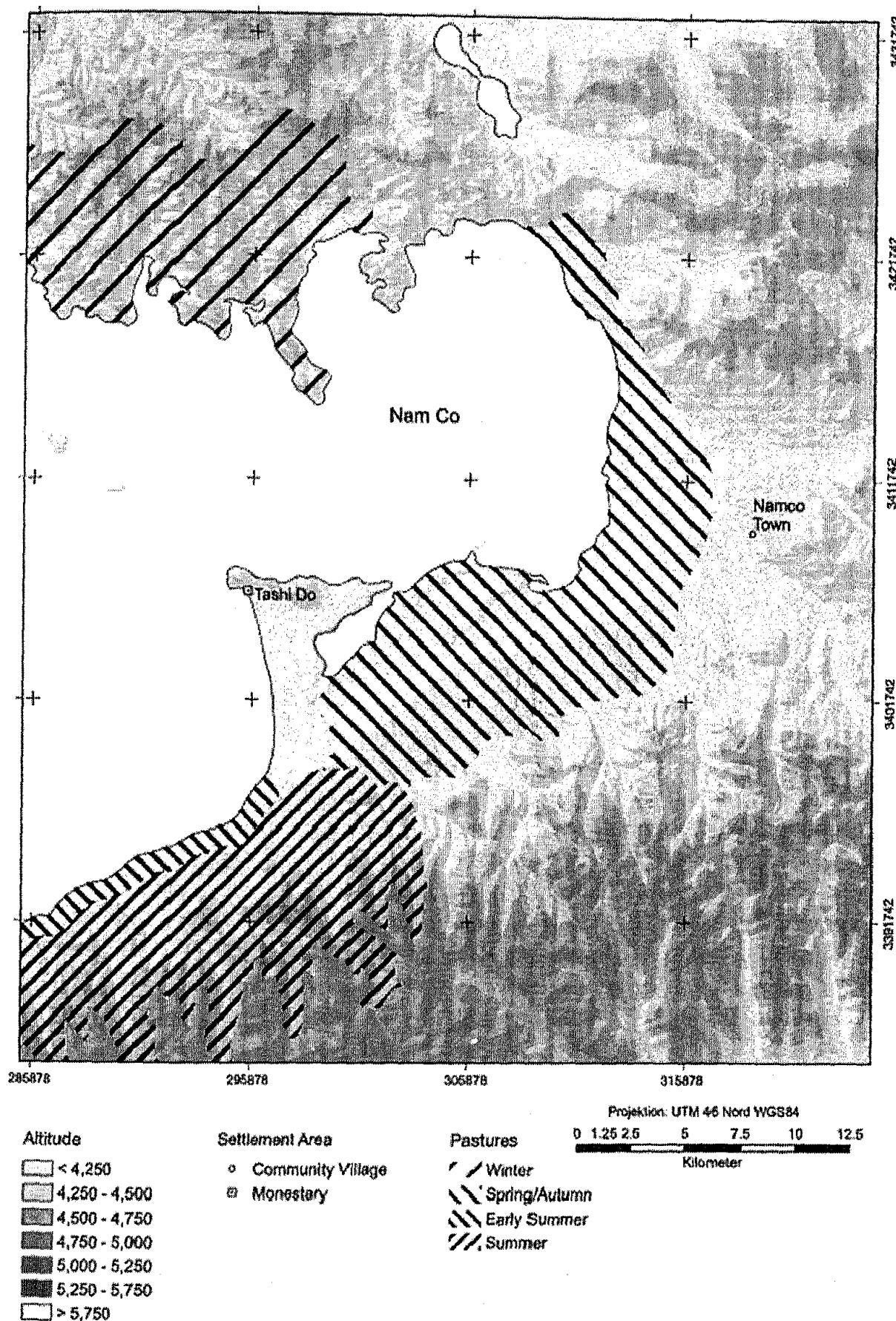


Figure 5. Seasonally changing livestock grazing pastures in the north-eastern Nam Co basin (after Behrendes 2008, changed).

According to local herders, this cyclic movement was established because of a) the high risk of snowfall in the valleys of the northern slope of the Nyenquettangla Shan and also the fairly high risk of snow east of the lake, b) the existence of *Kobresia schoenoides* swamps in the almost snow-free valleys north of the lake, c) the predominantly open vegetation and the absence of *Kobresia schoenoides* swamps in most of the eastern region, and d) the existence of widespread *Kobresia pygmaea* pastures along glacier-fed streams south of the lake.

As the vegetation shows no apparent gradients in grazing weed abundance, it is likely that all available pastures are exploited. It is to be feared that sedentarization will lead to smaller grazing radii leading to pasture degradation around the settlements and undergrazing on remote slopes.

Plant Community Characterization

The first vegetation survey of the area was undertaken by the „Comprehensive Science Investigation Team of the Chinese Academy of Sciences“ between 1973 and 1976 (Zhang, 1988, with a vegetation map at a scale of 1:3 million). The plant cover was classified according to dominant species. Vegetation maps for China on a scale of 1:1 million were edited by Hou (2001). Grazing impact assessments based on floristic vegetation records are still not available.

The records for this chapter extend over an area of 150 km from SW to NE and 200 km from E to W. In this direction, summer precipitation decreases from 267 to 204 mm (Figure 2), and altitude increases from 4350 m S of Damxung to 4750 m North of Nam Co, and to 5100 m in the Northeast watershed. The southernmost parts belong to the montane belt as shown by the northernmost outposts of the juniper forests of southern Tibet (Miehe et al., 2008d). The most north-eastern vegetation records, at 5100 m, are part of the alpine *Kobresia pygmaea* ecosystem, in the humid south-eastern highlands. The north-western records represent alpine steppe.

Vegetation surveys were conducted between 1995 and 2009. Plot size was 10 x 10 m. We recorded all vascular plant species in the plots and estimated their absolute cover percentages. We transformed abundance percentages to presence/ absence data during vegetation classification. Original cover percentages were used only as additional information to the classification of unranked communities. In total, 105 records are listed in Tables Appendix 1 and in Appendix 12. We chose plot sites in a deliberate manner, using those that were homogenous both in their species set in the abiotic habitat structure (e.g. slope inclination, exposure, soils). Sites were geo-referenced using a Garmin 12 XL GPS. Plant identification follows “Flora Xizangica” (Wu, 1983-87) or the volumes of “Flora of China” that have appeared so far (Wu and Raven, 1994 ff.). In a few cases, we had to combine closely related taxa (e.g. *Carex ivanoviae* / *C. montis-everestii*, *Stipa roborowskyi* / *S. purpurea*).

We applied a phytosociological classification to vegetation types following Mueller-Dombois and Ellenberg (1974). Arrangements of plot and species groups were supported by fidelity values using the phi coefficient of association (Φ) as implemented in JUICE 6.5, a software to sort phytosociological tables (Tichý, 2002). In order to analyze how communities were separated along environmental gradients, we performed a detrended correspondence analysis (DCA, Hill and Gauch, 1980), in the software PC-ORD (McCune and Mefford, 1999). Data were standardized by logarithmic transformation prior to the analysis (rare taxa were not downweighted). DCA was conducted with default program parameters (rescaled axes, rescaling threshold (0), and 26 segments).

It is almost impossible to differentiate altitudinal belts based on vegetation patterns in the Tibetan highlands due to the high human impact. This is especially true for the alpine belt (e.g. Herzschuh, 2006). We defined all taxa growing at altitudes higher than 5100 m as alpine species.

In order to assess to what degree communities were resilient or vulnerable to grazing, we assigned species to five different plant functional types (see Figure 9): plants (A) forming flat cushions, (B) growing with buds closely attached to the ground, or (C) with rosettes flattened to the ground, (D) being poisonous or unpalatable for herbivores during at least part of the year, and (F) taxa vulnerable to grazing, including most graminoids. E refers to the cover of all resilient plant functional types (sum of A to D). Vegetation cover of these types has been calculated for each plot as the sum of all single cover values in arid sites and as overlapping but independent cover values in the humid sites.

Satellite-Based Land Cover Mapping Assessment

Gaining information on the vegetation cover is one of the most pressing aims in studies of arid and semi-arid environments. Satellite-based assessments can provide valuable information but, unfortunately, these methods still need to be tested in many regions. The range of previously applied satellite-based methods varies from simple, unsupervised clustering algorithms to more sophisticated, supervised approaches like the widely used maximum likelihood estimation of neural networks (John et al., 2008; Lu, 2006; Mas and Flores, 2008; Govender et al., 2007; von Wehrden et al., 2006). Neural approaches have an advantage because they can handle the central problems of remote sensing in arid environments; according to Mas and Flores (2008), Artificial Neural Networks (ANN) can integrate the nonlinear relationships between the dependent and predictor variables in a learning process, and tend to generalize noisy and imprecise data. They incorporate *a priori* knowledge and constraints during the analysis, and handle data types other than remote sensing, as well as ancillary data from other sources.

We restricted the satellite-based land cover mapping to the central part of the study area where adequate satellite data were available (Figure 1, 916). Vegetation classification was based on ASTER (Advanced Spaceborne Thermal Emission and Reflection Radiometer) images and a Digital Terrain Model (DTM) from the Shuttle Radar Topography Mission (SRTM) dating from February 2000 (Rabus et al., 2003). These data were well calibrated and processed from reliable resources (<http://lpdaac.usgs.gov>). The used DTM version 4 (V4) from the Consortium for Spatial Information of the Consultative Group on International Agricultural Research (CGIAR-CSI), with a 3 arcsec (90m) spatial resolution (Jarvis et al., 2008). ASTER data were obtained from the Land Processes Distributed Active Archive Center (LP DAAC, USGS/EROS, Sioux Falls, SD, US). ASTER imagery has been available since 2000 from the NASA Terra satellite. In the current study, ASTER level 1B data (orthorectified) scene was acquired on November 10th, 2004 (UTM 46N, WGS-84, granules SC: AST_L1A.003: 2026149457, SC:AST_L1A.003:2026149457) and converted to radiances. The ASTER sensor acquires data in three band subsystems: Visible and Near Infrared (VNIR) bands 1, 2, 3 (resolution 15 m), Short Wave Infrared (SWIR) bands 4-9 (resolution 30 m), and Thermal Infrared (TIR), bands 10-1 (resolution 90 m). Additionally, a processed ASTER Digital Elevation Model (DEM) is available that is based on the VNIR bands 3b and 3n. It provides a significantly better resolution (15-30 meters) than the SRTM tiles but fails in areas of cloud cover (Toutin, 2008).

For the classification process, we derived from SRTM DTM V4 three basic terrain variables (elevation, slope, and aspect) that correlate significantly to distinct vegetation types and abundances, with an approximate resolution of 90 m. Moreover, we used the DEM derived from ASTER in the classification process to improve the cloud border identification.

Due to the high correlation between band subsystems, a Principal Component Analysis (PCA) was applied to remove redundant information. The first two VNIR components, band 1 (wavelength: 520–600 nm) and band 2 (630–690 nm) explained 99% of the image variability (Eklundh and Singh, 1993).

As the mosaic of *Kobresia schoenoides* mats was composed of open water, soil and vegetation, we calculated the Perpendicular Vegetation Index (PVI), an advanced soil-corrected Normalized Differenced Vegetation Index (NDVI). Specifically, we used the modified PVI of Bannari et al., (1995) to account for the water and soil background within the communities. The PVI was calculated using the ASTER bands 2 (WL 630 – 690 nm) and 3N (WL 760 – 860 nm) with the following equation:

$$PVI = \frac{(NIR - a) \times (Red + b)}{\sqrt{1 + a^2}}$$

where *Red* is the reflectance of ASTER band 2, Near Infrared (*NIR*) is the reflectance of ASTER band 3N, *a* represents the intercept of the soil line (*a*= -6.35), and *b* indicates the slope of the soil line (*b*= 0.89). Given that the image was taken in late autumn, thermal information can be expected to play a significant role in the classification process. During this time, *Kobresia pygmaea* is often brownish with low chlorophyll content.

Nevertheless, the turf blocks of *Kobresia pygmaea* can be expected to emit thermal data different from that of bare soil and alpine steppe. In the PCA, band 4 explained more than 99% of the thermal information in the SWIR subtype group of the sensor, and was thus chosen for vegetation classification.

Neural Networks have to pass through a learning process to obtain memory of patterns and iteratively identify the relationship between cause and effect (Hayking, 1999). There are no rules for the configuration and design of ANNs, and optimized results can be best achieved by structured trial and error (Chen and McNairn, 2006). Therefore, the performance and accuracy of ANNs have been evaluated during each learning step.

For training and testing, a Multi-layer Perceptron (MLP) procedure was chosen which provides an arbitrarily specified number of up to 100 pixels per class. The order of significance of each data layer was identified by a Canonical Component Analysis (Zhao and MacLean, 2000). This approach was preferred because the order of bands feeding in the MLP has a major influence on the quality of the training process and hence on the classification (Mas and Flores, 2008).

In a final step, we compared these results with independent ground truth data and we constructed an error matrix calculation for data validation. With respect to the mentioned shortcomings of georeferencing, record plots were treated as areas instead of points. Furthermore, we calculated Cramer's V index for data validation, which is an effective measure of similarity (Rees, 2008).

RESULTS

The Plant Communities

The analysis identified six plant communities (Appendix 1) that included a total of 229 species. Community 2, the dwarf shrublands of *Juniperus pingii* var. *wilsonii*, and community 6, the closed *Kobresia pygmaea* pastures, differ from the other communities because they present a single dominant species (Community 2: *Juniperus pingii* var. *wilsonii*, 36% mean cover; Community 6: *Kobresia pygmaea*, 87% mean cover). The remaining plant communities cover more than 90% of the study area and are characterized by a high proportion of bare soil and the absence of a closed plant cover (59% of the 177 species present a 1% cover or less).

The DCA indicates more than one complete species turnover between the most dissimilar sites (length of gradient is 6.2, Figure 6). Axis 1 shows a correlation with slope inclination ($r=0.54$) and the cover of unpalatable plant species ($r=0.78$). Axis 2 has a shorter gradient (2.9) and is correlated with elevation ($r=0.44$).

Community 1: Juniperus Tibetica tibetica Woodlands

Community 1 represents open and degraded *Juniperus tibetica* woodlands at the northern treeline ecotone. All eight records are located in the broad valley south of the Nyenquentangla Shan, at 4250 - 4550 m altitude, on exposed slopes with open rocky soil. At present, only a few turf patches with *Kobresia pygmaea* can be found on the south-facing slope, where *Juniperus* reaches its highest cover values (up to 70%).

Species richness is variable (5 - 31 species/ plot). The community structure has three layers, a tree, a shrub, and an herb layer. The gnarled trees hardly attain 3 m in height and exhibit a high proportion of dead wood. We detected only a few seedlings, possibly due to harsh climate and strong grazing and trampling.

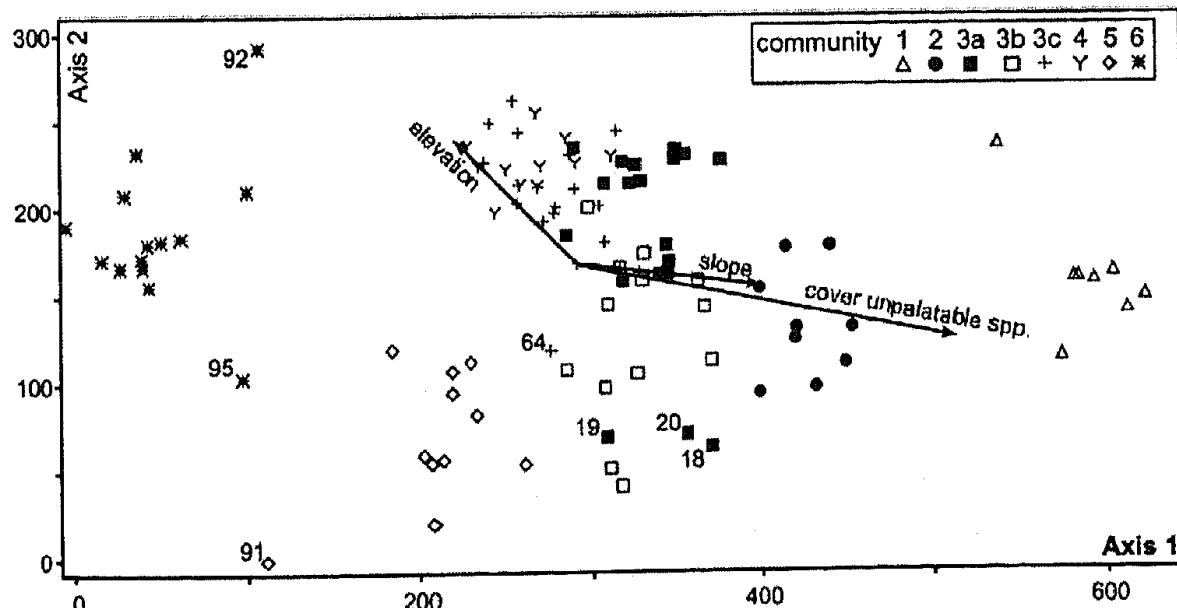


Figure 6. Detrended Correspondence Analysis (total inertia = 9.59, eigenvalue/ length of gradient axis 1 = 0.69/ 6.2, axis 2 = 0.28/ 2.9). Symbols indicate communities. Numbered records refer to the running numbers of the sites in the appendix.

Many of these sites are sacred for Tibetan Buddhists (especially the hill on which vegetation plots 1 to 7 were recorded, see Figure 7), which may have contributed to its conservation. According to the local community, these juniper forest remnants were once more widespread in the valley south of the mountain chain (Miehe et al., 2008d). Molecular evidence suggests this site is an Ice Age refugium because trees represent a unique haplotype (Opgenoorth et al., 2010). The pollen record supports these findings because *Juniperus* pollen was present deep in the studied core (13,000 years BP, Miehe et al., 2009). The pollen record indicates that grazing has prevailed in the last 8800 years and has increased in the last 2000 years (Miehe et al., 2009).

The shrub layer consists of *Juniperus pingii* var. *wilsonii* (3-70%) and a few dwarf shrubs, like *Caragana versicolor*, *Rosa sericea* and *Ephedra gerardiana*. These shrubs are the easternmost occurrence of semiarid thorny dwarf scrub that extends further westwards along the Yarlung Zhangbo into Ladakh (Hartmann, 1987). Even though *Caragana versicolor* reaches 4900 m in western Tibet, the shrub is absent around Nam Co.

The species composition of the herb layer is highly heterogeneous, with a mixture of species that are typically found in alpine steppe (*Arenaria bryophylla*, *Carex montis-everestii*), *Kobresia pygmaea* pastures (*K. pygmaea*, *Potentilla saundersiana*), montane pastures partly with C4 grasses (*Tripogon liouae*, *Orinus thoroldii*, *Pennisetum flaccidum*), and montane wastelands (*Dolomiae calophylla*, *Elsholtzia ciliata*, *Persicaria glacialis*, *Chenopodium nepalense*). Similar communities occur around Lhasa (3650 m). Poisonous and unpalatable plants are the most dominant functional type (mean cover of 57%, Figure 89). The mean cover of all grazing-resilient plants is 62%. These plants are never used as fodder, not even during late winter, when forage is scarce (*Stellera chamaejasme*, *Astragalus monbeigii*, *Iris potaninii*, *Delphinium* spp.). The abundance of grazing-resilient plants reflects pasture degradation and indirectly, strong human impact.



Figure 7. The northernmost woodlands of *Juniperus tibetica* (Community 1), with *Juniperus pingii* var. *wilsonii* and *Caragana versicolor* dwarf scrub on a south-facing slope. South-west of Damxung, 4250 m. September, 2009.

In the DCA, all sites of this community overlap with high disturbance and steep slope inclination. All sites are located on exposed slopes near settlements, thus receiving the highest impact of grazing and trampling.

Community 2: Juniperus pingii pingii Varvar. wilsonii wilsonii Open Dwarf Shrublands

Community 2 represents a dwarf juniper scrub (Figure 8) which is typical for the treeline ecotone of semiarid southern Tibet (Zhang, 1988). It is the northernmost vegetation type dominated by phanerophytes and the only source of wood in the region. Its character species, *Juniperus pingii* var. *wilsonii*, is a shrubby variant with a controversial taxonomical status (Farjon, 2005). It forms dense patches of up to 10 m diameter and 1.3 m height, and grows on rocky slopes with southern aspects. Individual shrubs may attain ages up to several hundreds of years (Liang et al., 2011). Growth is obviously rainfall limited as shown by dendrochronological analyses (Liang et al., 2011). Given that there are plenty sites around Nam Co with the same environmental properties, the vegetation of Community 2 may have once been much more widespread. On the southern slope of the Nyenquentangla, individual shrubs may form extensive, closed thickets. By contrast, around Nam Co and especially in the hills of its north-eastern catchment, only few isolated patches of this community can be found. Given that this vegetation type can be regularly found in the region, it is most probably natural. The vegetation composition reflects decreased humidity and stands in contrast to the southern slope of the Nyenquentangla Shan where dwarf shrubs such as *Lonicera rupicola*, *L. hispida*, *Ribes glaciale*, and *Rosa sericea* occur.

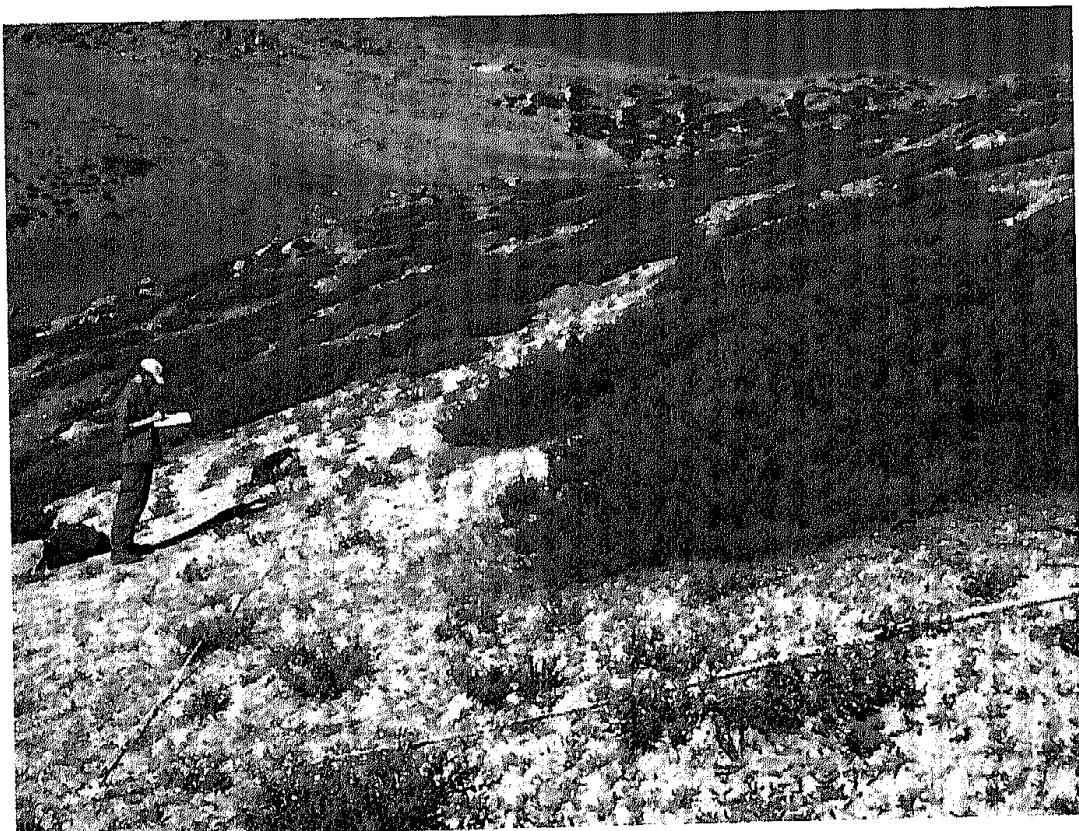


Figure 8. *Juniperus pingii* var. *wilsonii* open dwarf scrub on a southern exposed slope (Community 2). The juniper stands reach 6 m in diameter and 1.3 m tall. The surrounding pastures have a high cover of unpalatable plants. North-east of Nam Co., 4850 m. Sep. 2005.

Trees of *Juniperus tibetica* have so far not been discovered around Nam Co and it remains doubtful if trees were ever present here during the Holocene (cp. Herrmann et al., 2009). Community 2 has a mosaic structure with dense patches of shrubby junipers surrounded by open soil and isolated herbs and graminoids. The plant cover around the juniper patches ranges from 20 to 33%. On average, 39 species occur in each plot. Species of the *Kobresia* pastures are nearly absent, whereas alpine steppe species are commoner (*Stipa purpurea*, *Carex montis-everestii*, *Incarvillea younghusbandii*). These mosaics share a greater number of species with the juniper woodlands of southern Tibet (*Phlomis younghusbandii*, *Thalictrum rutifolium*, *Dracocephalum tanguticum*, *Elymus schrenkianus*, *Pedicularis alaschanica*, *Cryptothladia kokonorica*). The community is characterized by the abundance (71%) of poisonous and unpalatable plants which is five times greater than in the herbaceous communities 3 - 6 (Figure 9). Cushion plants are nearly absent from Community 2 (less than 1%). The mosaic structure and the intermediate species composition (see DCA, Figure 6) indicate a transitional status of this community that mediates between open woodland pastures and alpine steppe pastures. At present, stands are only used as winter pastures, when livestock feeds on the dry aboveground plants. Thus, the current level of degradation is relatively low, and the present species composition may reflect more intense grazing by livestock or wild mammals in the recent past.

Community 3: Alpine Steppe

Community 3 was recorded in 51 plots and is located in the north-eastern Nam Co catchment, at 4660 - 4890 m altitude (42% of all records were recorded at 4720 - 4750 m). Sites are located on moderately inclined, south-facing slopes, or in pediments and lake terraces. Loess is the common substrate on these sites. The average vegetation cover is 31%. Most plant species (65%) have a total cover of 1% or less. The community attains the highest graminoid cover (30%), Cyperaceae reach only a 9% cover. The altitude and the presence of cushion plants (Figure 10) in this community match the description of the 'High cold steppe' by Wang (1988) and justify its classification as alpine steppe. Only few species are taller than 10 cm (*Stellera chamaejasme*, *Cryptothladia kokonorica*, *Dracocephalum tanguticum*, *Iris potaninii*, *Thermopsis lanceolata*, *Stipa koelzii*, *Pennisetum flaccidum*). These taxa are mainly poisonous plants or grazing weeds reaching their altitudinal limits here. The majority of dicots are shorter than 5 cm.

The 51 plots belonging to this community can be further divided into three sub-communities. Sub-community 3a (running no. 18 to 37, see Appendix 1) is characterized by *Stellera chamaejasme*. It is mostly found in the hills and pediments of the northern side of Nam Co; 40% of the records are on south-facing slopes. Plants avoided by livestock and disturbance indicator species (*Dracocephalum tanguticum*, *Euphorbia stracheyi*, *Astragalus tribulifolius*, *Youngia simulatrix*, *Cryptothladia kokonorica*, *Sedum perpusillum*, *Lasiocaryum munroi*, *Rhodiola smithii*) reach high frequency values. It is possible that these stands replaced the *Juniperus pingii* var. *wilsonii* thickets from the south-facing slopes in the north-eastern Nam Co catchment that had been cleared for firewood.

Sub-community 3b is characterized by *Kengylia thoroldiana* (running no. 38 to 50). This community type was mainly recorded at the south-eastern sandy plains of Nam Co. The most common species are *Kengylia thoroldiana*, *Kobresia robusta*, *Dontostemon glandulosus*, and *Dracocephalum heterophyllum*. They are character species of eastern alpine steppes on sand dunes and are common in the sand fields around Madoi in the north-eastern highlands.

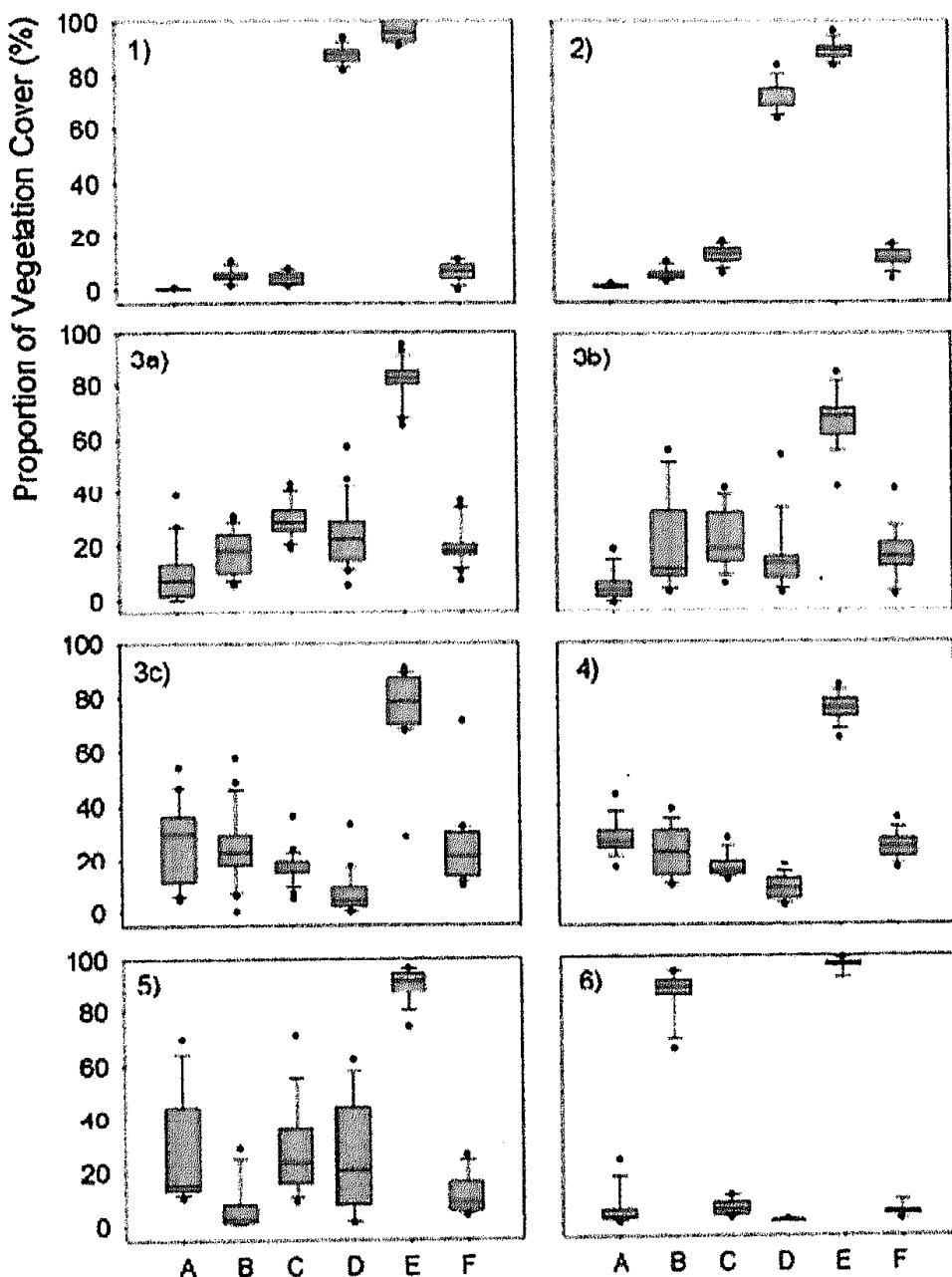


Figure 9. Mean cover values for the plant functional types in the communities. A-D and F represent plant functional types as described in the text. E refers to the cover of all resilient plant functional types (sum of A-D).

Sub-community 3c (running no. 51 to 68) is mainly distributed on loess covered hills and sandy plains north of Nam Co and reaches a mean richness of 25 species/ plot and mean vegetation cover of 36%. Graminoids, such as *Festuca valesiaca*, *Koeleria litvinowii*, and *Poa albertii* are frequent, with a mean cover of 17% (46% of the total plant cover). Cushion plants (*Astragalus arnoldii*, *Sibaldianthe adpressa*) have mean cover values of 10%. It is distinguished from sub-community 3b by four species (*Artemisa stricta*, *Astragalus arnoldii*, *Potentilla exigua*, *Koeleria litvinowii*).

Community 4: Alpine Steppe – *Kobresia Pygmaea pygmaea* Mosaic

This community is the most common vegetation type in the 2000 km ecotone. On a larger scale, it can be regarded as a transitional vegetation type with strong affinities to alpine steppes of Community 3 (Figure 6) and more limited affinities to closed *Kobresia* pastures in

the south-east (Community 6, Figure 6). The mean plant cover is 42%. Its intermediate nature is also reflected in the vegetation structure that is characterized by a mosaic of isolated turfs and *Kobresia pygmaea* patches, surrounded by open soil with scattered graminoids, rosettes and cushions. The turf sods resemble stepping stones and are scattered across the landscape (Figure 11). They are all 5 - 10 cm high and likely the remnants of a once closed turf cover (see description of Community 6 below).



Figure 10. Alpine steppe in an open plain. The total plant cover is 25%. Six graminoid species cover 20%. 31°23'N/94°40'E, 4680 m. August 1993.



Figure 11. *Kobresia pygmaea* turf that has been fragmented into stepping-stone-like turf sods (1). Pikas dug holes underneath the sods (arrow). The open soil among the turf sod is colonized by alpine steppe species (2). Qinghai (34°37'N/98°00'E), 4240 m. August 2009.

Humans have certainly had a negative impact in the recent past, by cutting sods for construction purposes (Figure 12). Yaks tear up the turf cover with their horns to wallow in the open soil. The closed *Kobresia* turfs, also called the “rhizomull”, are mostly resilient to trampling, a globally unique feature for an ecosystem that is subject to grazing impact and desertification (Kaiser et al., 2007). Abiotic processes, however, seem to have a negative effect. In the highest pastures of the region, gelifluction can break sods up during freeze-thaw events (Miehe, 1988).



Figure 12. *Kobresia pygmaea* sods have been cut to construct a protecting wall against precipitation in the vicinity of a newly built winter village. Nam Co, 4750 m. September 2007.

The remaining turf sods mostly have steep sides with dry roots, and lack any higher plants, algae, mosses, or lichens. This structure largely resembles the turf exfoliation cliffs caused by wind and needle-ice (Troll, 1973). The sides of these turf cakes sods are often undermined by burrowing pikas which probably take advantage of the stable sods and their insulating effects during winter. On steep slopes, the sides of such sods are even used by sheep for rubbing.

A widespread pattern throughout the entire altitudinal range of the *Kobresia* turfs are polygonal cracks caused by heavy frost (Zhang, 1988), or desiccation (Miehe et al., 2008b). They are widened by the joint impact of gelifluction, deflation, and digging by pikas (Figure 13). The relatively high richness (mean 38 species) and the mosaic structure in this community reflects its transitional position between the two major biomes, the relatively mesic *Kobresia pygmaea* grasslands and the alpine steppe. This notion is supported by the fact that plant functional types of both the alpine steppe and *Kobresia pygmaea* pastures are prevalent. Two of the most widespread grazing resilient species, *Androsace tapete* and *Leontopodium pusillum* attain highest frequency and cover degrees in this community.

The spatial species distribution follows a regular pattern. Whereas typical *Kobresia* mat species are confined to the turf sods, alpine steppe species grow among the sod fragments. However, the open patches around the *Kobresia pygmaea* stands are colonized by alpine steppe species. Both findings suggest that alpine steppe species could slowly replace the *Kobresia pygmaea* mats.

The plot data thus show the same aridification trend as the large-scale proxies derived from the palynological sediments in Tibetan lakes (e.g. Academia Sinica, 1990; Avouac et al., 1996; Zhu et al., 2008) which estimated a general trend towards lower monsoonal rainfall since 5600 years calibrated before present (Shen et al., 2008).

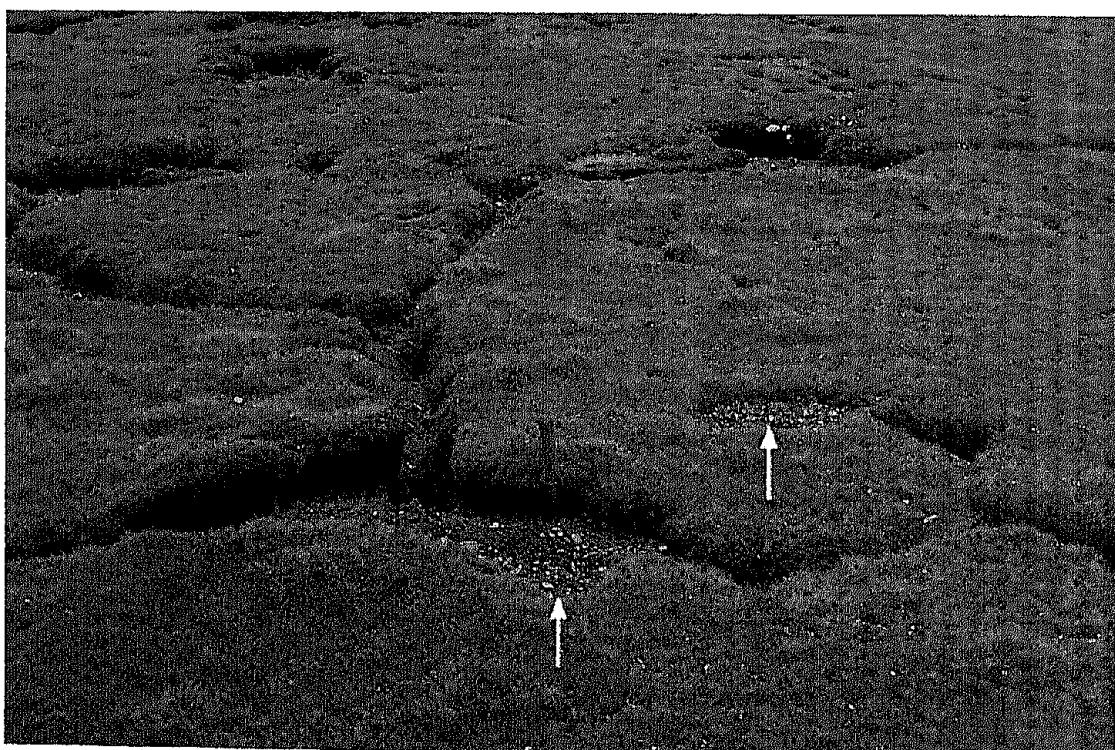


Figure 13. *Kobresia pygmaea* turf, split by polygonal cracks. Pikas have undermined the turf cliffs (knife). *Kobresia* fragments are carved by soil erosion (arrow). South of Nagqu, 4540 m. September 2009.

This explanation might be too simple, though. Increased levels of humidity in parallel with a cooling trend may enhance needle ice frequency and promote turf exfoliation. The same is true for a cooling trend: During the period 1951-80, a drop in temperature of 0.6-1.2 K (Böhner, 1996) resulted in intensified gelifluction as shown by screes overriding turfs or intensified frost breaking up the turf (Miehe, 1988). Probably, a long-term late-Holocene trend of decreasing humidity is currently being superimposed to short term thermal oscillations. Wind erosion might also have played a role in the retreat of exposed turf cliffs. A long-lasting deflation effect, however, is not evident because deflation pavements are missing in the study area. One possible conclusion is that the process of turf retreat is relatively recent and/or deflation is not as strong as in the southern Tibetan Foehn-exposed rain shadow of the High Himalayas (Miehe, 1988). In summary, Community 4 seems to represent an intermediate succession stage, from the closed alpine *Kobresia* turfs typical of a humid biome to the alpine steppe characteristic of a semiarid one.

Among the 132 species found in Communities 3 and 4, 45% form cushions (11%, e.g. *Androsace tapete*) or rosettes that are closely appressed to the surface (34%, e.g. *Taraxacum sherriffii*). Poisonous plants or grazing weeds avoided by livestock due to repellent characters (e.g. *Incarvillea younghusbandii*, *Dracocephalum heterophyllum*) make up 21 % of the species with a 15% cover. Graminoid species represent 18%, with an average cover of 13% (37% plant cover, cp. Figure 14 a, b). Their average growth height ranges between 3 to 5 cm (e.g. *Carex montis-everestii*) and 10 to 15 cm (e.g. *Stipa purpurea*, *Carex moorcroftii*). The latter are the main forage resource. Some 12% of the species with a cover percentage of 22% are resilient against overgrazing because their buds are closely attached to the surface and thus well protected (e.g. *Stipa purpurea*) or because they have rhizomes that are hidden in the soil (e.g. *Carex moorcroftii*). Only bunch grasses like *Festuca* or *Poa* spp. (2% of the species and 9% of the cover percentage) are prone to grazing. Thus, most alpine steppe species in the study area are more or less tolerant to grazing. The resilience against grazing and the absence of grazing gradients has been similarly detected in the mountain desert steppes of the Gobi Altai, in southern Mongolia (Stumpp et al., 2002), which share physiognomy and related flora.

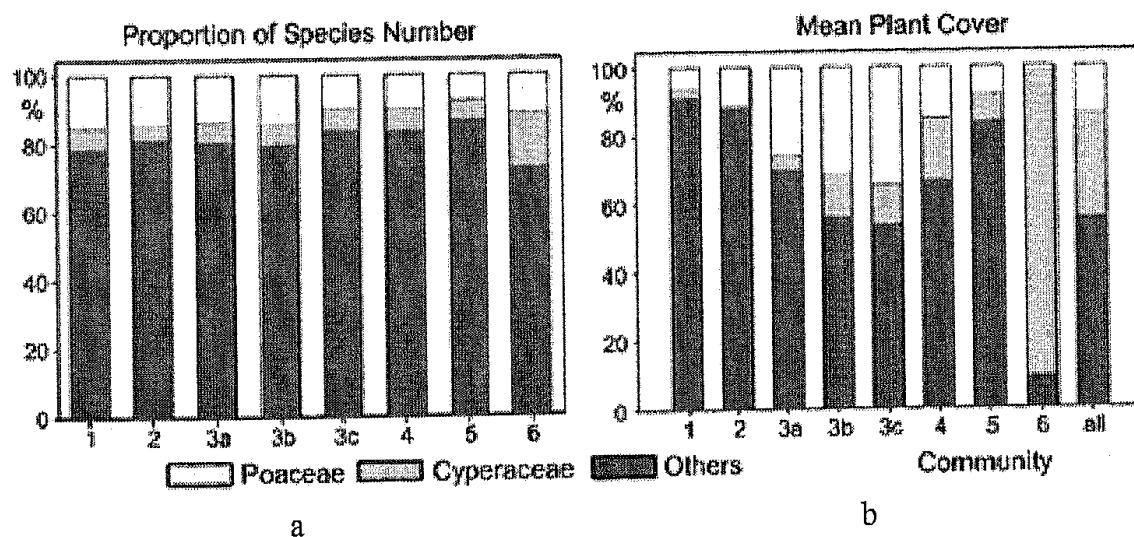


Figure 14. Proportion of species richness (a) and vegetation cover (b) by Poaceae, Cyperaceae and other families in each community.

Community 5: *Lancea Tibeticatibetica*-Wastelands

This community (11 plots) is a common vegetation type in Tibet's alpine pastures. It represents the final degradation stages following the destruction of a protecting turf cover. This vegetation type is also called "black soil" (Ma et al., 1999) in the north-eastern highlands due to the high humus content of the exposed loess. The community tends to be more common on exposed slopes, where inclination, shallow soils and presumably higher grazing pressure may increase damage and erosion. According to the DCA, this community is a transition between alpine steppes and *Kobresia pygmaea* pastures. The majority of sites are located at the left side of axis 1 with higher variability along axis 2 (Figure 6). They share plant species and environmental conditions with Community 3b and with some plots of Community 2 and 3a (running no. 18-20). Community 5 differentiates from Community 2 and 3a along an elevation gradient.

Dwarf shrubs (*Dasiphora parvifolia*) and *Artemisia* sub-shrubs (*A. tridactyla*, *A. santolinifolia*) occur in this community, the latter often heavily grazed. Some common species have rhizomes, like *Thalictrum rutifolium* and *Artemisia tridactyla*, which allows plants to cope with the unstable substrate.

A high proportion of the species of Community 5 (43%) are annual rosette plants, especially members of the Brassicaceae, Boraginaceae, Polygonaceae and Chenopodiaceae. This group reaches a high frequency in this vegetation type (26% of the plots). Some typical Tibetan grazing indicator plants are also present, including *Potentilla bifurca*, *Lancea tibetica*, and annual *Artemisia* species (*A. hediondii*, *A. stricta*). Where pikas are less common, small mats of *Leontopodium pusillum* spread and develop an "edelweiss semi-desert" (Holzner and Kriechbaum, 2000). Nearly all species in this community are endemic and some are even monospecific genera (e.g. *Microgynoecium*, Wu et al., 1981). More than 66% of the species of community 5 are found above 5100 m. They occur on regularly disturbed and open soils. Such sites are generated by large herbivores, especially the Tibetan wild ass and the wild yak, which wallow in open soil, and by smaller digging mammals like marmots and pika. Thus, these niches must have been available for long periods of time.

Vegetation structure is patchy in this community. Total plant cover is not very high (mean: 62%, range: 27 - 83%) and mean species richness is 29 species/ plot. Forage plants, if present, are heavily grazed by livestock and pikas. Pika density is highest in this community with an average of 34 pika holes per plot. Whether pikas actually cause the degradation or just follow the destructive impact of livestock is an important question for future research.

Community 6: *Kobresia Pygmaea pygmaea* Grazing Lawns

Community 6 (14 plots) is the intact, golf course-like pastures of *Kobresia pygmaea* which are commonly found in the south-eastern Tibetan highlands (Figure 15), the world's largest humid alpine biome. The community is characterized by a number of distinct features. It represents the world's highest plant community (Miehe, 1989) with 70% of the species having their upper limit of distribution above 5100 m (Figure 719). The rhizomes and roots build a characteristic soil type ("rhizomull", Kaiser et al., 2008) with a felty A-horizon. Soil blocks are so tough that they are used for construction purposes (cp. Figure 12). All species in this community are highly adapted to grazing. The species set differs from the other communities, as shown by the DCA (Figure 6).

This community type was recorded mainly in the north-eastern study area, in valley bottoms with loess and gravel substrates, at 4480 - 5100 m.



Figure 15. Detail of closed *Kobresia pygmaea* grazing mats (Community 6). 30°48'N/92°35'E, 4770 m. July 2004.

The community is made up almost entirely of a single plant species, *Kobresia pygmaea*, which covers more than 90% in nine of 14 samples. Species richness is low (mean: 17 species/plot). Plants are small, with their above-ground biomass near the soil surface.

Land Cover Assessment

The absolute classified area covers approximately 5656 km² (Table 1). In addition to gravel, snow, ice, clouds and water, six different vegetation classes were identified (Figure 16), based on 71 training areas. These classes were deliberately chosen so that the floristically classified vegetation types were represented.

Table 1. Relative and absolute cover percentages of the land cover classes

Type	Area/ km ²	Percentage
<i>Kobresia pygmaea</i> pastures	295.75	5.0%
<i>Kobresia pygmaea</i> turf/ alpine steppe mosaic	1612.12	27.1%
Dense alpine steppe	431.95	7.3%
Sparse alpine steppe	61.34	1.0%
Alpine scree plant communities	153.84	2.6%
<i>Kobresia schoenoides</i> swamps	650.19	10.9%
Gravel	420.19	7.1%
Snow/ ice	1462.17	24.6%
Clouds	229.64	3.9%
Water	635.33	10.7%

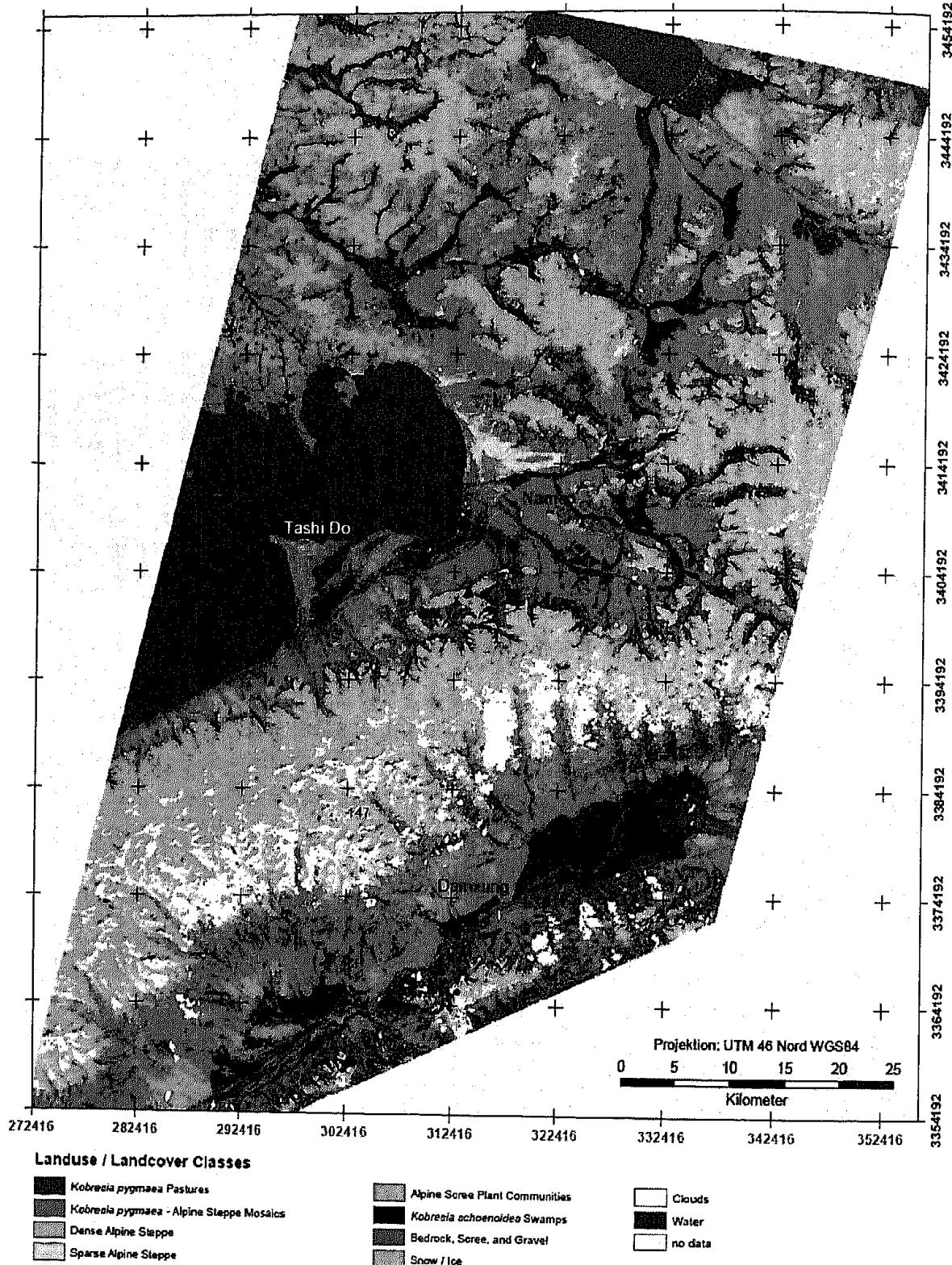


Figure 16. Land use/ land cover classes derived from supervised classification of satellite imagery.

Several runs of the Multilayer Perceptron procedure were performed, yielding classification accuracies of 69% - 79%. Finally, the VNIR bands 1 and 2, the scaled PVI (PVI*100), a PCA image of the ASTER DEM and the SRTM DEM and SWIR band 4 were used in the given order. The obtained accuracy of the training process was 76.2% and showed no tendency for overtraining.

Cramer's V index shows a correlation of 0.46 ($p= 0.02$) which shows that the classification was accurate. Furthermore, it provides a reliable estimation of the correspondence between plant community composition and vegetation formations.

However, whereas the floristic classification of plant communities focuses on species composition, the satellite based classification has to deal with both the response in vegetation cover and the abiotic surface signals. Thus, some of the floristically derived vegetation types had to be fused while others could be differentiated further. For example, Community 3 could not be distinguished from Community 4 using the spectral images from November. The *Kobresia pygmaea* turf/ alpine steppe mosaic and the *Kobresia schoenoides* swamps covered the largest areas of all identified vegetation types.

DISCUSSION

Is There Resilience or Vulnerability in an Equilibrium/ Non-Equilibrium Ecotone?

The study area stretches from a climatically stable equilibrium system in the east (Community 6, cp. Figure 1) to a highly variable non-equilibrium system in the west (Community 3).

Major parts of the area belong to an ecotone where species of both biomes intermix. The *Kobresia* pastures in the east have a closed plant cover, which stands in contrast to the naturally open alpine steppe in the west. Thus, the percentage of open substrate should be used as an indicator for rangeland health only in the east. The land cover map (Figure 16, see also Table 1) shows a high proportion of vegetation mosaics which can possibly be attributed to Community 4.

The vulnerability or resilience of a pasture is reflected in the prevalent plant functional types (Duckworth et al., 2000). In Communities 1 and 2, 19% of all species are graminoids which have buds closely attached to the ground or hidden in the soil. This group makes up 10% of the cover in this vegetation type (Figure 14a,b). Rosette species are especially common in Communities 3-6 (Community 3: 37%; covering 25%, Community 4: 33%; 17%, Community 5: 43%; 28%, Community 6: 45%; 5%). Taller plants, which are constantly avoided by livestock, like *Stellera chamaejasme*, *Cryptothladia* spp., and *Meconopsis horridula*, make up 6% of all species in the data set, having a mean cover of 1% across all records. These species reach their highest proportions in Communities 1 and 2 (24% and 86% of the cover, respectively). Poisonous grazing weeds attain very high cover percentages in some plots.

Today, most *Kobresia* pastures in the study area lack closed turf cover but it is possible that they once formed closed vegetation (see conceptual model in Figure 17). However, this hypothesis has yet to be proven. Compared to the alpine steppe, the *Kobresia* turfs in the eastern equilibrium system are likely to be more vulnerable than the non-equilibrium system of the west.

The answer to the question of whether a plant community is vulnerable or resilient to grazing relies on the chosen plant functional types. The present distribution, however, can be interpreted in different ways, depending on the question of the state of naturalness.

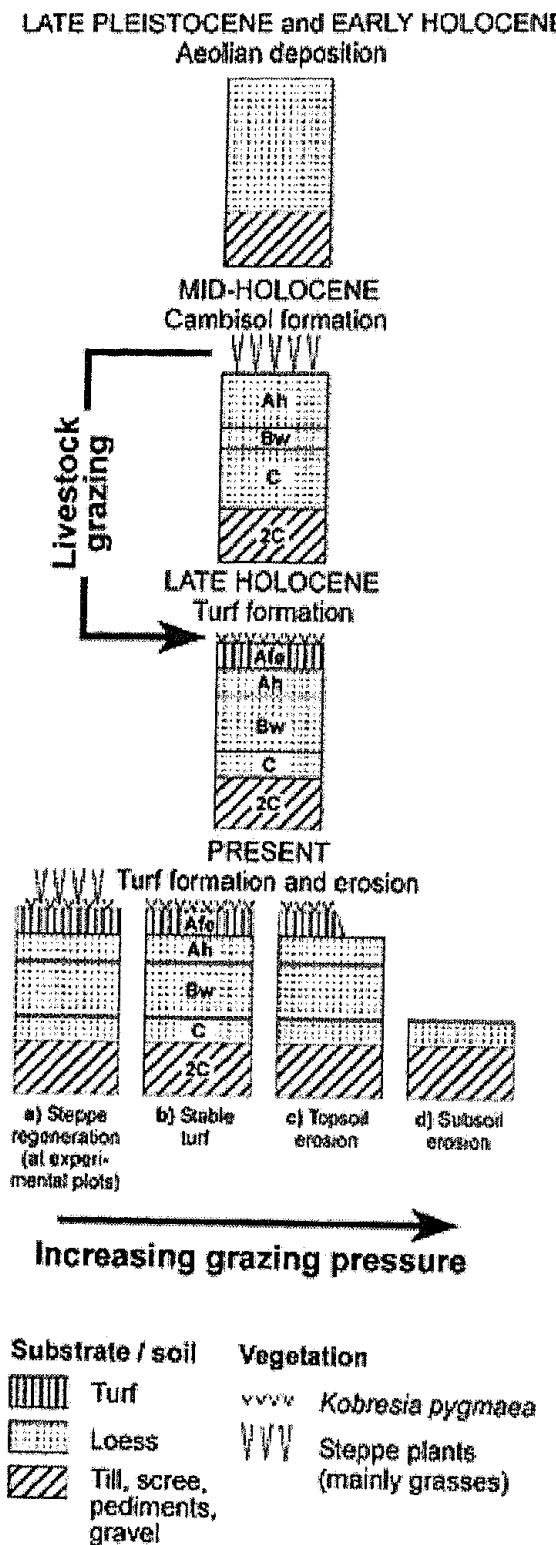


Figure 17. Conceptual model showing possible vegetation and soil dynamics in the mosaic of *Kobresia pygmaea* mats and alpine steppe in the Nagqu area (ca. 4500 m). Adapted from Kaiser et al., 2008.

The current physiognomy of the studied communities corresponds to what is generally defined as “alpine” plant communities (Körner, 1999). Consequently, it is not surprising that most authors regard the current state of Tibetan highlands as natural. However, such an assumption might not be correct for the *Kobresia* communities. Grazing exclosure experiments indicate that this community might have formed due to strong grazing effects, at least for the equilibrium systems of the *Kobresia* pastures (Miehe et al., 2008b, c).

Most of the current *Kobresia* pastures of the Tibetan highlands are at altitudes potentially suitable for tree growth, and most probably represent a synanthropic plagioclimax (Miehe et al., 2008a, c). Grazed plots resemble “alpine” short grasslands, whereas fenced plots differ by having tall grasses that overgrow the small sedge mats, rosette and cushion plants. Data from grazing exclosure experiments of truly alpine altitudes are still not available for the Tibetan highlands, because exclosure experiment plots in the southern (Reting 30°18'N/91°31'E) and north-eastern highlands (Xinghai 35°30'N/99°49'E) are located around 400 m below the upper tree line (Miehe et al., 2008b, c). However, the recently commenced privatization of rangeland with the fencing of winter pastures at alpine altitudes can be seen as a large scale fencing experiment. Even at 4340 m, the area outside the fence used as all-year round common grazing ground was covered by “natural alpine” *Kobresia pygmaea* vegetation. By contrast, the area inside the fence, where grazing is now excluded, was dominated by tall grassland that had overgrown the small “alpine” *Kobresia* mats (Figure 18).

Most of the species in this data set are endemic to the Tibetan highlands or at least to High Asia (Wu, 1983-87; Liu, 1996-99) which indicates that species must have their natural habitats here. This alpine endemism must have developed during the uplift and isolation of the highlands into alpine altitudes since the Tertiary (Rowley and Currie, 2008; Spicer et al., 2003; Tapponnier et al., 2001), as well as during the climatic changes in the Quaternary. Plants have likely adapted to the cold and partly dry conditions. The larger herbivores of the highlands are also endemic, and it is possible that the endemic plants have co-evolved with these herbivores.

It is known that plant species from different natural communities can be found in synanthropic communities (e.g. like in Central European meadows, Ellenberg, 1996).



Figure 18. Fenced winter grazing reserve in *Kobresia pygmaea* pastures. Outside the fence, “alpine” *Kobresia pygmaea* mats are maintained by grazing, whereas inside the fence, they have increasingly been overgrown by grasses. Qinghai (35°45'N/95°46'E), 4340 m. Sep. 2002.

As the *Kobresia*-pastures of the study area have a high number of endemic species and are in part a grazing-climax, the question arises of where these species may have their natural habitats. According to own records and regional accounts (Wu, 1983-87; Liu, 1996-99), 53% of the species listed in the supplement reach their upper distribution limit at 5100 m altitude or higher (Figure 19).

In Community 6, such "high alpine" species account for 70% of the regional species pool and attain a mean cover of 90%. They dominate the upper limit of the alpine belt and are typical species of the world's highest plant communities at 5960 m, on the northern escarpment of Mt. Everest (Miehe, 1989).

There, they form dense cushions made up mostly of *Kobresia pygmaea*, *Festuca tibetica*, *Saussurea graminea* var. *ortholepis*, *Arenaria bryophylla*, *Cortiella caespitosa*, and *Saussurea leontodontoides*, surrounded by boulders and scree of a periglacial environment. Approximately 35% of these species are rosette plants that closely hug the ground.

Free range grazing is the traditional rangeland management in the Tibetan highlands and it is still being practiced today. Animals, especially goats and sheep, selectively graze palatable plants that are available during the different seasons.

Taller and palatable forage plants are skimmed off except for their basal buds. Grazing favors shorter plants, like *Kobresia pygmaea*, over taller grasses that have more than three quarters of their above-surface biomass within the grazing reach of livestock.

It is likely that dwarf high alpine species and those from disturbed sites (e.g., pika burrows) have spread in response to high grazing pressure and reassembled to form the present pastures. The *Kobresia* pastures can thus be regarded as an assemblage of secondary vegetation composed of grazing tolerant plants (Grime, 1979; Diaz et al., 1992).

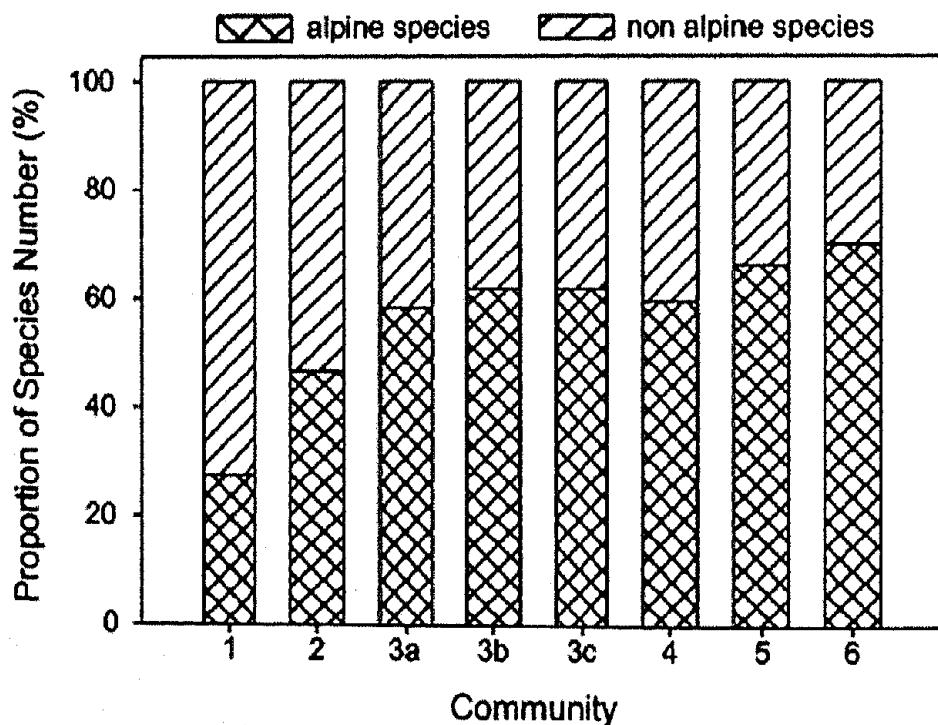


Figure 19. Proportion of alpine species (growing higher than 5100 m) within the communities (community numbers according to the table in the supplement).

The prime example is *Kobresia pygmaea* itself as an endemic and grazing adapted constituent of the pastures that is extremely resilient both against trampling and against grazing.

In conclusion, the eastern part of the study area is dominated by synanthropic *Kobresia pygmaea* rangelands, in which grazing adapted plant functional types prevail. This vegetation type is comparable to the *Cynodon dactylon* grazing lawns of the East African highlands (McNaughton, 1984).

Although the proportion of grazing adapted species is high, the fragmented turf cover indicates that habitat destruction is beyond the resilience of this system. Up to now, no evidence of turf cover recovery could be detected in the area of investigation. Possible detrimental effects are imposed by climate (gelifluction and needle ice, deflation, desiccation), animals (pika, destructive impacts of livestock), and humans (turf extraction). How much turf cover was destroyed has not been quantified yet, but probably extends throughout the entire biome in this region.

The natural extension of this vegetation type can only be reconstructed with the help of palaeo-ecological studies and long-term experiments.

In contrast to the *Kobresia* pastures, the alpine steppe vegetation is more open, having an average cover of 39% in the study plots. It is not known to what extent this vegetation type is natural. Data from grazing exclosure plots are not yet available for these communities. We also do not know to which extent the present livestock numbers exceed the former number of large wild herbivores as a natural disturbance factor. Climatic data imply the presence of a non-equilibrium system which is largely rain-driven.

We can assume that episodic heavy snowfall in winter is another factor to control livestock numbers. Most alpine steppe species in the study area are High Asian endemics. In Communities 3 and 4, 45% are cushion or rosette plants, while 20% of the species are poisonous or grazing-resistant weeds.

Graminoids are the main forage resource and make up 18% of the species, with an average cover of 13%. Their average growth height is 3 - 15 cm. Most graminoids (12% of all species in the community, 22% cover) are resilient to overgrazing.

Only bunch grasses are prone to grazing. Thus, alpine steppe species in the study area are more or less tolerant to grazing. We did not detect any clear grazing gradients and thus assume that the alpine steppe is a Central Asian non-equilibrium climax.

The high proportion of grazing-adapted plant functional types in *Kobresia* mats and alpine steppe suggests that both biomes are relatively resilient against degradation. Human impact may be monitored using the cover of unpalatable species as a measure of pasture degradation.

In contrast to the grazing resilience of the pastoral resources, the widespread *Kobresia pygmaea* turf is more vulnerable and subject to fragmentation. Future studies need to investigate whether this degradation process is natural or whether it was induced by overgrazing in the last decades.

APPENDIX 1

Vegetation table of relevés at lake NamCo comprising 105 records and 299 species

APPENDIX 1 (CONTINUED)

Shown are cover degrees in percent for the species in each record plot ('+' = cover < 1%; 'r' = rare incidence of the species; ':' = no occurrence of the species in this record).

APPENDIX 2

Categorical synoptic table for Communities 1 - 6. All species with frequency > 3%
(I=0.1-19%; II=20-39%; III=40-59%; IV=60-79%; V=80-100%) are included

Community No.	1	2	3a	3b	3c	4	5	6	
No. of relevés	8	9	20	13	18	12	11	14	freq.
Character species of Community 1									
<i>Juniperus tibetica</i>	V	6.7
<i>Caragana versicolor</i>	V	6.7
<i>Dolomiaea calophylla</i>	V	6.7
<i>Rhodiola sacra</i>	V	6.7
<i>Sedum roborowskii</i>	IV	5.7
<i>Piptatherum gracile</i>	IV	5.7
<i>Poa hylobates</i>	V	6.7
<i>Stellaria dianthifolia</i>	V	6.7
<i>Pleurospermum foetens</i>	IV	5.7
Character species of Community 1 and 2									
<i>Kobresia macrantha</i>	II	II	.	I	5.7
<i>Pennisetum flaccidum</i>	V	I	I	I	9.5
<i>Ephedra gerardiana</i>	IV	.	I	I	I	I	I	.	12.4
<i>Urtica hyperborea</i>	II	III	.	.	.	I	.	.	8.6
<i>Allium fasciculatum</i>	IV	II	I	.	.	I	.	.	9.5
<i>Astragalus tribulifolius</i>	IV	III	II	I	14.3
<i>Juniperus pingii var. wilsonii</i>	V	V	15.2
<i>Phlomis younghusbandii</i>	V	IV	II	.	.	II	.	.	22.9
<i>Dracocephalum tanguticum</i>	V	V	IV	I	.	III	.	.	34.3
<i>Stellera chamaejasme</i>	IV	IV	IV	II	I	IV	.	.	39
Character species of Community 2									
<i>Artemisia moorcroftiana</i>	.	IV	I	.	.	.	I	.	8.6
<i>Poa albertii ssp. poophagorum</i>	.	IV	5.7
<i>Poa araratica s.l.</i>	.	V	8.6
<i>Poa asperifolia</i>	.	III	3.8
<i>Stephanachne cf. pappophorea</i>	.	III	3.8
<i>Gentianella azurea</i>	.	III	3.8
<i>Rhodiola tangutica</i>	.	IV	.	.	.	I	.	.	7.6
<i>Allium przewalskianum</i>	.	II	.	I	3.8
Other species in Communities 2 – 4									
<i>Stipa penicillata</i> var. <i>penicillata</i>	.	III	I	I	7.6
<i>Microula tangutica</i>	.	V	I	II	-	-	.	.	15.2
<i>Salsola monoptera</i>	.	II	I	II	-	-	.	.	8.6
<i>Dontostemon glandulosus</i>	.	III	I	III	I	-	.	.	15.2
<i>Corydalis hookeri</i>	.	V	II	I	-	I	.	.	16.2
<i>Trikeria oreophila</i>	.	III	I	.	-	II	.	.	9.5
<i>Anaphalis nubigena</i>	.	III	III	.	-	IV	.	.	20
<i>Silene caespitella</i>	.	IV	II	.	I	V	.	.	21.9

APPENDIX 2 (CONTINUED)

Community No.	1	2	3a	3b	3c	4	5	6	
No. of relevés	8	9	20	13	18	12	11	14	freq.
<i>Pleurospermum aromaticum</i>	I	V	I	.	.	III	.	.	14.3
<i>Ajuga lupulina</i>	.	III	I	.	I	I	III	.	15.2
<i>Thalictrum rutifolium</i>	.	V	I	II	I	I	III	.	23.8
<i>Artemisia tridactyla</i>	.	V	III	II	I	III	IV	.	34.3
<i>Pedicularis cheilanthifolia</i>	.	III	III	II	I	IV	.	.	25.7
<i>Euphorbia stracheyi</i>	.	V	III	II	I	I	.	.	26.7
<i>Lasiocaryum munroi</i>	.	IV	III	II	II	I	III	.	35.2
<i>Carex stenophylla</i>	.	II	V	III	V	V	.	.	48.6
<i>Rhodiola smithii</i>	.	II	II	I	II	I	.	.	17.1
<i>Oxytropis stracheyana</i>	.	II	II	III	II	II	.	.	24.8
<i>Youngia simulatrix</i>	.	II	IV	II	II	V	.	I	37.1
<i>Saussurea leiocarpa</i>	.	II	IV	I	I	IV	.	.	29.5
Character species of Community 3 and 4									
<i>Festuca cf. valesiaca</i>	.	.	IV	III	V	IV	.	.	43.8
<i>Lomatogonium brachyantherum</i>	.	.	IV	II	IV	III	.	.	35.2
<i>Kengyilia thoroldiana</i> var. <i>thoroldiana</i>	.	.	II	IV	III	II	.	.	26.7
Character species of Community 3									
<i>Kobresia robusta</i>	.	.	I	IV	II	.	.	I	16.2
<i>Deyeuxia zangxiensis</i>	.	.	I	III	II	.	.	.	13.3
<i>Artemisia stricta</i>	.	.	I	I	IV	.	I	.	16.2
Character species of Community 3 and 4									
<i>Astragalus arnoldii</i>	.	.	I	.	IV	III	.	.	19
<i>Potentilla exigua</i>	.	I	.	I	IV	III	IV	I	27.6
<i>Koeleria litvinowii</i> subsp. <i>argentea</i>	.	.	I	I	IV	III	IV	.	28.6
<i>Sibbaldianthe adpressa</i>	.	I	I	I	III	I	II	II	23.8
<i>Taraxacum sherriffii</i>	I	.	II	I	II	III	.	II	23.8
<i>Allium cyaneum</i>	.	II	II	I	I	V	.	.	22.9
Character species of Community 4									
<i>Comastoma pedunculatum</i>	.	I	I	.	I	IV	.	I	16.2
<i>Delphinium caeruleum</i>	.	I	I	.	I	III	.	.	13.3
<i>Draba zangbeiensis</i>	.	I	I	.	I	III	I	.	9.5
<i>Aster yunnanensis</i>	.	II	I	.	.	III	.	.	8.6
<i>Kobresia capillifolia</i>	.	I	I	.	.	IV	.	I	10.5
<i>Eritrichium tangkulaense</i>	.	II	I	.	.	III	.	.	9.5
Character species of Community 4 and 5									
<i>Meconopsis horridula</i>	IV	I	.	8.6
<i>Dasiphora parvifolia</i>	.	I	.	I	I	III	I	II	14.3
<i>Kobresia pygmaea</i>	I	V	IV	V	31.4
<i>Potentilla saundersiana</i>	.	.	I	I	II	V	III	IV	33.3
<i>Veronica ciliata</i>	.	.	I	.	II	I	V	II	20
<i>Artemisia santolinifolia</i>	.	II	I	.	I	II	II	.	12.4

Community No.	1	2	3a	3b	3c	4	5	6	
No. of relevés	8	9	20	13	18	12	11	14	freq.
Character species of Community 5									
<i>Axyris prostrata</i>	.	I	.	II	II	.	IV	I	16.2
<i>Galium exile</i>	IV	.	.	I	.	.	III	.	11.4
<i>Persicaria glacialis</i>	I	I	I	.	.	.	V	I	13.3
<i>Heracleum millefolium</i>	.	.	I	I	I	.	III	.	8.6
<i>Draba ellipsoidea</i>	I	III	.	6.7
<i>Saussurea andryaloides</i>	IV	.	7.6
<i>Stellaria decumbens s.l.</i>	III	I	6.7
<i>Lagotis brachystachya</i>	III	I	6.7
<i>Microgynoecium tibeticum</i>	IV	.	6.7
<i>Anaphalis xylorhiza</i>	II	I	4.8
Character species of Community 5 and 6									
<i>Lancea tibetica</i>	V	II	12.4
<i>Astragalus strictus</i>	I	II	III	10.5
<i>Lamiophlomis rotata</i>	III	II	9.5
Character species of Community 6									
<i>Primula walshii</i>	IV	8.6
<i>Cortiella caespitosa</i>	III	7.6
<i>Kobresia vidua</i>	II	4.8
<i>Saussurea graminea var. ortholepis</i>	I	.	II	5.7
<i>Gentiana spp. indet.</i>	II	3.8
<i>Pedicularis muscoides</i>	II	3.8
<i>Oxytropis pauciflora</i>	II	3.8
<i>Festuca cf. forrestii</i>	II	2.9
<i>Thalictrum alpinum</i>	.	I	.	.	I	II	I	III	15.2
<i>Stipa rohmooiana</i>	II	2.9
<i>Pedicularis roylei</i>	II	2.9
<i>Aster flaccidus</i>	I	I	IV	12.4
<i>Kobresia royleana</i>	I	IV	12.4
Other species									
<i>Oreosolen wattii</i>	.	III	II	I	II	II	I	III	30.5
<i>Leontopodium pusillum</i>	.	.	IV	II	V	V	V	II	60
<i>Androsace tapete</i>	.	IV	II	I	III	V	III	IV	51.4
<i>Saussurea leontodontoides</i>	.	II	III	IV	II	II	I	IV	41
<i>Potentilla bifurca s.l.</i>	II	IV	III	III	III	IV	V	II	52.4
<i>Incarvillea younghusbandii</i>	.	IV	V	IV	III	IV	IV	.	56.2
<i>Stipa roborovskyi/ purpurea</i>	I	IV	V	V	V	V	III	I	73.3
<i>Poa albertii subsp. albertii</i>	.	IV	V	III	V	V	V	I	71.4
<i>Carex montis-everestii</i>	II	III	IV	III	V	V	II	I	60
<i>Chenopodium nepalense</i>	IV	III	II	III	II	.	III	I	31.4
<i>Iris potaninii var. potaninii</i>	III	.	II	I	III	II	IV	.	29.5
<i>Astragalus monbeigii</i>	V	II	II	III	IV	I	.	I	35.2
<i>Elymus schrenkianus</i>	III	V	II	I	II	V	.	.	35.2
<i>Cryptothladia kokonorica</i>	.	V	IV	IV	II	IV	.	.	43.8

APPENDIX 2 (CONTINUED)

Community No.	1	2	3a	3b	3c	4	5	6	
No. of relevés	8	9	20	13	18	12	11	14	freq.
<i>Gentiana hyalina</i>	.	III	IV	II	V	IV	.	I	46.7
<i>Heteropappus semiprostratus/ gouldii</i>	II	IV	IV	III	III	I	V	.	48.6
<i>Sedum perpusillum</i>	.	IV	IV	II	III	III	II	.	42.9
<i>Pedicularis alaschanica</i>	.	V	III	IV	II	III	.	.	40
<i>Callianthemum pimpinelloides</i>	.	II	IV	III	III	III	IV	.	39
<i>Dracocephalum heterophyllum</i>	.	II	II	V	I	II	IV	.	31.4
<i>Hypecoum leptocarpum</i>	.	III	I	II	I	-	II	.	16.2
<i>Stracheya tibetica</i>	.	II	II	II	I	III	II	.	21
<i>Ajania tenuifolia</i>	.	.	II	I	I	I	IV	.	18.1
<i>Arenaria bryophylla/ kansuensis</i>	.	.	I	I	II	III	IV	I	23.8
<i>Viola kunawurensis</i>	.	II	III	II	III	I	.	I	30.5
<i>Oxytropis chiliophylla</i>	.	.	II	I	II	IV	.	.	21
<i>Astragalus confertus</i>	.	.	II	I	III	III	I	.	24.8
<i>Gentiana pseudoaquatica</i>	.	II	II	.	II	I	.	II	19
<i>Carex moorcroftii</i>	.	.	I	II	IV	III	.	I	22.9
<i>Pleurospermum hedinii</i>	.	.	I	I	I	II	.	.	9.5
<i>Corydalis mucronifera</i>	.	I	I	II	.	-	.	.	7.6
<i>Anthoxanthum cf. glabrum</i>	.	.	I	II	.	-	.	.	5.7
<i>Polygonum sibiricum</i>	.	.	I	I	I	.	.	.	3.8
<i>Thermopsis lanceolata</i>	.	.	I	.	I	.	.	.	3.8
<i>Artemisia xigazeensis</i>	.	I	I	.	I	I	.	.	3.8
<i>Anemone imbricata</i>	.	.	I	.	.	I	.	I	3.8
<i>Oxytropis deflexa</i>	I	II	.	.	5.7
<i>Stipa koelzii</i>	.	I	I	I	I	I	.	.	7.6
<i>Draba ladyginii</i>	.	II	.	I	I	I	I	.	8.6
<i>Kobresia humilis</i>	I	.	.	II	3.8

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