The shaping of Tibetan grasslands:
Combined effects of livestock-grazing and environment
– a multi-site, interdisciplinary study

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Norther Winslow: I've been working on this poem for 12 years.
Young Ed Bloom: Really?
Norther Winslow: There's a lot of expectation.
I don't wanna disappoint my fans.
Young Ed Bloom: May I?
Young Ed Bloom: [Edward reeds the poem on the notebook]
"*The grass so green*
Skies so blue
Spectre is really great!"
Young Ed Bloom: It's only three lines long…..
Norther Winslow: This is why you should never show a work in progress.

Big Fish (2003)

Content

Extended summary

Livestock grazing is the dominant land use on Central Asian grasslands, where the increasing grazing pressure has been widely blamed as the main cause of grassland degradation. Livestock directly reduce plant aboveground biomass and change plant species composition through foraging. Trampling compacts soils and often negatively affects soil physical conditions, which may further influence soil carbon (C), nitrogen (N) and other nutrient contents. Livestock-mediated nutrient redistribution might reshape plant communities; in turn, grazing-induced alterations in plant communities also feedback on soil properties. Grazing influences animal communities by changing vegetation structure, soil conditions, and disturbing food chains.

Previous empirical studies from semi-arid grasslands have revealed that plant communities are not mainly structured by livestock impacts as classical equilibrium theories proposed. Climate conditions, especially precipitation patterns, might strongly control plant growth and population dynamics at certain temporal and spatial scales. Interactions with climate and topographic conditions could mitigate or intensify grazing effects by changing resource availability (e.g. food, water, light, heat) or modifying relationships within and among trophic levels. Disentangling environmental impacts from livestock grazing effects is not only important to understand rangeland theories, but also critical for grassland management and conservation.

As one of the largest grassland regions in the world, Tibetan grasslands host enormously varying physical environments along with an evolutionary history of grazing by large herbivores including wild, and now predominantly domestic animals. Grassland health in this region is relevant for local livelihoods and the environment of surrounding regions. The broadly held perception that increased grazing leads to extensive grassland degradation across the plateau is rooted in equilibrium theories and has overlooked the importance of environmental variability as non-equilibrium theories highlight. Accordingly, policies for grassland conservation and restoration mostly focus on reducing livestock numbers and restricting mobility of pastoralism.

Besides the insufficient theoretical considerations, several methodological problems exist in previous degradation assessments of Tibetan grasslands. First, field studies mostly focus on controlled grazing experiments from single sites, and hardly consider interactions with physical environmental factors. Even among those which do, the limited study duration often

restricts the possibility of detecting long-term responses. Whether the typically employed clipping could represent the natural grazing situation is still questionable. Second, large-scale studies are typically based on remote sensing data or modelling approaches, thus are often too generalized, simplified and lack of proper field calibrations. Although there are several multi-site field surveys on plant communities and soil conditions along large environmental gradients, grazing effects are rarely taken into account. Finally, inconsistent definitions and standards of degradation and non-standardized sampling methods make the interpretation of general patterns difficult, as shown from the extensive review focused on grazing effects on vegetation and soils (Chapter 3).

Baring these inadequate aspects in mind, this thesis presented a multi-site study on five indicator groups (vascular plants–hereafter plants, small mammals, ants, soils and hyperspectral data) across two main habitats (alpine meadow, steppe) and one transitional ecotone (steppe-meadow) on Tibetan grasslands. Four levels of livestock activity (piosphere directly adjacent to herder camps, heavy, moderate and light grazing) were considered. Plant communites (626 species, six functional groups) and soil conditions (eight chemical properties) from 173 plots/28 sites were compared among all these four levels. In the course of partner projects, ants (15 species), small mammals (15 species) and hyperspectral data (15 indices) were sampled from heavy-light grazing pairs at 18 sites within the same standardized sampling strategy (Chapter 2). Environmental factors include climate conditions of mean annual precipitation total (hereafter precipitation, P, 110–660 mm) and the coefficient of interannual variation (cvP, 14–42%), mean annual temperature (hereafter temperature, T, −6.1–3.2 °C), accumulative temperature above 0 °C (acT0, 478–1816 °C) and shortwave incident radiation (srad, 190–260 w/m^2); and topographic conditions of elevation (Elev, 2820–5150 m), inclination (incl, 0–16 °), relief positions and aspects.

The main aim was to investigate which indicators were sensitive to intensification of livestock activity after disentangling influences from various climate and topographic factors across and within habitats. The following general questions were specifically addressed:

1. Which characteristics of vegetation and soils are sensitive to increasing grazing intensity according to the previous publications?
2. Do these reported grazing responses still hold after considering the large-scale environmental influences? If so, are the patterns in line with equilibrium or non-equilibrium theories? Specifically, are responses stronger in wetter alpine

meadows and weaker in drier steppes, and how is the situation for the transitional habitat? If not, what are the possible reasons?

3. Besides plants and soils, how do small mammals and ants respond to grazing intensification, and can hyperspectral signals detect these responses when environmental interactions are accounted? Which climate and topographic factors are important for each indicator group among and within habitats?
4. Do responses of biotic groups correlate to each other, and how do they relate to soil properties and hyperspectral signals? What lessons can be learned from the interdisciplinary approach?
5. Which suggestions can be provided for future grassland management?

Accordingly, Chapter 1 started with a general introduction of rangeland theories. Chapter 2 introduced the basic natural and social backgrounds of the study region, and summarized the methodology of sampling and data analysis. Chapter 3 provided a comprehensive review across the most important pastoral grasslands in China to answer question 1. Heavy grazing generally had negative effects on most vegetation and soil characteristics, but with strong interactions of climate. Several existing methodological problems and research gaps were highlighted.

Chapter 4 continued with an analysis focusing on vegetation and soils to answer question 2. Plant species compositions and soil fertility indeed changed by livestock grazing, but the prominent differences were only restricted to piospheres in the immediate vicinity of herder camps. Few indicators responded to grazing intensification only in meadows, such as reduced soil organic carbon (SOC) and total nitrogen (tN) concentrations. Environmental influences varied among habitats and also differed between plant communities and soils. A series of plant species indicating strong trampling and excessive nutrient inputs from livestock excreta were provided for future ecological monitoring and grassland management.

Chapter 5 subsequently attempted to answer question 3 and 4 by presenting a joint analysis of five indicator groups. Results confirmed that grazing only explained a small proportion from the total variation of compositions of plant species, plant functional groups, small mammal and ant species, while larger share was explained by environmental impacts. Heavy grazing only reduced vegetation cover, SOC and tN, and then reflected by some hyperspectral indices. Following Chapter 6 gave a remote-sensing assessment across three spatial resolutions based on field-calibrated vegetation cover, and discussed advantages and limitations of different upscaling methods. To explain the weak correlations among indicator groups requires further detailed studies with an integrative ecosystem view in which interactions between various biotic and abiotic factors are acknowledged.

Finally, with the synthesis in Chapter 7, I am confident that current results can shed a light on several essential but so far unnoticed ecological patterns in this region, and also contribute to a better understanding of non-equilibrium theories by filling the research gaps in regions with high elevations and dry-cold combined winters. Moreover, I particularly addressed couple of implications for grassland management in the end of the overall discussion, and followed with a brief conclusion (Chapter 8) and an outlook for future studies on plenty of unclear and unsolved questions (Chapter 9). The key message is that current results do not support widespread claims that grassland degradation is largely caused by grazing intensification, however, future grassland assessments should pay more attentions on environmental influences and interactions among different trophic levels.

Ausführliche Zusammenfassung

Beweidung durch Nutztiere ist die dominierende Landnutzungsform in den Weideländern Zentralasiens, und wachsender Beweidungsdruck wird als die Hauptursache für Degradation des Graslandes gesehen. Beweidung reduziert die oberirdische Pflanzenbiomasse, führt aber auch zu veränderter Artenzusammensetzung. Durch Nutztiere bedingte Verdichtung der Böden und entsprechend verschlechterte bodenphysikalische Bedingungen, können zu Veränderungen in den Gehalten an Kohlenstoff (C), Stickstoff (N) und anderen Nährstoffen führen. Außerdem verlagern Nutztiere Nährstoffe, was ebenfalls Veränderungen in der Vegetation bedingen kann, die dann weitere Änderungen im Boden nach sich ziehen. Beweidung beeinflusst Tiergemeinschaften durch Veränderungen der Vegetationsstruktur, der Bodeneigenschaften, sowie durch Störungen der Nahrungsketten.

Bisherige Studien aus semi-ariden Grasländern haben gezeigt, dass die Zusammensetzung der Pflanzengemeinschaften nicht nur durch Weidetiere bestimmt wird, wie dies klassische *Equilibrium*-Theorien annehmen. Die klimatischen Bedingungen, insbesondere die Niederschlagsverhältnisse, haben starke Auswirkungen auf Wachstum und Populationsdynamik der Pflanzen auf verschiedenen räumlichen und zeitlichen Skalen. Interaktionen mit Klima und Topographie können die Effekte der Beweidung abschwächen oder auch verstärken, indem sie die Ressourcenverfügbarkeit verändern (z.B. Futter, Wasser, Licht, Wärme) oder indem sie Beziehungen zwischen trophischen Ebenen modifizieren. Eine saubere Unterscheidung von Effekten der physikalischen Umwelt und der Beweidung ist aber nicht nur wichtig, um die Weideland-Theorien zu verstehen, sondern auch um Management- und Naturschutzstrategien zu entwickeln.

Als eine der weltweit größten Graslandregionen zeigen die tibetischen Grasländer eine große Spanne von physikalischen Umweltbedingungen. Zudem haben sie eine evolutiv lange Beweidungsgeschichte und sind heute weitgehend komplett durch Nutztiere beweidet. Die Intaktheit dieser Grasländer ist wichtig für die lokalen Gesellschaften und die Umwelt- und Lebensbedingungen in den umgebenden Regionen.

Die weitverbreitete Ansicht, dass die intensive Beweidung zu flächenhafter Degradation in Tibet geführt hat, wurzelt in der *Equilibrium*-Theorie und vernachlässigt die Bedeutung der Variabilität der Umweltbedingungen wie sie *Non-equilibrium*-Ansätze betonen. Als Folge konzentrieren sich aktuelle Strategien für Graslandschutz und -renaturierung auf die Senkung der Viehzahlen und Sesshaftmachung der Pastoralnomaden.

Neben den Lücken im theoretischen Hintergrund gibt es auch methodische Probleme bei der Bewertung von Degradation in den tibetischen Grasländern. Erstens konzentrieren sich Geländestudien meist auf Beweidungsexperimente an Einzelflächen, so dass übergreifende Interaktionen mit physikalischen Umweltfaktoren nicht untersucht werden können. Selbst in den wenigen Ausnahmen übergreifender Experimente begrenzt deren eher kurze Zeitdauer die Möglichkeiten, Langzeiteffekte zu dokumentieren. Ob das typischerweise genutzte experimentelle Abschneiden natürliche Beweidung angemessen simuliert, ist unklar. Zweitens basieren großräumige Studien häufig auf Fernerkundung oder Modellierung und sind oft zu generalisierend oder leiden unter dem Fehlen guter lokaler Kalibrierung. Es gibt zwar einige Studien zu Pflanzengemeinschaften und Bodenbedingungen entlang von großräumigen Klimagradienten über mehrere Untersuchungsorte, aber diese berücksichtigen dann selten Beweidungseffekte. Schließlich fehlen klare Definitionen und Standards für Degradation und ihre Erfassung, was die Ableitung allgemeiner Muster stark erschwert. Dies zeigt ein umfassender *Review* der aktuellen Literatur zu Auswirkungen der Beweidung auf Vegetation und Böden (Kapitel 3).

Basierend auf diesen Überlegungen wird in vorliegender Arbeit eine in mehreren Untersuchungsgebieten durchgeführte Studie vorgestellt, bei der fünf Indikatorgruppen (Gefäßpflanzen – im Folgenden Pflanzen –, Kleinsäuger, Ameisen, Böden und hyperspektrale Daten) für zwei Hauptlebensraumtypen („alpine Matten“, „Steppen“) und einen Übergangstyp („Steppen-Matten“) in Tibet untersucht wurden. Vier verschiedene Intensitäten von Nutztiereinfluss (Piosphäre mit starken Tritteffekten, sowie starke, mittlere und schwache Beweidung) wurden berücksichtigt. Die in 173 Plots (28 Untersuchungsgebiete) aufgenommenen Pflanzengemeinschaften (626 Arten, sechs funktionelle Gruppen) und Bodeneigenschaften (acht chemische Parameter) wurden über alle vier Intensitäten verglichen. Im Zuge der Partnerprojekte wurden Ameisen (15 Arten), Kleinsäuger (15 Arten) und hyperspektrale Daten (15 Indices) mit dem selben standardisierten Aufnahmedesign (Kapitel 2) in 18 der Untersuchungsgebiete aufgenommen, wobei aber nur stark beweidete Flächen mit schwach beweideten verglichen wurden. Die verwendeten Umweltvariablen umfassten mittlere Jahresniederschlagssumme (im Folgenden Niederschlag, P, 110−660 mm) und ihre interannuelle Variabilität (Varianzkoeffizient, cvP, 14−42 %), die Jahresmitteltemperatur (im Folgenden Temperatur, −6,1−3.2 °C), die Temperatursumme über 0 °C (acT0, 478−1816 °C) und die kurzwellige Strahlung (srad, 190−250 W/m²), sowie die Topographie mit Meereshöhen (Elev, 2820−5150 m NN), Neigung (incl, 0−16°), Reliefposition und Exposition.

Das Hauptziel war zu testen, welche Indikatoren auf veränderte Nutztieraktivität reagieren, und zwar unter Berücksichtigung der Effekte von Klima und Topographie. Die folgenden übergreifenden Fragen wurden untersucht:

1. Welche Parameter der Pflanzengemeinschaften und Böden sind laut verfügbarer Literatur empfindlich gegenüber erhöhter Beweidung?
2. Bleiben die gezeigten Beweidungseffekte sichtbar, wenn großräumige Umweltunterschiede berücksichtigt werden. Wenn dies so ist, entsprechen die Muster eher der *Equilibrium* oder der *Non-Equilibrium*-Theorie? Sind die Effekte in feuchten alpinen Wiesen stärker als in den trockenen Steppen, und wie ist die Situation im Übergangsgebiet? Wenn Ersteres nicht so ist, was sind die möglichen Gründe?
3. Wie reagieren Kleinsäuger und Ameisen im Vergleich zu Pflanzen und Böden auf Beweidungsintensivierung, und können mit hyperspektralen Indices relevante Veränderungen gemessen werden? Welche topographischen und klimatischen Faktoren beeinflussen jede Indikatorgruppe innerhalb und zwischen Habitaten?
4. Korrelieren die Muster zwischen verschiedenen biotischen Indikatorgruppen, und wie hängen sie mit Bodeneigenschaften und Hyperspektraldaten zusammen? Welche neuen Erkenntnisse bringt ein interdisziplinärer Ansatz?
5. Welche Empfehlungen können für das zukünftige Graslandmanagement abgeleitet werden?

Entsprechend beginnt das erste Kapitel mit einer Einführung in die wichtigen Theorien der Beweidungsökologie. Kapitel 2 führt die wesentlichen Umwelt- und Sozialbedingungen in der Studienregion ein, und fasst den Untersuchungsansatz zusammen. Kapitel 3 beinhaltet eine umfassende Studie der verfügbaren Literatur zu wichtigen Weidegebieten Chinas, um Frage 1 zu beantworten. Starke Beweidung hat überwiegend negative Effekte auf Vegetation und Bodeneigenschaften, allerdings in starker Interaktion mit dem Klima. Darüber hinaus werden verschiedene methodische Probleme und Kenntnislücken herausgestellt.

Im Anschluss widmet sich Kapitel 4 mit einer umfassenden Analyse der Auswirkungen auf Vegetation und Böden den unter 2. angesprochenen Fragen. Die Artenzusammensetzung und die Bodenfruchtbarkeit änderten sich in der Tat unter Nutztiereinfluss, allerdings waren die starken Effekte auf die Piosphäre beschränkt, also auf die direkte Umgebung der Hirtencamps. Nur wenige Indikatoren reagierten auf unterschiedliche Beweidungsintensitäten im engeren

Sinne, und diese Reaktionen waren auf die alpinen Matten beschränkt, wie z.B. niedrigere Konzentrationen an Bodenkohlenstoff (SOC) und Gesamtstickstoff (tN). Die Auswirkungen der physikalischen Umwelt unterschieden sich zwischen den Hauptlebensräumen und auch zwischen Pflanzengemeinschaften und Böden. Eine Reihe von Pflanzenarten können als signifikante Indikatoren für Tritt und übermäßige Akkumulation von Dung und Urin genutzt werden; sie sind von Bedeutung für zukünftiges Degradationsmonitoring und Graslandmanagement.

Kapitel 5 versucht, Fragen 3 und 4 gemeinsam zu beantworten, indem eine umfassende Analyse von 5 Indikatorgruppen vorgestellt wird. Die Ergebnisse bestätigen, dass Beweidung nur einen kleinen Teil der Gesamtvarianz in der Artenzusammensetzung von Pflanzen, Funktionellen Pflanzenartengruppen, Kleinsäugern und Ameisen erklärt, der weitaus größere Anteil korreliert mit Umwelteigenschaften. Starke Beweidung wirkt sich nur negativ auf Vegetationsdeckung, SOC und tN aus, was sich insgesamt auch in den hyperspektralen Indices abbildete. Das folgende Kapitel 6 stellt die Ergebnisse einer mit Hilfe von Felddaten zur Vegetationsdeckung kalibrierten und auf drei verschiedenen räumlichen Auflösungsniveaus durchgeführten fernerkundlichen Erfassung vor. Die Vorteile aber auch die Grenzen verschiedener Extrapolationsmethoden werden diskutiert. Für eine genauere Erklärung der relativ schwachen Korrelationen zwischen den verschiedenen Indikatorgruppen sind aber weitere Studien nötig, die ein integriertes Ökosystemverständnis erfordern, und in denen die Interaktionen zwischen biotischen und abiotischen Faktoren berücksichtigt werden.

Mit dem Synthese-Kapitel 7 hoffe ich schließlich zeigen zu können, dass die vorliegenden Ergebnisse wichtige und in einigen Fällen essentielle neue Einsichten über ökologische Muster in der Region ergeben und auch zu einem besseren Verständnis von *Non-Equilibrium*-Theorien beitragen, indem sie Datenlücken für Hochregionen und Gebiete mit kalt-trockenen Wintern schließen. Am Ende der allgemeinen Diskussion habe ich besonders einige Implikationen für das Beweidungsmanagement herausgegriffen. Hierauf folgen kurze Schlussfolgerungen (Kapitel 8) und ein Ausblick auf mögliche weitere Forschungen zu den vielen weiterhin ungeklärten Fragen (Kapitel 9).

Die zentrale Aussage ist, dass die vorliegenden Ergebnisse kaum Unterstützung für die weitverbreitete Meinung liefern, dass Beweidungsintensivierung zwangsläufig zu flächenhafter Degradation führt. Zukünftige Grasland-Erfassungen sollten stärker auf die Bedeutung der abiotischen Umwelt und auf Interaktionen über verschiedene trophische Ebenen hinweg achten.

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Abbreviations

acT0	Average annual accumulated temperatures above 0°C (°C)
AGB	Aboveground biomass (g/m^2)
ANPP	Aboveground net primary production
aP	Plant available phosphorus in soils (mg/kg)
BD	Soil bulk density (g/cm^3)
BGB	Belowground biomass (g/m^2)
BNPP	Belowground net primary production
CAS	Chinese Academy of Science
cvP	Coefficient of interannual variation of precipitation (%)
East	Eastness=sin(aspect), aspect is the compass direction that a slope faces
EC	Electrical conductivity (µs/cm)
Elev	Elevation (m, a.s.l.)
GE	Relative grazing effects defined as (heavy−light)/light grazing
GLMM	Generalized Mixed Linear Models
incli	Inclination angle of a slope(°)
Lat	Latitude (°)
Lon	Longitude (°)
MANOVA	Multivariate Analysis of Variance for testing the difference in two or more vectors of means
NDNI	Normalized Difference Nitrogen Index
NDVI	Normalized Difference Vegetation Index
NMDS	Non-metric multidimensional scaling
North	Northness=cos (aspect), aspect is the compass direction that a slope faces
NPP	Net primary production
P	Mean annual precipitation sum (mm)
PCA	Principal Component Analysis
PCoA	Principal Coordinates Analysis
REP_LE	Red-Edge Position through Linear Extrapolation
rsRatio	Root/shoot ratio
SOC	Soil organic carbon (% or g/kg)
srad	Shortwave incident radiation (w/m^2)
SU	Sheep unit
T	Mean annual temperature (°C)
tN	Soil total nitrogen (% or g/kg)
TP	Tibetan Plateau
tP	Soil total phosphorus (g/kg)
yearTdiff	Difference between the average temperature of the warmest month and coldest month throughout the year (°C)

Chapter 1 Introduction

Grassland systems and relevant theories

The sun burns the snow high on the mountains
It runs and it flows as it falls
Silt and soil down it boils
Down to the valley the gold river rolls
To the plains
The rangeland lies high up from the river
The coolies are dry where the short grass grows
……
The long river winds through green years and dry years
Brand them in the spring ship them in the fall
The new colt foled--the mare grows old
Cycles of changes in this changeless land
Where the short grass grows in this changeless land

From Ian & Sylvia, "Short grass"
Album <Play One More>, 1966

Grasslands, as one of the largest ecosystems in the world, cover approximately 40% of Earth's terrestrial area (excluding Antarctica) and sustain huge biodiversity, adjust global nutrient cycling and foster various human cultures (White et al. 2000). Nearly all grasslands are modified by different kinds of disturbance, such as grazing either by wildlife or livestock or fires lit by nature or humans (Asner et al. 2004; Bone et al. 2015). Disturbance has affected and continues to impact grassland conditions in many aspects, such as productivity, diversity, species composition and community structure of various biotic groups. Changes in biotic groups also feedback on soil conditions (Hobbs & Huenneke 1992; Burke et al. 1998; Roxburgh et al. 2004; Joern 2005; Metera et al. 2010). From central Asia to America, Africa and Argentina, no matter if grasslands are called as steppes, plains, prairies, savannas or meadows, humans always have close relationships with plants, animals and various resources from grasslands (Bone et al. 2015; Kelaidis 2015). They are not only wonderful landscapes with intriguing natural beauty, but also support rich human cultures of fascinating histories and colorful livelihoods.

Every life form is inevitably affected by various environmental factors: abiotic ones such as topography and climate which influence the historical and current resource availability (water, heat and light), and biotic competitions or facilitations with surrounding species and individuals across different trophic levels (Van Dyne 1969; Golley 1996). Furthermore, soils, as the primary and direct resource (water and nutrient) pools for plants, are also influenced by physical environments directly or indirectly through changes of plant communities (Hobbs & Huenneke 1992; Ordoñez et al. 2009; Brevik 2012). Grasslands are typical ecosystems with various species of plants, animals and microbes, all of which have their own niche but also affect each other interactively at the ecosystem level (Polis et al. 1997; Bone et al. 2015). Understanding spatial patterns of biodiversity is one of the most fundamental tasks for ecologists (Gaston 2000; Kikvidze et al. 2005), but it's never easy in a natural ecosystem, not to mention the systems with disturbance.

When humans migrated to places with ample water, grasses and relatively favourable climate for cultivation, they started to settle down and aimed for sedentary agriculture. In contrast, in regions with harsh environments where crops could not survive, they kept going, chasing the good pastures to raise livestock which provide a variety of food and non-food products for people (Miller 2000; White et al. 2000; Suttie 2003; Bone et al. 2015). Grazing by large herbivores, no matter wild or domestic, influence grassland ecosystems, by directly reducing forage, changing the energy balance at soil surface, removing or redistributing nutrients and modifying inter- and intra-species competitions (Grime 1973; Hobbs & Huenneke 1992; Trlica et al. 1993; Anderson et al. 1995). Not all changes are necessarily detrimental from a human perspective, and the major concern for rangeland ecologists and managers is to distinguish whether biotic or abiotic factors are more important in certain systems and which indicators and their characteristics are more sensitive to specific factors in order to make sensible and sustainable conservation and management strategies (Ellis & Swift 1988; Ellis 1995; Vetter 2005; Overbeck 2014).

Vegetation responses

Grazing responses vary across diverse grassland systems and strongly interact with local productivity (Milchunas & Lauenroth 1993). From a theoretical perspective, classical equilibrium models which are based on rangeland succession theory assume that vegetation dynamics are controlled by plant-herbivore feedback processes, and are thus more sensitive to grazing in relatively stable and productive systems. In contrast, non-equilibrium models suggest that climate controls override grazing effects in grasslands of low forage productivity, particularly in Africa and Central Asia (Illius & O'Connor 1999; von Wehrden et al. 2012). Similar to non-equilibrium concepts, state-and-transition models suggest rangeland condition could shift from certain state ("equilibrium") to another when grazing regimes (intensity, type or timing of grazing) change or extreme weather events happen. These transitions between states can be reversible or irreversible (Westoby et al. 1989; Cingolani et al. 2005).

The evolutionary history of grazing also plays a key role in explaining grazing effects on plant species composition. In grasslands with long grazing history, resilience which allows reversible changes in plant communities could have been evolved, so plant species composition might be similar between grazed and ungrazed conditions. However, systems with short grazing history tend to be more sensitive to grazing, thus show contrasting plant communities (Milchunas & Lauenroth 1993). Moreover, impacts of grazing histories further interact with environmental conditions, such as moisture. A widely-cited generalized model demonstrates how the competitions within plant community are expressed under grazing in consideration of this interaction (Fig. 1, Milchunas et al. 1988). This model was developed based on both advantages and shortcomings from former hypotheses related to disturbance, i.e. predator, intermediate-disturbance, and Huston hypothesis. Four response patterns were summarized: 1) Grazing has relatively small effects on plant communities which have been shaped by both semiarid climate and a long evolutionary grazing history; 2) In subhumid grasslands with a long evolutionary history of grazing, changes of plant diversity with increasing grazing intensity typically follow the intermediate disturbance hypotheses, indicating highest plant diversity under moderate grazing intensity and lowest diversity with no-grazing or heavy grazing; 3) Plant communities with short grazing histories from semiarid regions exhibit a slight increase in diversity when grazing intensities are low, then following a decrease from the peak as grazing intensifies; 4) Subhumid grasslands with short grazing histories are primarily under a single selection pressure for canopy dominance without grazing, so light grazing increases diversity due to the competition relaxation while heavy grazing results in rapid decline of diversity. Examples for these four response patterns have been found in different grassland systems (Milchunas & Lauenroth 1993; Adler et al. 2004; Cingolani et al. 2005; Milchunas et al. 2008). The further modification incorporates state-and-transition models (Noy-Meir 1975; Westoby et al. 1989) and additionally describes when and which kind of changes are reversible (Cingolani et al. 2005).

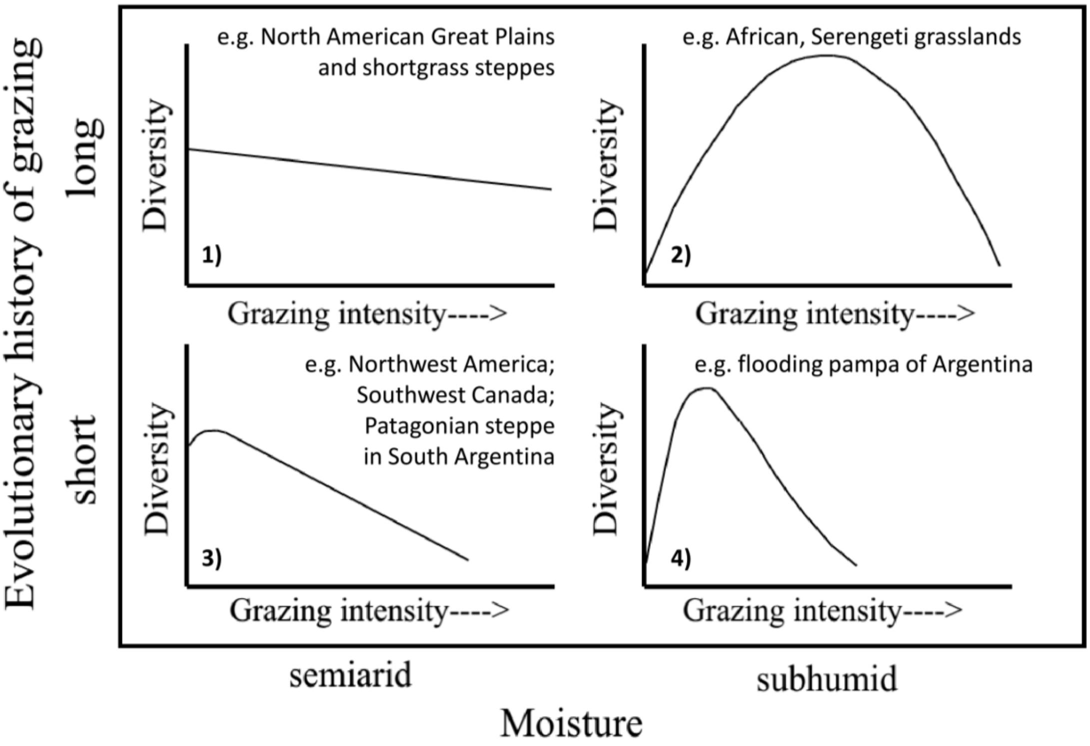

Fig. 1 Change of plant diversity (Shannon diversity) in response to increase of grazing intensity in relation to grazing history and moisture gradient. Modified from Milchunas *et al*. 1988.

Accordingly, grassland management strategies depend on which factors are shaping grasslands. Where the uncertainty and variability of the environment are higher, dynamics of livestock density and plant diversity or productivity might be decoupled (Ellis & Swift 1988; von Wehrden et al. 2012), rendering the concept of fixing a certain carrying capacity and stocking rate without consideration of climate variability inadequate and less effective in maintaining productivity.

Soil response

It's difficult to generalize the overall pattern of grazing effects on soil conditions among different grassland systems as several reviews suggested (Milchunas & Lauenroth 1993; Piñeiro et al. 2010; McSherry & Ritchie 2013; Schrama et al. 2013). Inconsistent response patterns to grazing indicate the strong context-dependency and highlight that many important factors are affecting soil C and N cycling, such as climate, physiography, natural disturbance, human use and biotic interactions with soil animals and soil microbes (Soussana et al. 2004; Burke et al. 2008).

Soil organic C (SOC) formation is controlled by various factors and their interactions at different time scales. Grazing affects SOC simultaneously through three complicated pathways (Fig. 2): 1) changes of net primary production (NPP); 2) decomposition of organic matter; 3) nitrogen stocks (Piñeiro et al. 2010). The first pathway indicates the changes of inputs of SOC. All SOC is plant derived, and the main contributors are root and shoot remains (Kuzyakov & Domanski 2000). Grazing often reduces aboveground NPP (ANPP), and has inconsistent effects on belowground NPP (BNPP), but tends to increase C allocation to belowground organs (McNaughton et al. 1998; Chen et al. 2006; Giese et al. 2009; Klumpp et al. 2009; Piñeiro et al. 2010). In contrast to pathway 1, the second pathway is focusing on outputs of SOC (i.e. soil respiration during decomposition), which is closely related to finer scale biotic interactions between soil animals, microbes and litter (Bardgett et al. 2001; Klumpp et al. 2009; Li et al. 2013a; Smith et al. 2014). This path is strongly related to soil physical conditions such as bulk density, infiltration rates, moisture and temperature, as well as the quality and quantity of litter (Burke et al. 1999; Su et al. 2005; Piñeiro et al. 2010; Dong et al. 2012a). The third pathway highlights the close coupling of C and N cycling and both inputs and outputs of SOC are affected by N availability (Holland & Detling 1990; Hobbie 1992; Baron et al. 2002; Knops et al. 2002; Wei et al. 2011) .

Additionally, some unnoticeable procedures need more attention. For example, besides the direct grazing effects on ANPP and BNPP, changes in plant species composition also alter the C allocation patterns, and potentially modify litter quality and quantity, and thus change decomposition rate, resulting in SOC changes (Chaneton & Lavado 1996; Barger et al. 2004; Li et al. 2008; Semmartin et al. 2010; Jing et al. 2014). Moreover, soil–plant feedback processes make grazing effects on plants and soils form a complicated circle. Grazing-induced changes in soil physical-chemistry conditions by trampling and nutrient translocation from livestock will change water and nutrient availability of plants then trigger plant community shifts, and these shifts will in turn modify soil conditions and lead to continuous changes of soil–plant system (Greenwood & McKenzie 2001; Drewry et al. 2008).

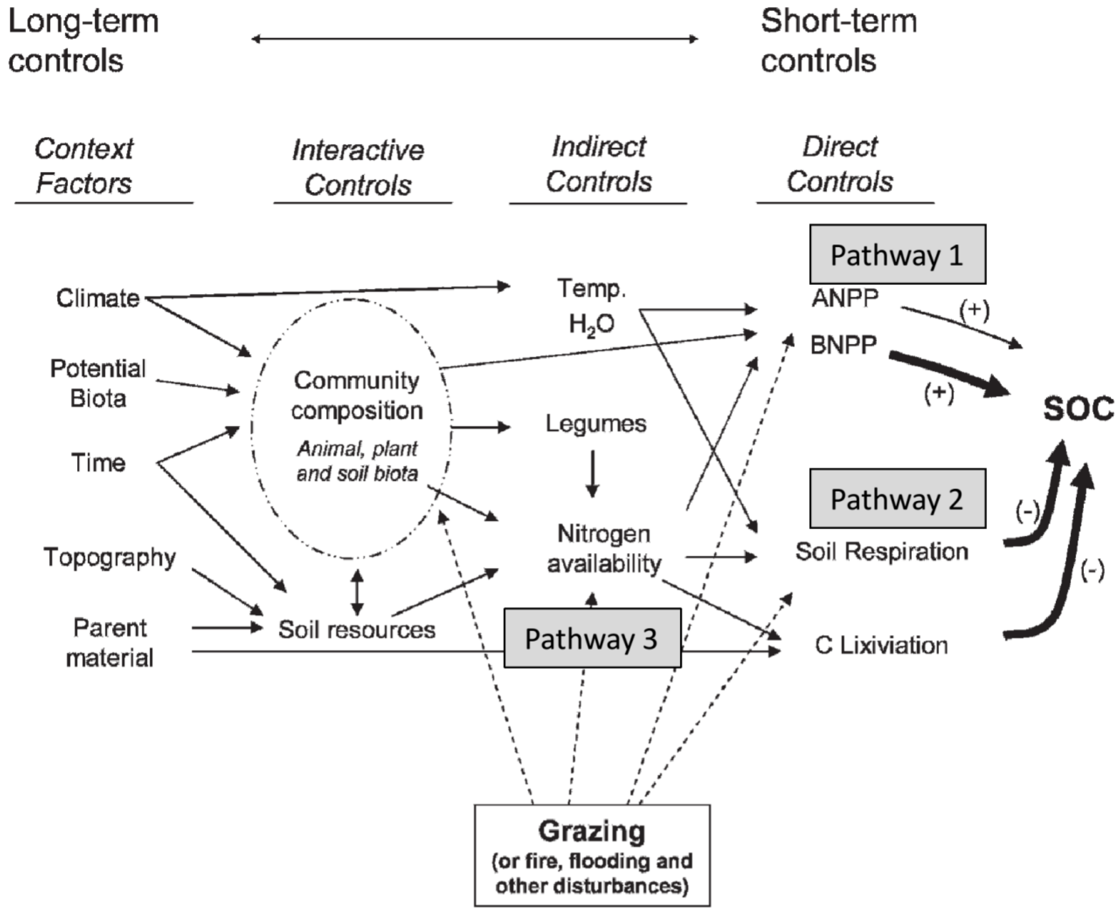

Fig. 2 Main factors and three pathways which controll soil organic carbon (SOC) formation. Dashed lines show grazing effects. ANPP and BNPP are aboveground and belowground net primary production. Modified from Piñeiro *et al*. (2010).

Couple of context factors have influences on SOC formation. For examples, precipitation is assumed to have positive impacts on SOC formation because aboveground biomass and litter often increase with water availability and lead to greater C inputs into soils (Semmartin et al. 2004; Derner & Schuman 2007; Luo et al. 2010). However, grazing effects interact with precipitation influences. Grazing might result in greater and more active microbial biomass C and more labile organic matter pools which could promote C turnover at sites with a mean annual precipitation of 600 mm or less (Derner & Schuman 2007). In contrast, most studies from semiarid grasslands in Central Asia indicate negative grazing effects on SOC contents (Su et al. 2005; Pei et al. 2008; Zhao et al. 2008; Golluscio et al. 2009). A global review demonstrates that grazing effects on soil C density shift along precipitation gradient, but also interact with soil texture : as precipitation increases, grazing effects decrease on fine texture soils, while increase on sandy soils (McSherry & Ritchie 2013). Grass type (C3 vs. C4 pathway), study duration and sampling depth, as well as interactions between these factors are also important to explain the inconsistent grazing effects on SOC (McSherry & Ritchie 2013).

Dynamics of soil N in grassland systems (Fig. 3) are as complicated as those of SOC. Total N (tN) is stable and indicates long-term effects in comparison with many other N forms which easily and rapidly change from one to another (Parton et al. 1988; Brady & Weil 1996; Jones et al. 2004). The most straightforward way in which grazing changes soil tN is the direct removal of plant N and spatial redistribution of nutrients within ecosystems by grazers (Whitehead 1995; Frank & Evans 1997). It's easy to understand that grazing is expected to have positive effects on soil N because the increase of grazers' activity often leads to higher N inputs from dung and urine. Moreover, changes of soil physical conditions (temperature, moisture, aeration and salinity) through soil compaction and increasing soil exposure will interact with the N mineralization in grazed grasslands (Schrama et al. 2013).

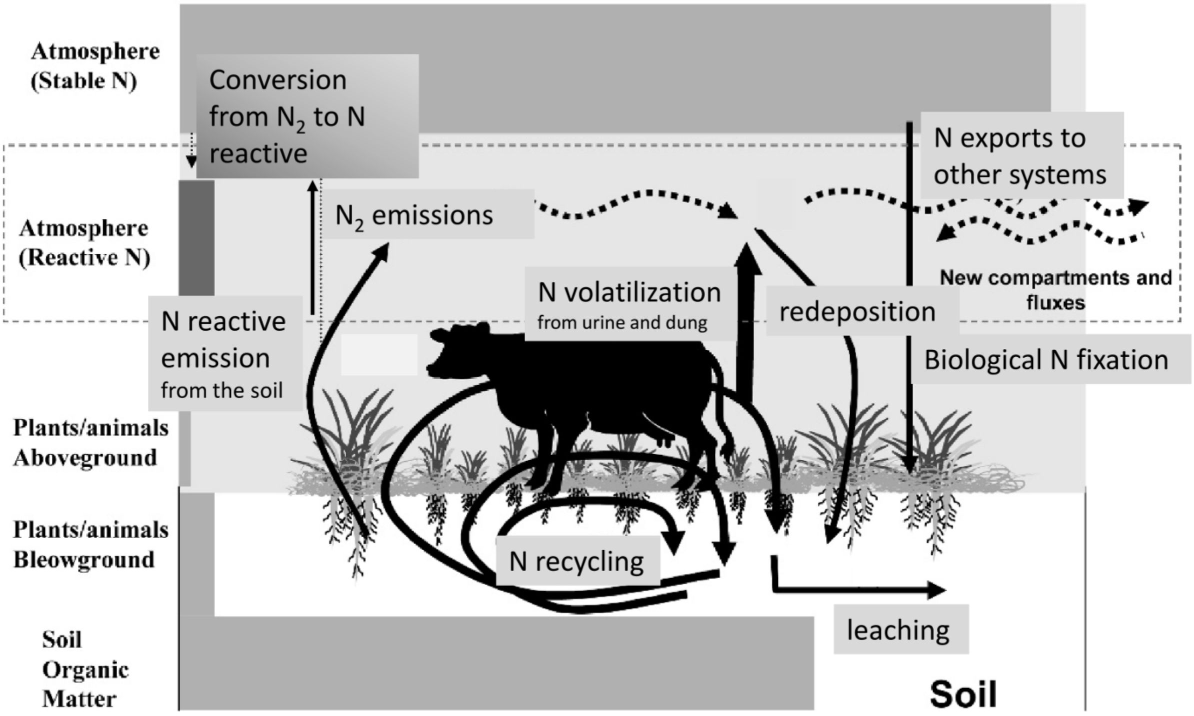

Fig. 3 Nitrogen cycles in grazed ecosystems. Solid arrows show traditional fluxes and light gray boxes indicate traditional pools, while dashed lines and dark gray boxes are new fluxes and pools to better understand N cycling at regional scales. Modified from Piñeiro *et al*. (2010).

Generally, whether grazing will speed up or slow down N cycling in the soil is strongly depending on the answers to the following questions (Frank & Evans 1997): 1) Does grazing increase or decrease litter turnover by trampling processes (Raiesi & Asadi 2006; Garibaldi et al. 2007); 2) does grazing accelerate N mineralization which then provides more available N to plants and soil microbes compared with ungrazed conditions (Stanford & Smith 1972;

Singer & Schoenecker 2003; Schrama et al. 2013); 3) how do litter and soil C–N ratios change by grazing (Garibaldi et al. 2007; Piñeiro et al. 2010); 4) how is microbial immobilization affected by grazing (Ruess & McNaughton 1987).

In addition to these traditionally fundamental processes, livestock could also promote N loss through ammonia volatilization from patches of urine and dung (Frank & Evans 1997; Piñeiro et al. 2010) and leaching are more likely to happen in systems with more rainfall (Ryden et al. 1984; Piñeiro et al. 2010). Soil fertility is another determinant of livestock effects on grasslands because nutrient availability decides how many resources plants can invest in developing tolerance or resistance mechanisms to livestock-grazing (Bardgett & Wardle 2003; Augustine & McNaughton 2006). Additionally, study period (i.e. non-growing season, early or peak growing season) is also closely related to grazing-caused changes in soil temperature and moisture and also aboveground biomass (AGB), N allocation pattern and N use efficiency (Shan et al. 2011). Soil P cycling is also extremely complicated (Shen et al. 2011), but grazing effects on soil P are much less studied thus are not specifically summarized here. In general, understanding the C, N cycling needs an integrative ecosystem view with consideration of several biotic and abiotic factors, which will be further discussed in later chapters.

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Chapter 2 Study region and general methodology

Tibetan grasslands: natural and social backgrounds

by Jun Wu, the driver from the field excursion in 2011

Since the 19th century, many explorers have written fancy stories about the lush pastures, amazing wildlife and large herds of livestock in wild Tibet and triggered great interest of many geologists, palaeontologist and archaeologists. The unique geological background formed by Himalaya determines its striking significance in controlling climate conditions of surrounding Asia, especially for monsoon developments (An et al. 2001). It's the most extensive high-elevation region on earth and among the best grazing lands in whole Asia (Miller 2005).

The term "Tibetan grasslands" used in this thesis refers to natural and semi-natural/secondary pastures which may have replaced forest due to human disturbance (Miehe et al. 2009; Miehe et al. 2014). The geographical regions include the Qinghai-Tibetan plateau within China, comprising the whole Tibetan autonomous region (hereafter Tibet), most parts of Qinghai and Northwest Sichuan, Southwest Gansu and Northwest Yunnan where Tibetan people are living. The evolutional origins and development of those grasslands share some similarities. Grasslands here are **grazing lands including herbaceous species dominated areas and also some alpine and/or semi-arid shrublands**. The extensive parts of Tibetan steppes in Bhutan, Nepal and India were not considered here. Areas of agricultural lands with barley, wheat, pea, rape and potato are also excluded because they only cover less than 1% of the Tibetan grasslands (Miller 2003).

The estimations of the area of grasslands depend on the definition of grassland, the border of the area defined by the authors and the year when assessments take place. Generally, Tibetan grasslands cover nearly a quarter of China's land area (about 1500 km from north to south, and 3000 km from east to west) and are estimated to constitute 42% of China's rangelands (Miller 1999; Sheehy et al. 2006), supporting 13 million yaks, 30 million sheep and goats, and 5 million pastoralists and agropastoralists (Long 2003; Miller 2005).

Tibetan grasslands present a unique platform to study how general rangeland theories apply along large environmental gradients and various grazing management strategies. As one of the most important parts of the Central Asian grasslands, ecosystem health in Tibetan grasslands, especially in headwater regions, is critical for downstream areas of several major Asian rivers. How these grasslands can be managed is mainly decided by soil and climate conditions, which are fundamentally determined by geological backgrounds. All biotic groups are relying on the availability of resources, including water, heat and food, which are also dependent on climate and topological conditions.

1 Geology, climate and soils

The Tibetan Plateau (hereafter TP) is the largest, highest and flat plateau in the world. It ia often called the "roof of the world", "third pole" or "water tower", with an average elevation of more than 4000 m a.s.l. The Indo-Asian collision over the last 70-50 Ma created the Himalaya, and attracted geologists' attention as a natural laboratory for testing theory of continental dynamics (Yin & Harrison 2000). A series of high mountains surround the TP: the Himalayas at the southern and partly western boundary; Kunlun, Arjin and Qilian Mountains at the northern border; Karkoram, Kunlun and Pamir Mountains join in western Central Asia; and the Henduan Mountains at the eastern parts connecting to Yunnan, Sichuan, Qinghai and Gansu (Fig. 1). These mountain chains not only decide the circulation of water and heat on the plateau, but also determine substrates and topological conditions for plants and animals to inhabit. Some regions have drainages and parallel mountain ranges, while many large lake basins locate in Tibet are without outlets and enclosed by circular mountain chains.

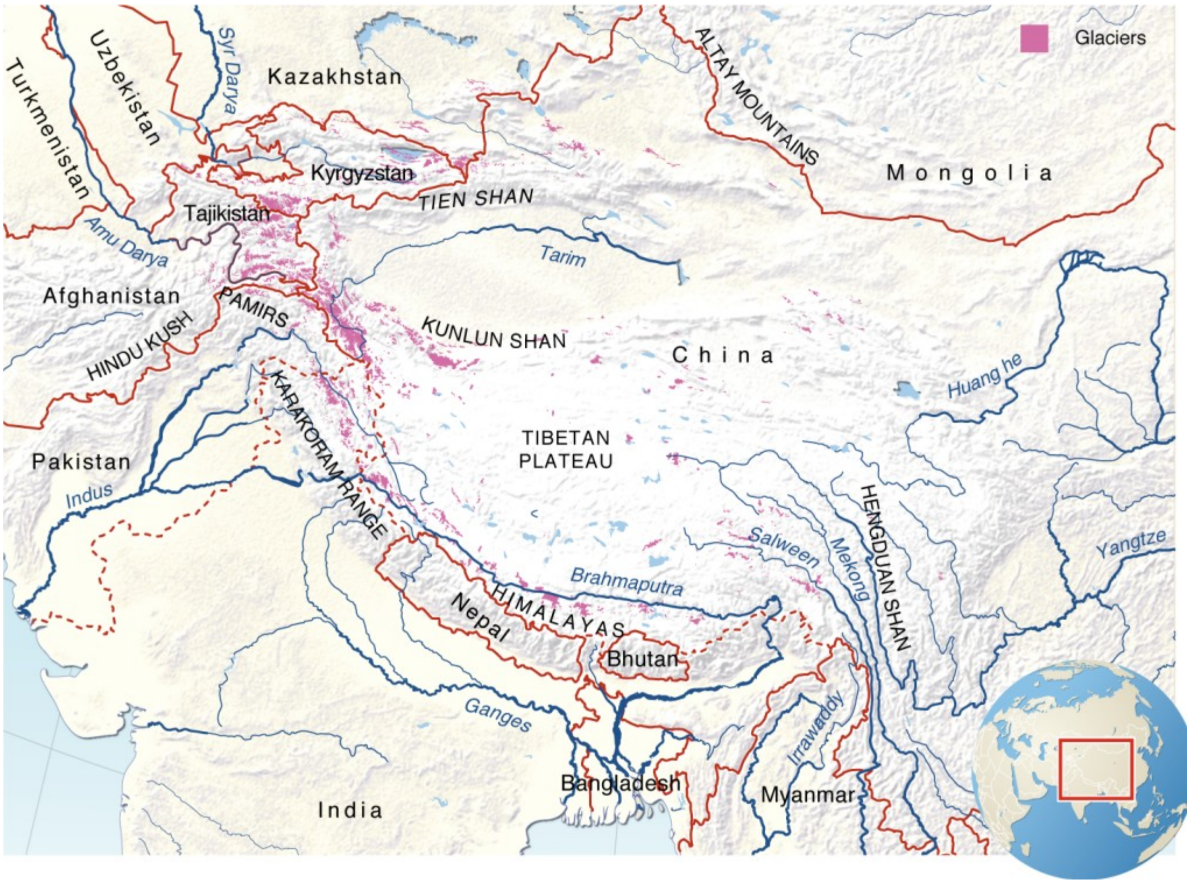

Fig. 1 Rivers and bordering mountain ranges of the Tibet Plateau. © Hugo Ahlenius, UNEP/GRID-Arendal. (From http://www.yowangdu.com/tibet-travel/where-is-tibet.html).

Climate conditions on Tibetan grasslands are determined by the unique geological settings (Fig. 2). A typical continental climate is characterized by wet summers controlled by the South Asian and East Asian monsoons and cold and dry winters influenced by the Westerlies and Siberian High that accumulates on the northeastern part of Eurasian terrain (Huang 1987).

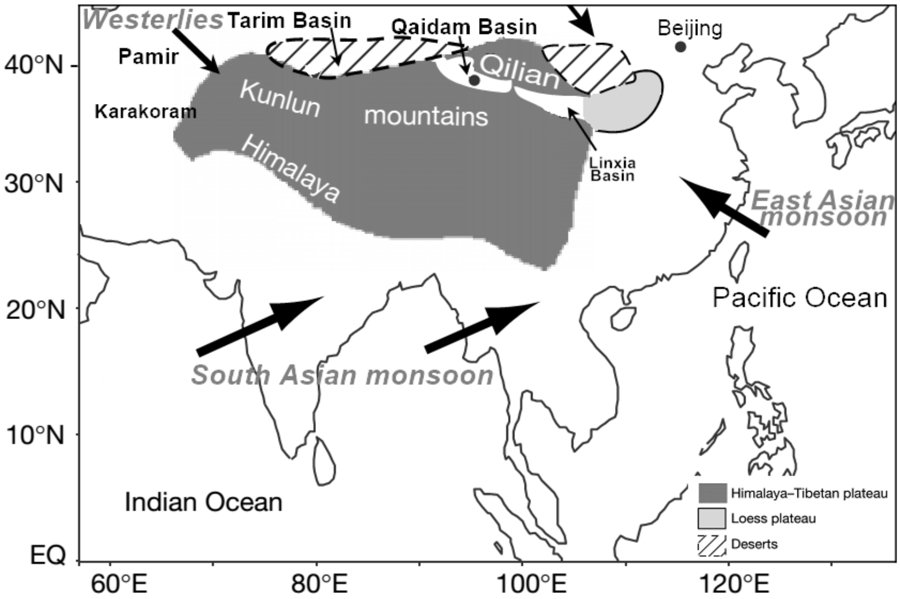

Fig. 2 Main controls of climate conditions on the Tibetan Plateau. Modified from An *et al*. (2001).

General climate conditions on the TP show longitudinal and latitudinal gradients as the relative strength of monsoons and Westerlies change. Particularly, mean annual precipitation (P) decreases from the east to the west and also from the south to the north. Precipitation is the most important factor for grasslands as it's defined in Oxford dictionary of plant sciences (Allaby 1998):

> *"Grassland constitutes a major world vegetation type and occurs where there is sufficient moisture for grass growth, but where the environmental conditions, both climatic and anthropogenic, prevent tree growth. Its occurrence therefore correlates with a rainfall intensity between that of desert and that of forest, and the range of grassland is extended by grazing and/or fire to form a plagioclimax in many areas that were previously forested."*

Most precipitation falls as rain in summer from May to September. Large parts of the central plateau receive less than 400 mm rainfall per year. Unlike tropical and subtropical dry rangelands such as savannahs, cold winter is typical for this region (Wu & Yan 2002), especially in the western high-elevation, cold and semi-arid areas. Considerable amount of precipitation falls as snow in winter and occasional heavy snowfall and low temperature exert additional stress on livestock. Snow depth and cover could also affect vegetation dynamics (Chen et al. 2008; Chen et al. 2009; Peng et al. 2010), and snow disaster is a crucial issue for local livelihoods (Miller 2000; Shang et al. 2012; Yeh et al. 2013). Due to the overall high elevation and thinned and purified atmosphere, the annual solar radiation is 50–100% higher on the TP than lowlands in the same latitude (Zheng et al. 2000). Strong winds also affect plants, animals and local livelihoods, especially in the western part of the plateau where wind speed could be over 17 m/s for 100-150 days in a year (Miller 2005).

Climate conditions also differ vertically along the elevation gradient and vary between various topographic conditions such as the enclosed valleys or basins and the exposed plains. Climate variability affects grassland productivity, socio-economic adaptations and decision-making processes (Wu & Yan 2002). As one of the most sensitive regions to global climate changes, the temperature has increased at about 0.32 °C/decade during 1960–2012 (CAS, 2015), and warming was stronger at higher elevations (Liu & Chen 2000). Climate changes could have negative effects on Tibetan pastures by changing water and heat availability, increasing risks of drought, as well as erosions caused by heavy rainfall, strong wind and melting permafrost.

Soils are results of long-term interactions of geological and climatic impacts. The main soil types on Tibetan grasslands mentioned in the literature are largely named after the main vegetation types, such as alpine meadow soil, subalpine meadow soil and alpine meadow steppe soil. Alpine meadow soils are rich in organic matter, and the surface layer is full of roots forming a substantially disturbance-resilient turf. Alpine steppe soils, as variants of soils from temperate steppes have developed under cold conditions. They are often with gravel and coarse sandy loam lacking the turf layer and more sensitive to wind and rainfall erosions (Huang 1987). There is a high diversity and variety of substrates, geomorphological processes and soil forming factors. Leptic Cambisols and Leptosols occur mainly on steep upper slopes, while Gleysols are often found close to rivers or lakes. Gelic Gleysols, Gelic Cambisols, and Permagelic/Gelic Histosols are dominant at permafrost sites (Baumann et al. 2009).

Soils on Tibetan grasslands form a huge C pool, which has been reported to store about 23.4% of China's total soil organic C and 2.5% of the global soil C pool (Ni 2002; Wang et al. 2002). More recently, based on published data from 2004–2014, about 29.37 Pg C (1 Pg=10^{12} kg) was estimated to be stored in the 0–100 cm soil layer in Chinese grasslands and nearly half (14.18 Pg C) was from alpine grasslands on the Qinghai–Tibet Plateau (Ma et al. 2016). Changes of soil conditions have profound effects on global C and N cycles under climate change processes. Specifically, more than half of the total area of the TP is with permafrost, representing the largest high-elevation and low-latitude permafrost region on earth (Cheng 2005). These permafrost areas are more sensitive to climate change and surface disturbance than those at higher latitudes such as in Russia and North America because they are warmer and less deep (Wang & French 1995). Degradation of Tibetan permafrost will change soil hydrology and soil moisture–temperature regimes, and thus affect soil biochemistry processes and plant communities in grassland systems (Baumann et al. 2009).

2 Grassland types, plant and fauna diversity

Since the 1960s, the Integrated Survey Team of the Chinese Academy of Science (CAS) started to investigate grasslands in Tibet, Gansu and Qinghai. From 1979, further progresses have been made by publishing the Atlas of China's Rangeland Resources and the Map of Grassland in China (Chen & Fischer 1998). However, classifications of grassland types vary among authors and studies. Climate zones, the humidity index and the importance to livestock industry are often criteria for distinguishing grassland types (Chang 1981; CAS 1990; Ellis 1992; Hou 2001; Sun 2005; Kang et al. 2007). Considering the scope of the present thesis, the classification and the terminology will not be discussed here. Only two major grassland habitat groups and one transitional ecotone will be considered in the following chapters: steppes, (sub) alpine meadows and steppe-meadows.

Alpine and subalpine meadows cover nearly 45% of the total plateau (Sheehy et al. 2006), and mainly occur on mountain slopes in eastern parts of the plateau (Fig. 3a-d), and in valleys or riparian areas with meltwater runoff in the west (Miller 2005). The word "meadow" refers to the unmown but only grazed moist pastures instead of the mown grassland in European understanding. Hereafter I keep the term "*alpine meadow*" as it has been widely introduced in the literature and widely accepted among researches working on the TP. Alpine and subalpine grasslands are not strictly differentiated here due to the focus of the current the study.

Steppes include alpine steppes (Fig. 3 e-f), which are mostly called "*Tibetan steppes*" as the most cited and representative habitat for western explorers and researchers, and are typically found in the Changtang (meaning "*the empty highland of the north*" in Tibetan language). In a wider sense, "*Tibetan steppe"s* sometimes refer to all kinds of Tibetan grasslands (Miller 2005; Sheehy et al. 2006), including cold alpine deserts, alpine or sub-alpine shrublands (Fig. 3g) and even the typical temperate semi-arid steppes which are similar to steppes in (Inner) Mongolia (Fig. 3h).

The transitional ecotone, steppe-meadows, typically comprise a mixture of plant species from the above two habitats but the general environmental conditions are similar as in alpine meadows. However, it's worth noting that steppe-meadows are different from the typical Mongolian meadow steppes (Hilbig 1995).

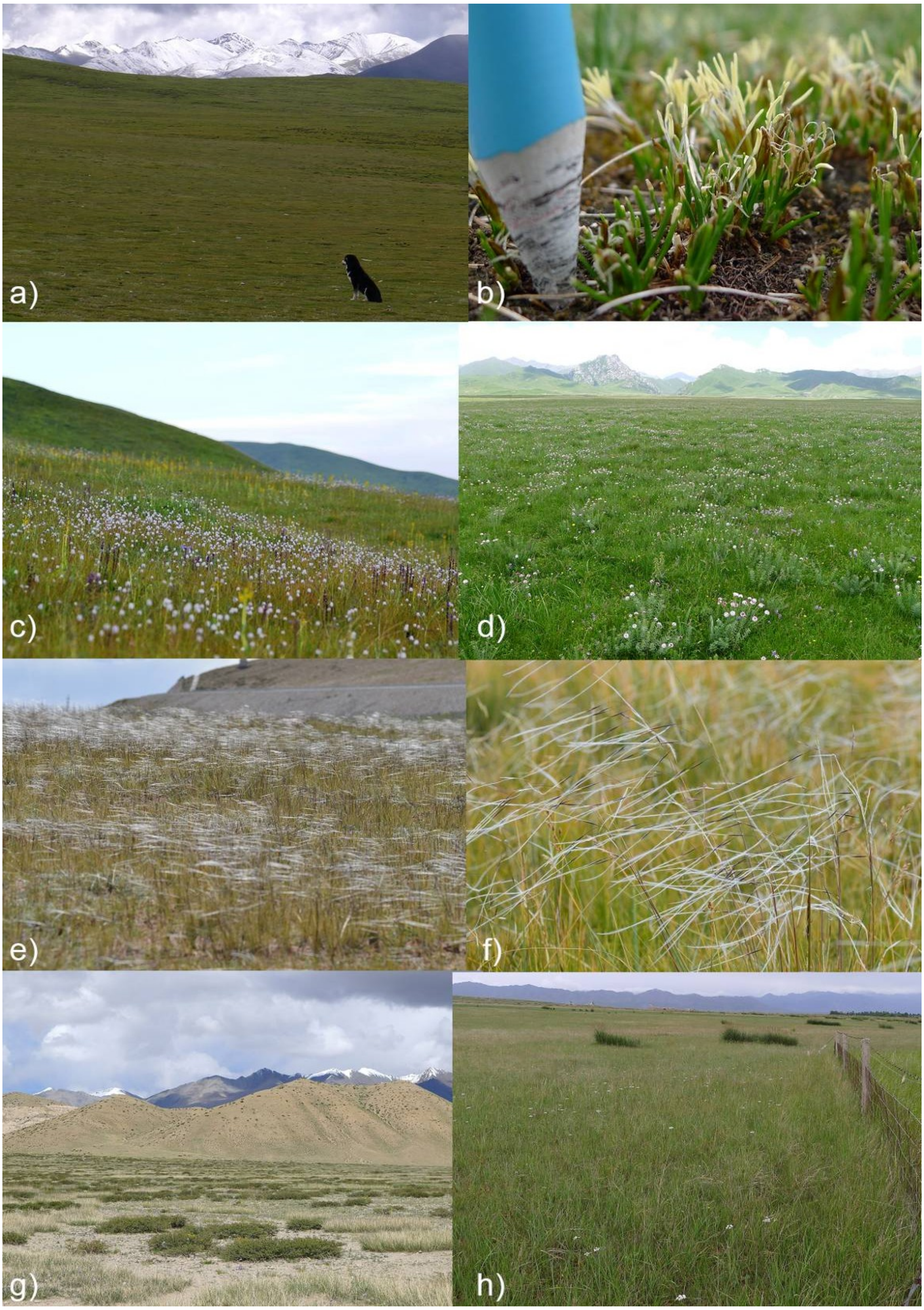

Fig. 3 Main grassland types on the Tibetan Plateau. a) moist alpine meadows dominated by sedge species *Kobresia pygmaea* in central Tibet; b) a close look at *K. pygmaea*; c) moist alpine meadows dominated by a mixture of sedges and forbs, such as *Polygonum macrophyllum* (the white flowers); d) alpine meadows with grazing weed *Stellera chamaejasme* in eastern parts of the TP; e) and f) semi-arid alpine steppes dominated by *Stipa purpurea* in western parts of Tibet and Qinghai; g) alpine steppes dominated by the shrub of *Caragana versicolor* and grass *Orinus thoroldii* in western parts of Tibet; h) temperate steppes dominated by grasses of *Orinus kokonorica* and *Stipa sareptana* var. *krylovii* in western parts of Qinghai. The large tussock grasses are *Achnatherum splendens*.

The Flora on the TP, as determined by the unique geological and climate backgrounds, comprises species elements of Central Asian (semi-) desert, temperate East Asian and Himalayan groups (Chang 1981, 1983). The dominant herbaceous species are not always grasses, but are frequently sedges of *Kobresia–Carex* species especially from alpine meadows, such as *K. pygmaea*, *K. humilis*, *K. capillifolia* and *C. atrofusca*. Alpine steppes are often dominated by *Stipa* species of Gramineae, for example *S. purpurea* (Fig. 3e-f) and *S. subsessiliflora*. Other related species include xeric and meso-xeric grasses such as *Poa alpina*, *P. crymophila*, *Agropyron cristatum*, *Orinus thoroldii* (Fig. 3g) and cushion plants. Halophytes, such as dwarf shrub *Krascheninnikovia compacta* (syn. *Ceratoides compacta*) and the sedge *Carex moorcroftii*, are common in cold alpine desert steppes (Miller 2005; Sheehy et al. 2006). More than 2000 plant species have been indentified in Tibet, of which 86% are forage plants and occur mainly in the humid and subhumid pastures of eastern Tibet, while 540 species occur in the arid and semi-arid rangelands (Gu 2000). Most frequent families and genera according to our three-year field vegetation surveys are listed in Fig. 4.

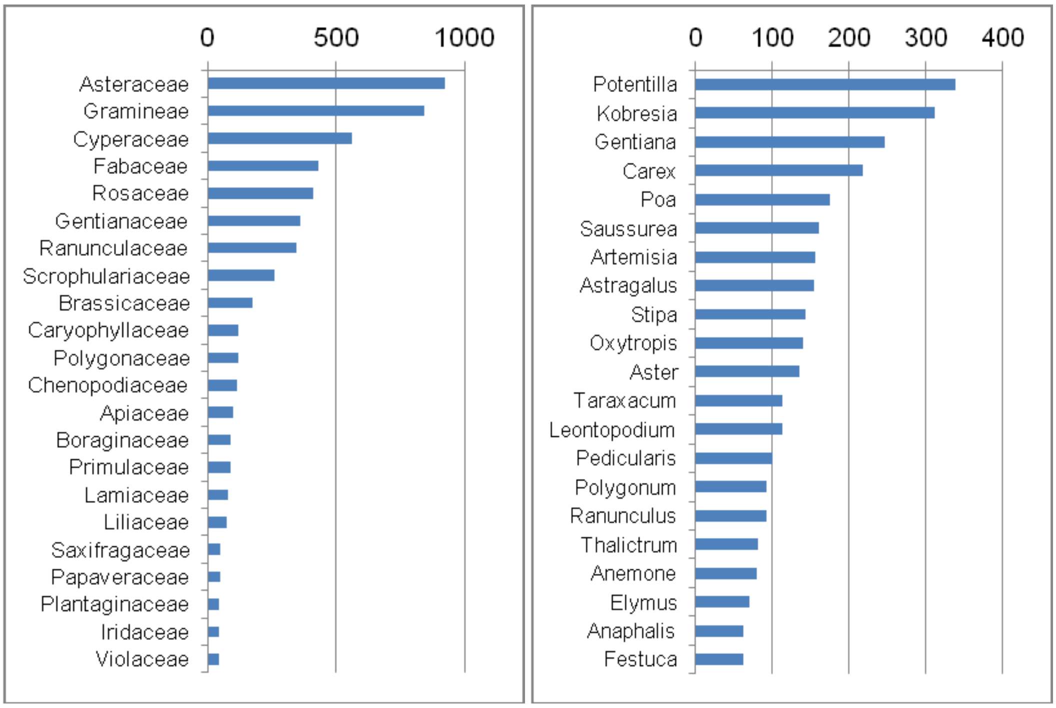

Fig. 4 Frequencies of most common families and genera from field vegetation surveys across 28 sampling sites on the TP. Plant biodiversity was high as shown from 626 species/185 genera/46 families. Meadows (523 species) and steppes (292 species) shared 189 species. The most common families were Asteraceae, Gramineae, Cyperaceae, Fabaceae and Rosaceae and 31 families occurred more than 10 times. Families include more than 10 genera are Gramineae (24 genera), Asteraceae (20 genera), Brassicaceae (15 genera), Apiaceae and Ranunculaceae (11 genera). Fourteen genera occurred more than 100 times.

Besides the rich flora, diverse fauna groups and especially several endemic species are also important for *in situ* preservation of biodiversity and genetic resources (White et al. 2000). Several unique mammals are found in Tibetan steppes (Fig. 5), such as Tibetan wild ass (*Equus kiang*), wild yak (*Bos grunniens*), Tibetan antelope (*Pantholops hodgsoni*) and Tibetan gazelle (*Procapra picticaudata*). Some species prefer to inhabit mountain habitats, e.g. blue sheep (*Pseudois nayaur*) and Tibetan argali (*Ovis ammon hodgsoni*). Other speices include brown bear (*Ursus arctos*), wolf (*Canis lupus*), snow leopard (*Uncia uncia*), lynx (*Felis lynx*), Tibetan steppe fox (*Vulpes ferrilata*) and red fox (*Vulpes vulpes*), as well as more common small mammals including marmot (*Marmota bobak*) and plateau pika (*Ochotona curzoniae*). Typical bird species are steppe eagles (*Aquila nipalensis*), upland buzzards (*Buteo hemilasius*), saker falcons (*Falco cherrug*), goshawks (*Accipiter gentilis*), black kites (*Milvus migrans*) and some waterfowl as black-necked cranes (*Grus nigricollis*), bar-headed geese (*Anser indicus*) and ruddy shelduck (*Tadorna ferruginea*).

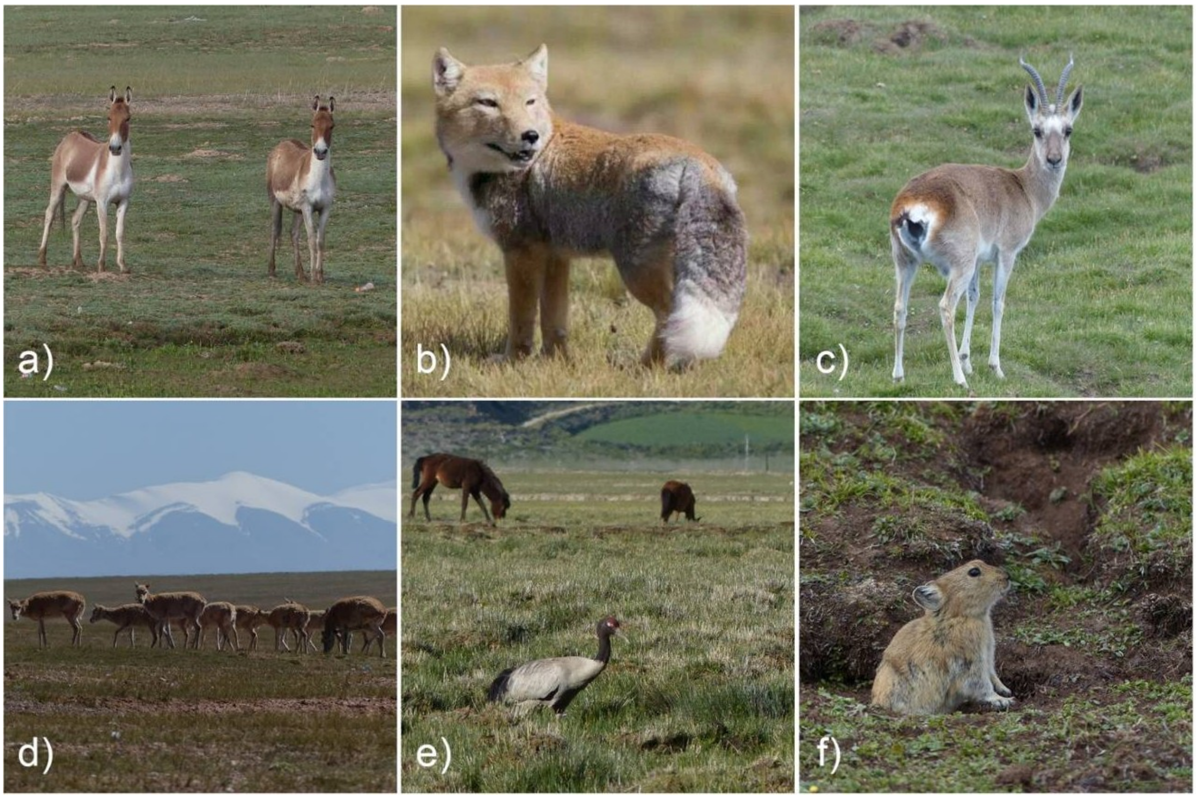

Fig. 5 Typical wild animals on Tibetan grasslands. a) Tibetan wild ass (*Equus kiang*); b) Tibetan steppe fox (*Vulpes ferrilata*); c) Tibetan gazelle (*Procapra picticaudata*); d) Tibetan antelope (*Pantholops hodgsonii)*; e) black-necked crane (*Grus nigricollis*) and f) plateau pika (*Ochotona curzoniae)*. ©J. Schmidt and Huaben Duo.

3 Grazing systems, livestock and management

Similar to other mountains such as Altai, Caucasus, Alps, Scandinavia and Andes (Speed et al. 2013), seasonal rotation is typical for traditional grazing management on the TP. Livelihoods in these regions are strongly dependent on availability of natural resources and especially restricted by high elevations, steep slopes and dramatic annual or seasonal climate changes. Winter pastures are often situated at lowlands, and summer pastures are at highlands (Fig. 6a-b, f). In different regions, settings of spring and autumn pastures show a wide variation depending on the local climate and productivity. The well-organized pastoral societies also keep special pastures against emergent extreme events, such as snowstorms in hard winters (Fu et al. 2012). In humid areas, winter pastures are often alpine swamps where taller plants (e.g. *Kobresia tibetica*) are still possible to be assessed by livestock even under snow cover, while summer pastures usually locate at higher elevation, with more precipitation and thus higher productivity.

Livestock play central and multiple roles in nomadic cultures by providing basic materials for food (meat, milk), clothes (wool, fibre) and fuels (yak dung), and also represent subsistence, savings and even social status of their owners. In pastoral areas, products from livestock are also the connection to agricultural communities through the exchange of barley, which is another staple in the diet of Tibetan people but can’t be grown in most areas of the TP because of the low temperatures at high elevations. Unlike most of other pastoral regions in the world where water shortage is the limiting factor for primary productivity, high elevation and low temperature are the main restrictions which make the conversion of Tibetan grasslands to croplands impossible (Miller 2000).

The domestic yak, which is well adapted to environments with cold temperature, low oxygen content and strong radiation (Wiener et al. 2003), is the most common herd on the TP (Fig. 6b, g). As the 10th Panchen Lama said, “No yak, no Tibetan people”, yak is not only the foundation of the local livelihoods by providing milk products and meat for food, fur for clothes, and dung for fuel, but also represents wealth for Tibetan nomads (Miller 2000). The evolution of yak could be traced back to 400 000 years ago and the historical range of wild yak includes the whole TP, northwestern Mongolia, the Lake Baikal region in Russia and Nepal (Miller et al. 1994). The most recent study based on whole-genome resequencing of wild and domestic yaks have revealed several behaviour and tameness related genes, indicating that yak domestication happened 7300 years before present (Qiu et al. 2015). Tibetan sheep/goats

(*Ovis aries*) and the second main herd group (Fig. 6c, e, h), particularly for steppes, and horses also account for part of the grazers (Goldstein & Beall 1989).

Fig. 6 Typical livestock and seasonal pastures. a) yaks at a winter pasture in central Tibet; b) yaks at a summer pasture in southern part of Qinghai; c) yaks, sheep and goats at a summer pasture in southern part of Gansu; d) summer camps with the traditional yak hair tent; e) sheep and goats in northern part of Qinghai; f) winter settlements in southern part of Qinghai; g) yaks in alpine steppes in western part of Tibet; h) sheep and goats in western part of Tibet; a) -f) are from alpine meadows and g) -h) are from alpine steppes.

Herd composition varies across the TP according to local conditions of plant community and physical environment or historical reasons (Miller 1999, 2000; Miller 2005). Type of herd is relevant to grazing effects on vegetation because different grazing habits cause various consequences in plant vigour and lead to shifts of competition patterns, especially in grasslands where resource availability is high and reliable (Anderson et al. 1995). For instance, yaks are versatile foragers and are adaptive for grazing long grasses and sedges by their tongues as cattle do, but also grazing short grasses and creeping stems and roots of grasses by their incisor teeth and lips as sheep do (Wiener et al. 2003). Yak diet usually comprises tender branches of shrubs and rough stems and leaves of sedges. In spring pastures, even the wilted stems and leaves of grasses from last winter could be grazed. More specifically, they are able to select against poisonous or thorny plants (Wiener et al. 2003). In contrast, sheep and goats are more selective than yaks. They prefer for grasses, legumes and other forbs (Wang 1999), and only browse with lips and teeth to browse (Cincotta et al. 1991). Furthermore, herd composition could also change plant species composition by selective foraging on specific plant species, or different plant parts, such as seed and other reproductive parts (Li et al. 2013b).

Like all other grassland systems over the world, livelihood changes are not only caused by nature, but more frequently, by humans. Although local people from remote areas are short of infrastructure, health and education services and are relatively isolated from modern society, relationships between people and nature have been peaceful and sustainable for a long time before changes in economic and administrative systems started. Modern civilization brings in opportunities and challenges, from both social and environmental aspects. Governmental interventions in local livelihoods may result in social problems because contradictions often exist between tradition and developments

Before assessing the current health conditions of Tibetan grasslands, it's necessary and useful to review when and what kind of changes happened on the TP in the past. Due to the prominent climate changes and environmental issues in eastern part of China, researchers and policy makers have put much attention and efforts in this region to explore the causes of degradation and the effective strategies for restoration (Gao et al. 2006; Feng et al. 2009; Gao et al. 2010; Dong et al. 2012). Overgrazing is commonly recognized as the main cause of grassland degradation (Zhou et al. 2005; Liu et al. 2006; Akiyama & Kawamura 2007; Li et al. 2013a) as statistic data indicate an increase in livestock number from 1950s to 2000s (Fig. 7a). There are, however, great differences among livestock species, administrative units and even counties (as shown by livestock numbers reported from statistical yearbooks for the studied sites from Qinghai in later chapters, Fig. 7b). Unfortunately, larger livestock number does not necessarily indicate higher grazing pressure because this might only reflect the forage productivity from certain grassland systems is generally higher. For example, the suitable grassland area for livestock grazing in Tibet is twice larger than in Qinghai, so livestock numbers follow the similar pattern. At county or site level, statistical number often cannot be directly translated to grazing intensity because the grassland area which is available for livestock is unknown at the corresponding spatial scale.

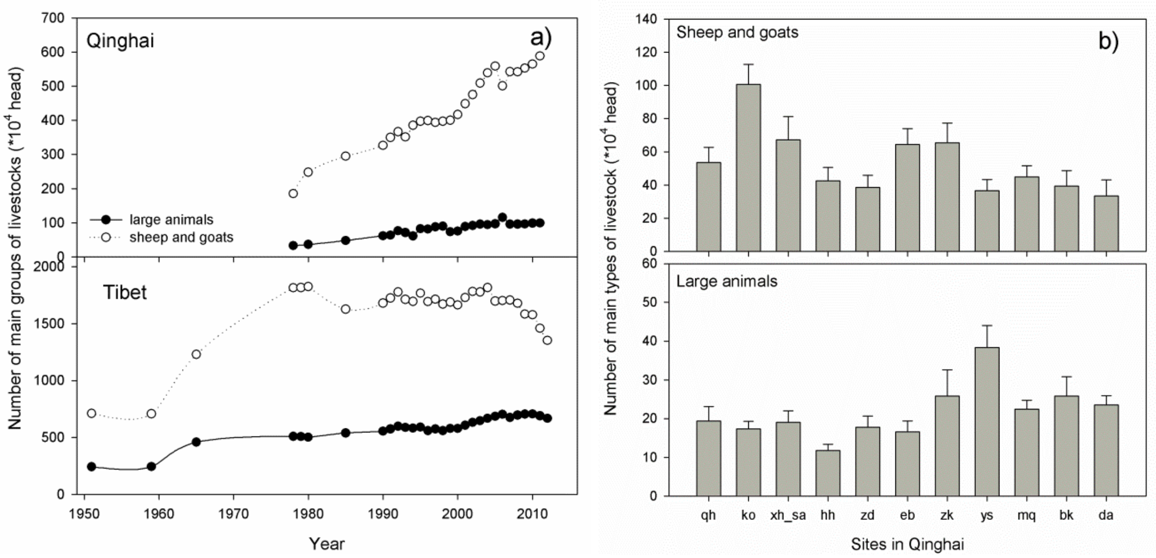

Fig. 7 Changes of livestock numbers. a) large animals (including yaks, cattle and horses), sheep and goats from the statistical yearbooks of Qinghai (1978–2012) and Tibet (1951–2012); b) differences among counties that were investigated in field excursions in Qinghai based on the data of 1970–1996. Data are from the statistical yearbooks of Qinghai and Tibet of the corresponding years (published in Chinese).

Most grassland management policies on Chinese grasslands are based on the equilibrium concept that livestock density mainly controls plant species composition, cover and productivity. Although non-equilibrium theories have been widely discussed in semi-arid grassland systems over the world since later 1980s, they are surprisingly and rarely acknowledged in China (Ho 2001). The central idea of the equilibrium-based management is adjusting herd size to the optimal carrying capacity, which is defined as the maximal number of herbivores that the vegetation can support within a given time without degradation (McCabe 2004). Accordingly, several policies implemented by government in the last decades on Chinese grasslands tried to change the communal and pastoral management and to reduce the grazing intensity (Yan et al. 2005; Nyima 2015). However, the effectiveness of these policies is still under debate from both conservation and socio-economic perspectives (Table 1). To avoid the “tragedy of commons” and achieve economic efficiecy, management of common resources were framed by contracts and with enclosures (Cao et al. 2013b). The proposals of reducing livestock numbers and the flexibility and mobility of the nomads to restore grassland condition are widely adopted, but the impacts of these policies on social, economic and ecological aspects of grassland ecosystems are still greatly debated (Yan et al. 2005; Klein et al. 2011; Gongbuzeren et al. 2015). Although grassland restoration could be achieved by grazing exclusion in terms of vegetation cover or productivity, whether fencing will improve richness of plant and animal species from other trophic levels in a long run is nonetheless still questionable (Shang et al. 2013; Shang et al. 2014). Moreover, studies are mostly conducted at moist alpine meadows (Cincotta et al. 1992; Yan & Wu 2005; Fu et al. 2012; Wu et al. 2012; Cao et al. 2013a; Cao et al. 2013b), while investigations are rare from relatively dry grassland systems (Yan et al. 2005; Xu et al. 2008).

Table 1 Important rangeland policies and their general impacts on ecosystem health in Chinese grasslands. (+) and (–) mean positive and negative effects. The time when certain policy started to be implemented differs among different administrative regions and is indicated (Goldstein & Beall 1989; Wu & Yan 2002; Fu et al. 2012; Wu et al. 2012; Cao et al. 2013a; Gongbuzeren et al. 2015; Nyima 2015).

Period	**Policies/projects**	**Changes of livelihood**	**General effects**
1960s–early 1980s (same for Qinghai and Tibet)	Collectivized ownership of agricultural capital after the People’s Republic of China was established	Livestock and other resources became collective property; pastoralists lost decision-making rights on pasture management, although many communes still followed traditional management patterns.	Maybe “tragedy of commons”, or still sustainable
Since 1990s (same for Qinghai and Tibet; experiments started in1980s at few sites following West Sichuan and South Gansu)	decentralization/decollectivization; “Grassland household responsibility”; by 2013, the contracted grassland covered 71% of total grassland area in China	Grassland user rights began to be contracted to individual households, although grassland remained state-owned; Fences (Fig.8b) were introduced to separate different grazing units; inequality caused conflicts	(–) on ecosystem, animal husbandry, pastoralist livelihoods
1980s only in Qinghai, 2006 in Tibet, 2009 in Qinghai (for widely building new settlements)	Sedentarization of pastoralists (Fig. 8a)	Old people are likely to stay in the settlements for whole year; migration radius of livestock was reduced depending on the distance to winter settlements	(+/–) pastoral livelihoods (+) animal husbandary (–) ecosystem
Since 2002 (Qinghai: 2003; Tibet: 2004)	Grassland retirement program (“Tui Mu Huai Cao” or “grass for green”)	Livestock number and the corresponding amount of diary products reduced	(+) on ecosystem (–) on pastoral society
Since 2011 (same for Qinghai and Tibet)	Projects for grassland ecological constructions, “subsidy” system for grassland conservation	Cause social problems	No information

Fig. 8 Rangeland polices of a) sedentarization project with newly built settlements close to winter pastures in Yushu, south of Qinghai, b) fences for separating seasonal rotating pastures in Qilian, north of Qinghai.

4 General methodology

Considering the long evolutionary grazing history of Tibetan grasslands and the main interest in cumulative grazing effects, comparing different grazing intensities is more realistic than investigating short-term grazing exclusion effects. Moreover, long-term grazing exclusion experiments are hardly available across large environmental gradients. Therefore, the local gradient of livestock activity was qualitatively determined by the distance to grazing hotspots, such as camps, settlements and water resources. This approach has been criticized because the distance to a grazing hotspot has only explained a relatively small share of the total variation in grazing intensity at one site in central Tibet (Dorji et al. 2013) and might be oversimplified to capture the non-linear relationship between grazing intensity and distance to grazing hotspots (Manthey & Peper 2010). However, this approach is representative for cumulative and historical grazing pressures (Adler & Hall 2005) and has been applied in several alpine (Spehn et al. 2006; Haynes et al. 2012; Qian & Shimono 2012; Wen et al. 2013) or semi-arid grassland systems (Fernandez-Gimenez & Allen-Diaz 1999; Khishigbayar et al. 2015).

At each sampling site, one to four transects radiating from a grazing hotspot were set up depending on the movement-range of livestock. Strictly speaking, these transects were not exact straight lines but only the general directions away from one grazing hotspot at a given site. Four levels of livestock activity were considered: 1) P–piospheres with high levels of nutrient inputs and mechanical disturbance by trampling of (resting) livestock. Piospheres were distinct from the other three levels of grazing intensity in that livestock did not move and forage freely; 2) H–heavily grazed plots relatively close to camps where livestock could move and forage, but within a small area; 3) L–relatively lightly grazed plots where herds spread over a larger area relatively far from the camps; 4) M–moderately grazed plots located between and with roughly equal distance from heavily and lightly grazed plots.

Within each transect, two to five vegetation plots were surveyed depending on the local grazing range and corresponding soil samples from each plot were collected. To validate the recent livestock activity, dropping from yaks, sheep, goats and horses were counted from three randomly placed quadrats (1x1m^2) within each vegetation plot and calculated into total dung cover (%).

The main datasets were compiled from late June to early September in 2011–2013. Sampling of five indicator groups (plants, soils, ants, small mammals, hyperspectral data) were conducted jointly by a German-Chinese team, with the helps and supports from several persons, institutes and universities. Plant specimens were largely identified according to eFloras (2008) and related works, and cross-checked in the Herbarium of the Kunming Institute of Botany, CAS by me and difficult taxa were sent to specialists. Vegetation and soil samples were processed by me, while other samples were handled and processed by the joint subprojects. The sampling and statistical approaches are summarized in Table 2 and Fig. 9.

Table 2 Summary of response variables for each indicator group, explanatory variables and main statistical methods.

Indicator group	**Multivariate indicator**	**Univariate indicator**	**Sample unit**	**No of plots**	**Sample processing**
Plants	species composition	species richness, total cover	10 x 10 m^2	173	identify plant specimen
	functional group composition (shrubs, grasses, sedges, perennial forbs and annual forbs)	Richness and relative cover of each functional group			
	Plant functional trait matrix	e.g. life form, growth form, clonality, tissue C, N contents		104	plant tissue nutrients, SLA
Soils	soil physical and chemistry properties	pH, EC	0~5 cm; 3 replicates / 10 x 10 m^2 plot	161	pH/EC meter
		SOC, tN			CN-Analyser
		plant available P, Ca, K, Mg			Olsen-P, ICP-OES
Ants	species composition	species richness	40~150 m^2	62	details see Chapter 5
		nest density			
Small mammals	species composition	species richness	100 x 100m^2	44	
		abundance			
Hyperspectral data	Hyperspectral data matrix	NDVI, NDNI, REP_LE	5 quadrats/ plot, 3 replicates/ quadrat	68	
Dung	dung cover from yak, sheep and goat, horse, others	total dung cover	3 quadrats of 1 x 1m^2	173	details see Chapter 5-6
Environmental factors	Climate factors: P, cvP, T, acT, srad, yearTdiff				
	Topographic conditions: Lon, Lat, Elev, aspect (East, North), inclination, relief position				
Statistic analyses	**Multivariate analyses**		**Univariate analyses**		
	Within indicator group: PCoA, NMDS, PCA (dissimilarity matrix: Bray-Curtis, Euclidean, Spectral Angle Mapper), multivariate permutation MANOVA		Pearson correlation, GLMMs, multiple Turkey HSD test		
	Among indicator groups: Mantel correlation, Procrustes test				

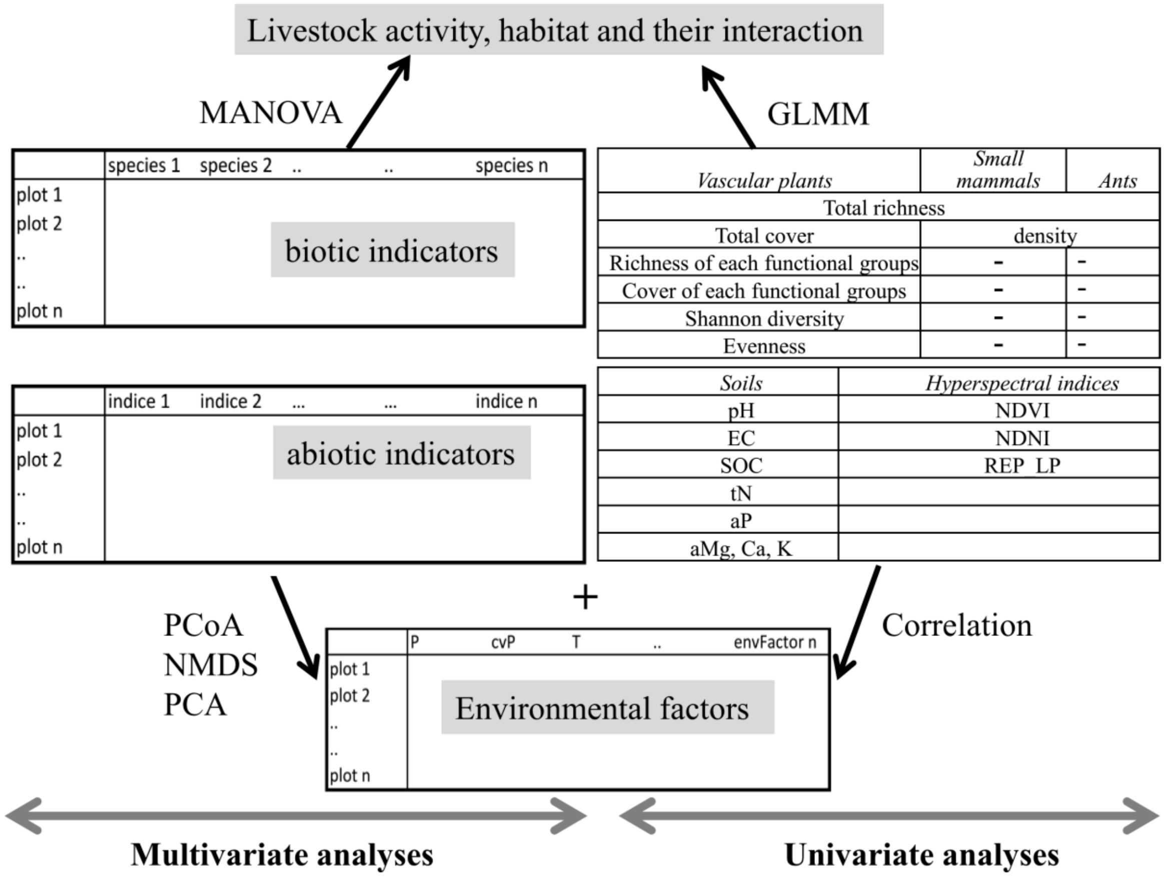

Fig. 9 Summary of main datasets and corresponding approaches for statistic analyses.

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Chapter 3 Literature review

Vegetation and soil responses to livestock grazing in Central Asian grasslands: a review of Chinese literature

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Abstract

Grasslands in northern China and the Qinghai-Tibetan plateau are particularly important to both ecosystem functioning and pastoral livelihoods. Although there are numerous degradation studies on the effect of livestock grazing across the region, they are largely only published in Chinese, and most focus on single sites.

Based on case studies from 100 sites, covering a mean annual precipitation gradient of 95 to 744 mm, we present a comprehensive, internationally accessible review on the impact of livestock grazing on vegetation and soils. We compared ungrazed or slightly grazed sites with moderately and heavily grazed sites by evaluating changes in two indicator groups: vegetation (plant species richness, vegetation cover, aboveground biomass, belowground biomass and root/shoot ratio) and soil (pH, bulk density, organic C, total N, total P and available P).

Most indicators declined with intensified grazing, while soil pH, bulk density and belowground biomass increased. Available P showed no clear response. Variables within indicator groups were mostly linearly correlated at a given grazing intensity. Relative grazing effects on different indicators varied along specific abiotic gradients. Grazing responses of plant species richness, aboveground biomass, soil bulk density, total N and available P interacted with precipitation patterns, while grazing effects on belowground biomass were influenced by temperature. Elevation had impact on grazing responses of aboveground biomass and soil organic carbon.

Complex grazing effects reflect both methodological inconsistency and ecological complexity. Further assessments should consider specific characteristics of different indicators in the context of the local environment.

Keywords

Abiotic control; Climate; Degradation; Inner Mongolia; Nutrients; Plant diversity; Qinghai Tibetan Plateau; Soil organic carbon

1 Introduction

Grasslands cover 30–40% of the Earth's terrestrial surface. Of these, 8.9 million km² are situated in Asia, with nearly 4 million km² occurring in China (White et al. 2000), and mainly in the northern and western cold and arid regions. These grasslands support diverse plants, animals and ethnic communities, providing animal products including meat, milk, wool and furs for local pastoralists (Kang et al. 2007). The grasslands on the Qinghai-Tibetan plateau (QTP) have a unique ecological importance as upper watersheds for large rivers such as the Yellow, Yangzi and Mekong Rivers, and they are considered to be particularly sensitive to climatic changes and human impacts (Chen et al. 2013). Much effort has been put into grassland degradation/desertification assessments in this region after environmental problems such as sand and dust storms, flood and drought have intensified across eastern China (Zhou et al. 2005; Li et al. 2013b). However, conclusions of assessments do differ widely in their estimates of the degradation status. The most frequently quoted values are 30% degraded grasslands on the QTP, while others consider 90% of all grasslands in China to be degraded (Shang & Long 2007; Harris 2010).

Estimations of degradation extent and magnitudes vary because there is a lack of consistent definition for degradation and varying baselines, indicator systems and methodologies for assessment. The spatial and time scale of the study might lead to different results (Oba et al. 2003). In spite of conceptual differences, researchers often did not distinguish desertification from grassland degradation (Wang et al. 2008; Cui and Graf 2009), and the influences of climate change and human activities on grasslands are rarely differentiated (see Chen et al. 2014; Zhou et al. 2014; He et al. 2015 for positive exceptions). Large scale assessments based on remote-sensing data and models are sometimes questionable due to the misinterpretation of spectral data (Yang et al. 2005). Fine-scale changes in vegetation (species composition) and soils (physical and chemical properties) represent appropriate indicators for local, site-based assessments, but they are not easily detected by spectral data. Moreover, reductions in vegetation cover and aboveground biomass on a short time scale can be reversible in the long run, so they do not necessarily indicate degradation (Khishigbayar et al. 2015). Although degradation has been demonstrated for different parts of the QTP, especially in southern Qinghai, northern Tibet and the Qaidam Basin (Li et al. 2013a), the extent and causes of degradation in whole region are still under debate (Harris 2010).

Such uncertainties also reflect more fundamental theoretical problems, such as whether vegetation dynamics in grasslands are primarily driven by herbivores or climate factors. The classic equilibrium models emphasize internal density-dependent factors (livestock-vegetation feedbacks) and acknowledge climatic effects within mean resource availability. Non-equilibrium models focus on the controls of stochastic abiotic factors in arid, highly variable and unpredictable ecosystems, where the threat of degradation caused by grazing seems to be limited. Empirical studies from Africa and Central Asia (in the biogeographical sense and thus including Mongolia and northern China, Cowan, 2007) demonstrate non-equilibrium dynamics, especially where interannual rainfall variability is greater than 33% (Ellis and Swift 1988; Ellis 1995; von Wehrden et al. 2012). Most grassland systems, however, show both equilibrium and non-equilibrium characteristics (Fernandez-Gimenez and Allen-Diaz 1999; Cheng et al. 2011b). Traditional nomadic systems acknowledge environmental heterogeneity and resource availability, but government interventions are mainly based on livestock-vegetation dynamics and assume overgrazing as the main cause of grassland degradation. Policies on destocking and sedentarization often reduce the mobility and flexibility inherent in traditional grazing systems (Vetter 2005). Experimental studies over large climatic gradients are therefore needed to gain a better understanding of the mechanisms behind interactive impacts of climate and grazing on vegetation dynamics (Overbeck 2014). Especially in the vast and environmentally diverse grasslands of Central Asia, investigating vegetation–soil–climate dynamics under grazing is both of high theoretical importance and of relevance to management.

Various indicators are employed to assess grazing effects and show different response patterns. Plant species richness typically shows a unimodal response to disturbance (Grime, 1973; Huston, 1994), however, the relationship between grazing intensity and richness depends on grassland productivity (Lezama et al. 2014). Vegetation cover and aboveground biomass are commonly reduced by grazing, but both may recover quickly under grazing exclusion (Sasaki et al. 2008). Belowground biomass shows complex response patterns (Milchunas and Lauenroth 1993; McNaughton et al. 1998; Frank et al. 2002). Soils are closely related to productivity, but responses to grazing and environmental changes are generally slower than plants. Once soils are degraded, they are also much more difficult to restore. Grazing affects soil physical properties through trampling and biomass removal, with soil pH tending to increase (Steffens et al. 2008; Li et al. 2011a) and bulk density increasing or remaining stable (Teague et al. 2011; Sun et al. 2014). Soil nutrients are often directly redistributed by the uneven release of dung and urine (Stumpp et al. 2005), and indirectly affected by grazing-induced changes in soil temperature, aeration and insolation, which influence their decomposition rates (Bagchi and Ritchie 2010). Global reviews reveal complicated grazing effects on soil C and N (Piñeiro et al. 2010; McSherry and Ritchie 2013; Schrama et al. 2013); case studies also show inconsistent grazing responses for soil P (Chaneton et al. 1996; Barger et al. 2004; Li et al. 2008; Steffens et al. 2008; Rui et al. 2012; Li et al. 2013b).

Moreover, vegetation and soil indicators interact with environmental factors in various ways. Plant species richness correlates with productivity at global and regional scales (Waide et al. 1999; Ma et al. 2010). Climate and soil conditions also independently and interactively influence vegetation dynamics, as demonstrated for arid grasslands (Le Houerou et al. 1988; Bai et al. 2008). Precipitation controls plant species richness, composition and productivity (Milchunas and Lauenroth 1993), especially in Mongolia and China (von Wehrden and Wesche 2007; Chou et al. 2008; Ma et al, 2010; Zhang et al. 2012). Water availability determines the distribution of *Kobresia* pastures in eastern Tibet, and it explains most of the spatial variation in belowground biomass on the QTP (Li et al. 2011b). Soil nutrients are also sensitive to climate, as showed for soil organic matter in general (von Lützow and Kögel-Knabner 2009), and especially in Chinese grasslands (Yang et al. 2008; Fang et al. 2010). Relationships among vegetation, soil and climate variables can vary from being linear to non-linear with increasing grazing intensity (Zhou et al. 2002), and grazing also modifies the climate sensitivity of nutrient cycling (Han et al. 2005; Paz-Ferreiro et al. 2012; Sun et al. 2014).

A large number of case studies focusing on grassland degradation in China, especially on the QTP, were published in Chinese and are difficult to access for an international readership. The few available reviews are mainly descriptive summaries (Akiyama and Kawamura 2007; Harris 2010; Cao et al. 2013a). Here, we synthesize the effects of livestock grazing on vegetation and soils along large environmental gradients mianly from recent Chinese publications. Specifically, we address the following questions:

1. How do commonly used vegetation and soil indicators respond to grazing?
2. Are there relationships among grazing responses within or between vegetation and soil indicators?
3. How do indicators and their grazing responses change along large environmental gradients (elevation, precipitation and temperature)?
4. Does grazing change the pattern and magnitude of correlations among vegetation, soil and environmental variables?

2. Methods

2.1 Data extraction

Considering that our focus was on overcoming language barriers and enhancing the knowledge based in the English language, we searched Chinese publications instead of performing a full search of the TR Web of Science (formerly ISI Web of Knowledge). In the CNKI (China National Knowledge Infrastructure) database, we searched for various combinations of the terms “grassland/meadow/steppe/pasture”, “vegetation/plant/soil” and “grazing effect” either in the keyword list or the title. We took “grassland” instead of the classic term “rangeland”, because “rangeland” in Chinese translation does not necessarily include non-grass dominated grazing lands, such as the shrublands in the Dzungarian basin of northwest China. We included studies published between January 1st, 2000 and June 28th, 2014, and we covered the main pastoral regions including Qinghai, Gansu, Yunnan, Sichuan and the autonomous regions of Tibet, Inner Mongolia, Xinjiang and Ningxia (Fig. 1).

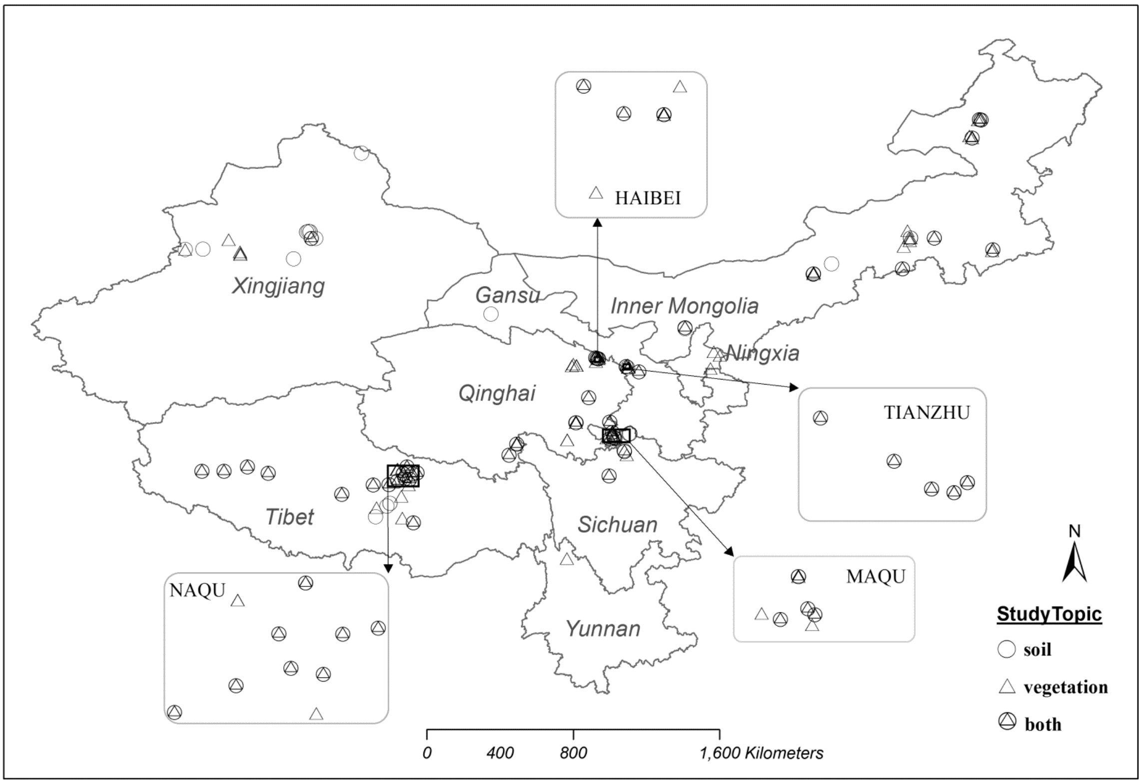

Fig. 1 Locations and research focus (vegetation and/or soil indicator group) for all study sites.

We excluded studies from artificial grasslands sown for hay or for restoration. Addionally, we also considered English publications referring to the same sites as those in Chinese studies, or those appearing in the reference lists of the retrieved publications. In total, we extracted 131 datasets from 103 publications (Online Resource 1, 92 papers and 9 Master/PhD theses; also Online Resource 2 in .xml format for exporting into reference management software) based on 100 distinct locations (Online Resource 3). Studies on different vegetation types and grazing regimes (i.e. summer vs. winter) were treated as ecologically independent experiments, even when the respective sites were very close to each other and shared the same macro-climate. Indicators collected at the same locations from the same working group but published in different papers were considered jointly. Most studies did not measure all varibales, so each dataset includes one or several vegetation or soil indicators corresponding to the respective abiotic parameters. Sample sizes for each indicator under a certain grazing intensity are given in Tables 1 & 2.

Authors surveyed plant species richness in different sizes of plot, which were usually small quadrats of 50 x 50 cm^2 or 1 x 1 m^2 (3–6 replicates, e.g. Fan et al. 2009; Ma et al. 2010; Shi et al. 2013) or, occasionally, larger plots of 5 x 5 m^2 or 10 x 10 m^2 (e.g. Li et al. 2008). Moreover, whether estimates were based on the sum or the mean species number from subplots was not always reported. So we expect species richness will show experimental artifacts. Reported vegetation cover was usually visually estimated from the small sample areas as described above. Aboveground biomass (AGB) was estimated based on clipped standing biomass from 50 x 50 cm^2 plots (3 – 5 replicates), and mostly from grazed sites (e.g. Wu et al. 2009; Sun et al. 2014) rather than from livestock exclusion plots (e.g. Li et al. 2008), which provides values of residual biomass rather than primary productivity. Where authors reported AGB values over the whole growing season, we selected the peak biomass (late July or early August). Belowground biomass (BGB) was usually derived using soil augers with differing diameter sizes or from plots corresponding to AGB (e.g. Gao et al. 2007; Li et al. 2013b). Methods for sieving soils differed among studies, and sampling depths were inconsistent, ranging from 4 to100 cm depending on vegetation types and dominant species (e.g. Li et al. 2013b; Sun et al. 2014). Most authors did not state whether roots were alive or dead; where they did, we pooled live and dead roots and samples from all depth layers as a representative BGB. Where possible, we recorded the reported root/shoot ratio or calculated it as total BGB/AGB.

Authors used soil–water suspensions or KCl solutions (soil/solvent=1:1, 1:2.5 or 1:5) to measure pH, and they calculated soil bulk density as the ratio of dry soil weight to sampled volume. Methodologies for obtaining nutrient concentrations varied among studies and sites. The dichromate-acid wet oxidation method was generally employed to determine soil organic carbon (SOC, e.g. Zou et al. 2007). Some authors measured total carbon by dry combustion and gas chromatography, and then deducted inorganic carbon (e.g. Li et al. 2008). Not all studies mentioned whether they had corrected for inorganic carbon. Where values for soil organic matter (SOM) were reported, we calculated SOC as 58% of the SOM (Pribyl 2010). Total nitrogen was mostly extracted by the semi-micro Kjeldahl procedure (e.g. He et al. 2011), while total phosphorus was generally measured by the H_2SO_4–$HClO_4$ or NaOH digestion and available phosphorus was extracted with the Olsen–P method ($NaHCO_3$), with few studies selecting alternative methods (e.g. Li et al 2008). Data on nutrient pools (mass per unit area) were excluded in our datasets because relevant bulk density data were not always available to convert nutrient concentration on a weight basis to a unit area basis.

Latitudes, longitude and elevation (Elev) were usually directly reported in publications. Wherever not, we used Google Earth to estimate elevation from specific coordinates. Climate information was not always recorded by authors, and when it was, the timescale for the reported data was often missing. As such, we extracted mean total annual precipitation (P, mm) and mean annual temperature (T, °C) from the China Meteorological Forcing Dataset (CMFD, 1979.01.01-2012.12.31; Chen et al. 2011; He and Yang 2011). The spatial resolution of the CFMD model is 0.1°, so we got similar climate values for sites that were geographically close to each other, even for those with different vegetation types or experimental designs. In total, 88 precipitation datasets and 98 temperature datasets were compiled for the 100 sites. The CFMD datasets correlated well with the originally reported data from the reviewed publications (Pearson correlation $r_{P.}$=0.95, n=88; r_T=0.79, n=98, Online Resource 4, Fig. S1). The interannual coefficient of variation for precipitation (cvP, %) was further calculated from the extracted precipitation data. We performed the same analyses for those 88 datasets as we had for the total 131 datasets. Results were broadly similar and confirmed that climatic pseudo-replication did not affect the analyses.

In summary, we included the following 11 indicators (five for vegetation and six for soil) in the analyses: plant species richness (Richness), vegetation cover (Cover), aboveground biomass (AGB), belowground biomass (BGB), root/shoot ratio (rsRatio), soil pH, soil bulk density (BD), soil total organic carbon (SOC), soil total nitrogen (tN), soil total phosphorus (tP) and soil available phosphorus (aP). Primary environmental factors include mean annual precipitation (P) and its interannual variance (cvP), mean annual temperature (T) and elevation (Elev).

2.2 Data processing

Authors either quantified grazing intensities by assessing livestock numbers within a given fenced-off area during a fixed period, or by assessing numbers qualitatively along transects for studies without fences. In general, grazing pressure was assumed to decrease with increasing distance from a settlement or waterhole. However, some studies only evaluated grazing intensity by comparing plant communities or bare soil cover. Authors usually qualitatively classify grazing intensities as light, moderate and heavy grazing. There were three experimental designs employed in the reviewed studies: (1) exclosure vs. grazing; (2) transects with ≥3 grazing intensities without an exclosure; (3) transects with ≥2 grazing intensities with an exclosure. Most publications originally reported vegetation types. When transitional types such as steppe-meadow, meadow-steppe and subalpine meadow were mentioned, we merged them into the class of the dominating vegetation. In total, six vegetation types were distinguished: 1) DS=desert steppe, 2) S=steppe, 3) ADS=alpine desert steppe, 4) AS=alpine steppe, 5) AM=alpine meadow and 6) ASW=alpine swamp. In this terminology, steppes refer to typical grass-dominated vegetation, whereas alpine meadows are not pastures dominated by Cyperaceae and without mowing. The prevailing environmental conditions differed among these vegetation types (Online Resource 4, Fig. S2).

We collected the reported value for all vegetation or soil indicator from each independent experiment. When experiments were repeated for ≥2 years, we calculated the mean value for a given site because in perennial-dominated habitats, interannual variability in indicators is low except in biomass and cover (Wesche et al. 2010). When several experiments were carried out by different researchers for a given study “hotspot”, we treated them independently. We also considered experiments from different grazing seasons as being independent, because summer and winter pastures are subject to different grazing regimes and also typically differ in vegetation and micro-habitat conditions. When exclosure studies were continued for extended periods of time, we used data from the shortest exclosure period to exclude effects of long-term succession. All absolute values were directly extracted from the text and tables or digitized from clear figures with PlotDigitizer (http://plotdigitizer.sourceforge.net/). We deleted one dataset of extremely high AGB and BGB values, as the author did not mention whether values referred to dry weight, and we also excluded one dataset of highly implausible SOC data.

We started to examine grazing effects on vegetation and soil indicators by their absolute values, comparing them along all available grazing intensities. We sorted responses into six groups: neutral, negative, positive, unimodal, reversed-unimodal and fluctuating (see Online Resource 4, Fig. S3 for graphical explanation). Subsequently, we only focused on three grazing intensities, i.e. non-to-lightest, second heaviest and heaviest grazing (hereafter: light, moderate and heavy) in our main datasets. Because the absolute values of indicators varied tremendously among studies due to inconsistant sampling methods, we calculated site-based relative grazing effects as GE=(heavy−light)/light grazing, which is similar to that used in Milchunas and Lauenroth (1993). Similarly, we also analyzed datasets for GE1=(moderate−light)/light grazing, because some experiments might have employed unrealistically high levels of “heavy” grazing, which would have led to 100% removal of AGB. GE and GE1 thus indicate the relative changes in certain vegetation and soil indicators following heavy and moderate grazing compared to light grazing. Positive or negative values of GE or GE1 suggest that grazing increases or decreases the absolute values of the indicators, and larger values of |GE| indicate stronger grazing effects.

Besides qualitative grazing intensity, information on exact quantitative grazing pressures was limited as only a few studies reported livestock types, numbers and grazing duration. When those data were available, we converted different types of livestock into sheep units (SU) based on province-wise adoptions from the national standard (Ren 1998; Ministry of Agriculture of the People’s Republic of China, 2002; Xin et al. 2011): 1 yak=3 SU in Gansu and Sichuan, 1 yak=4 SU in Tibet and Qinghai and 1 cattle=6 SU in Xinjiang. In Inner Mongolia, authors directly reported livestock numbers in SU, so no conversion was needed. Grazing pressure was then calculated as SU x month/ha. We took AGB values from exclosures as the potential productivity. Results implied that grazing pressure increased with increasing productivity (Fig. 2), so “light” grazing in productive grasslands could be “heavy” in less productive grassland, which suggested absolute values of forage consumption among sites were incomparable. We therefore only considered qualitative grazing intensities in further statistical models. Procedures of data extraction are summarised in Online Resource 4, Fig. S4.

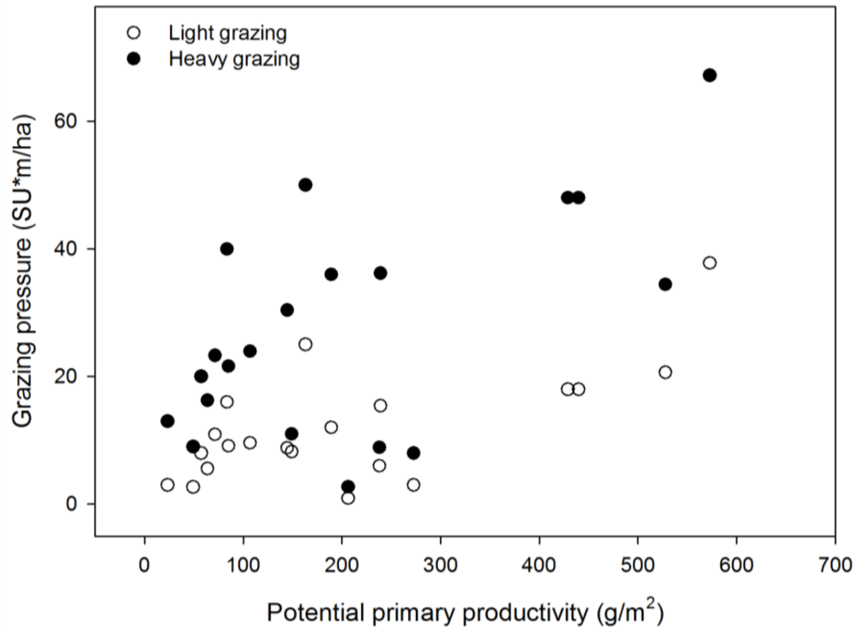

Fig. 2 Grazing pressures (sheep unit x month/ha) for light and heavy grazing employed in the literature, and their changes along the gradient of primary productivity (aboveground biomass obtained from the fenced-off plots).

2.3 Statistics

We did not choose the formal meta-analysis approach because we preferred to address ecological patterns rather than evaluate statistical significance. We neither deleted any statistical outliers for absolute values of indicators because those data were collected with different methods from diverse grazing systems where livestock types, topographic conditions and grazing management might differ. For absolute values of indicators, we 1) summarized the number of experiments showing neutral, negative, positive, unimodal, reversed-unimodal and fluctuating responses; 2) compared any pair from the three grazing intensities (light, moderate and heavy) by three sets of site-based paired t-tests (because multiple tests within the same dataset were not independent, we set the significance level at 0.05/3, i.e. $p < 0.015$ in accordance with Bonferroni corrections); 3) explored Pearson correlations between indicators and environmental factors for each grazing level. Further on, focused on relative grazing effects, we 4) tested influences of environmental factors (scaled to zero mean/unit variance) on grazing responses by multiple linear regression models. Interaction terms were not included because multiple environment-grazing interactions are difficult to be interpreted due to the lack of specific ecological hypotheses. We started with the full model including all environmental factors and obtained estimates of effects for each of them. Then we manually simplified the full model by progressively removing the least significant factor until we arrived at a null model. We compared the full model with all subsequently reduced models in an ANOVA framework by comparing the proportion of the explained variance. Based on

ANOVA results, we reported the minimum adequate model in which all the remaining predictors were significant. Models were visually assessed by residual plots for normality and variance homogeneity. We fitted specific linear models for each indicator since relative grazing responses were rarely linearly correlated (Online Resource 4, Table S1). All vegetation types were combined for multiple regressions because the uneven numbers of studies for each vegetation type will produce unreliable relationships. Analyses were performed in R (R Core Team 2015).

3. Results

3.1 Vegetation and soil responses to different grazing intensities

The majority of studies reported declining vegetation cover, AGB, BGB, SOC and tN under heavy grazing. Richness, soil tP and aP showed varying responses, while soil pH and BD mostly increased with increasing grazing intensity. Unimodal responses were mainly found for plant species richness, while inverse unimodal responses occasionally occurred for soil pH and aP. Only one study found no change at all (Table 1). Heavy grazing had an overall negative effect on R, cover, AGB and BGB, and a positive effect on soil pH and BD, while effects on rsRatio, tP and aP were not significant. Moderate grazing only affected cover, AGB, BD and SOC (Table 2).

Table 1 Numbers of experiments according to different grazing response types (see Online Resource 4, Fig S3 for graphical explanation). Richness=plant species richness, Cover=total vegetation cover, ABG=aboveground biomass, BGB=belowground biomass, rsRatio=root/shoot ratio, pH=soil pH, BD=soil bulk density, SOC=soil organic carbon, tN=soil total nitrogen, tP=soil total phosphorus, aP=soil available phosphorus, Sample size=total numbers of each response variable from all experiments

Response Trend	Negative	Positive	Unimodal	Reversed unimodal	Fluctuating	Neutral	Sample Size
Richness	23	12	21	5	6	0	67
Cover [%]	58	1	6	2	3	0	70
ABG [g/m²]	74	1	3	4	6	0	88
BGB [g/m²]	21	5	6	4	0	0	36
rsRatio	7	13	7	5	1	0	33
pH	6	14	4	9	2	0	35
BD [g/cm³]	6	28	8	4	2	1	49
SOC [g/kg]	51	10	8	1	1	0	71
tN [g/kg]	34	12	6	5	3	0	60
tP [g/kg]	12	11	3	5	5	0	36
aP [mg/kg]	10	6	4	7	1	0	28

Table 2 Values for indicators under different grazing intensities (mean [95% confidence interval]); different superscript letters indicate significant differences based on paired t-tests (Bonferroni-corrected at P value=0.05/3, abbreviations are the same as in Table 1 and sample sizes are indicated as N).

Mean [95% CI]	Light grazing	N	Moderate grazing	N	Heavy grazing	N
Richness	26 [23-30] ^{a}	67	31 [26-35] ^{a}	46	23 [20-27] ^{b}	67
Cover [%]	78 [69-87] ^{a}	70	71 [62-81] ^{b}	36	55 [46-64] ^{c}	70
AGB [g/m²]	202 [173-231] ^{a}	88	159 [126-191] ^{b}	46	106 [89-123] ^{c}	88
BGB [g/m²]	1751 [1330-2172] ^{a}	36	1633 [1157-2110] ^{a}	22	1187 [841-1532] ^{b}	36
rsRatio	8.1 [6.4-9.8] ^{a}	33	9.3 [5.2-13.4] ^{a}	19	10.1 [7.6-12.7] ^{a}	33
pH	7.2 [6.9-7.5] ^{a}	35	7.1 [6.7-7.4] ^{a}	25	7.4 [7.2-7.7] ^{b}	35
BD [g/cm³]	1.09 [0.99-1.20] ^{a}	49	1.16 [1.07-1.30] ^{b}	27	1.20 [1.11-1.30] ^{b}	49
SOC [g/kg]	68.92 [47.06-89.67] ^{a}	71	44.11 [36.90-51.60] ^{b}	38	49.5 [31.10-67.29] ^{c}	71
tN [g/kg]	4.68 [3.64-5.72] ^{a}	60	3.72 [2.92-4.51] ^{ab}	35	3.82 [2.99-4.66] ^{b}	60
tP [g/kg]	0.74 [0.53-0.94] ^{a}	36	0.83 [0.59-1.06] ^{a}	23	0.65 [0.50-0.81] ^{a}	36
aP [mg/kg]	8.02 [5.34-10.69] ^{a}	28	8.32 [5.73-10.91] ^{a}	25	6.81 [4.73-8.90] ^{a}	28

3.2 Correlations among environmental, soil and vegetation variables

Precipitation was strongly positively associated with vegetation cover, soil tN and tP, while it was negatively associated with soil BD and pH for light and heavy grazing both (Online Resource 4, Table S2). Soil organic carbon only increased with precipitation under light grazing. As precipitation was negatively correlated with cvP, relationship between indicators and cvP essentially showed qualitatively similar but reciprocal pattern. Temperature and elevation were not correlated with any indicator.

Within the vegetation or soil indicator group, specific variables were mostly linearly correlated (Online Resource 4, Table S2). Plant species richness showed no correlation with any other indicator, presumably because inconsistent plot sizes made the absolute values incomparable. Aboveground biomass and cover were always positively correlated, same as for BGB and rsRatio, and BGB also correlated with AGB and cover under heavy grazing. Soil indicators showed similar patterns under both grazing levels: soil BD was negatively correlated with SOC and tN; SOC and tN were positively correlated; soil tP and aP were not correlated.

Correlations between soil and vegetation indicators were weaker for heavily grazed sites in comparison to lightly grazed sites (Online Resource 4, Table S2). Under both grazing levels, richness showed no correlation with any of the soil indicators, cover was positively related to SOC, tN and tP, but negatively to soil BD. AGB behaved in a similar way to cover and showed closer correlations with SOC and tN under heavy grazing. Available P was not correlated with any of the vegetation indicators.

3.3 Dependence of grazing effects on the local environment

Given that absolute values for indicators are affected by methods of sampling and measurement used by different authors, relative changes in vegetation and soil variables caused by heavy or moderate grazing may provide less biased information. Grazing responses of specific indicators did not differ much among vegetation types as we expected (Fig. 3), so we pooled all vegetation types together for the analyses.

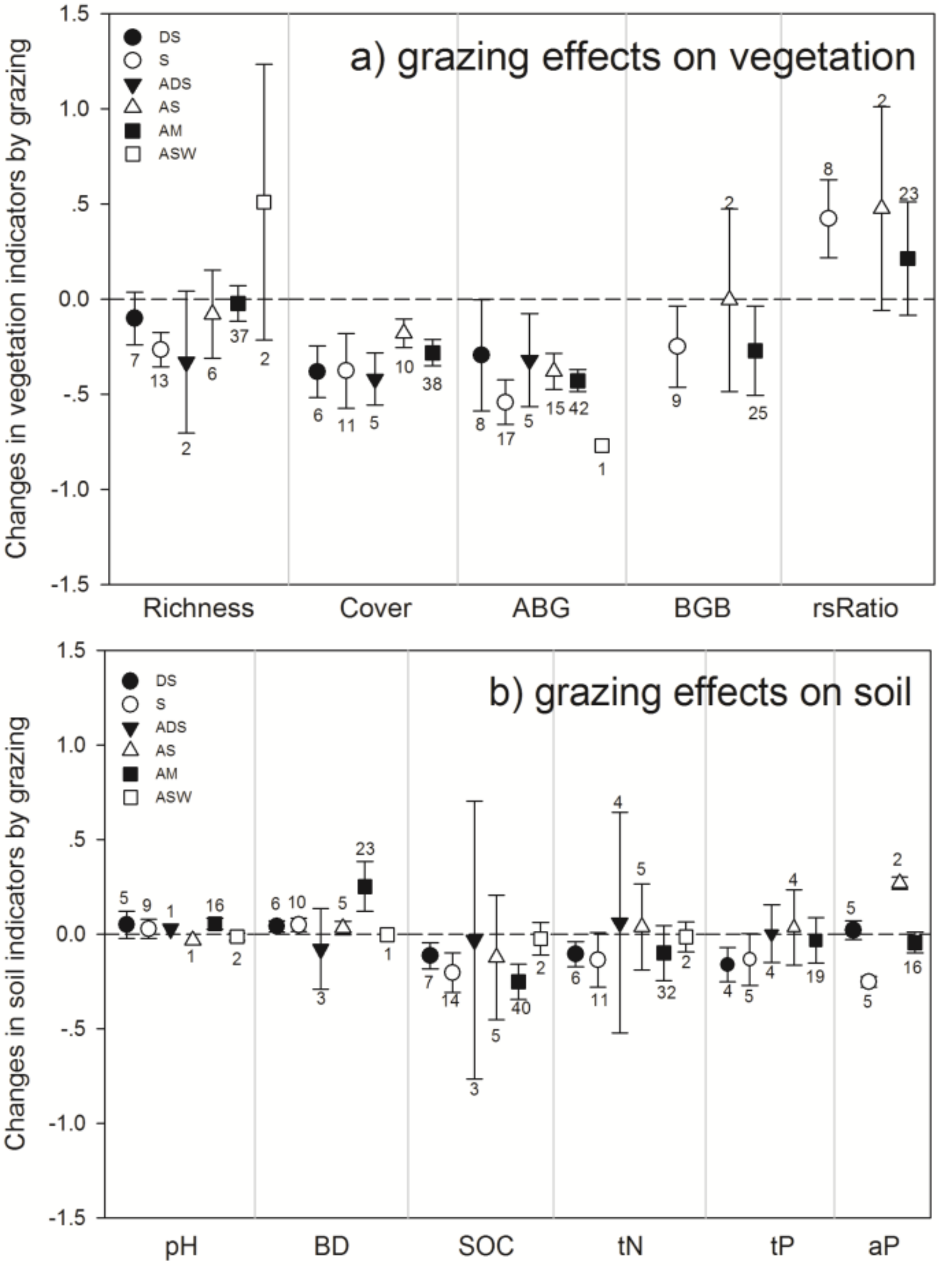

Fig. 3 Relative grazing effects on a) vegetation, b) soil indicators from different vegetation types (symbols abbreviations are the same as in Fig. 3). Error bars indicate standard deviation and numbers close to the error bars represent sample sizes.

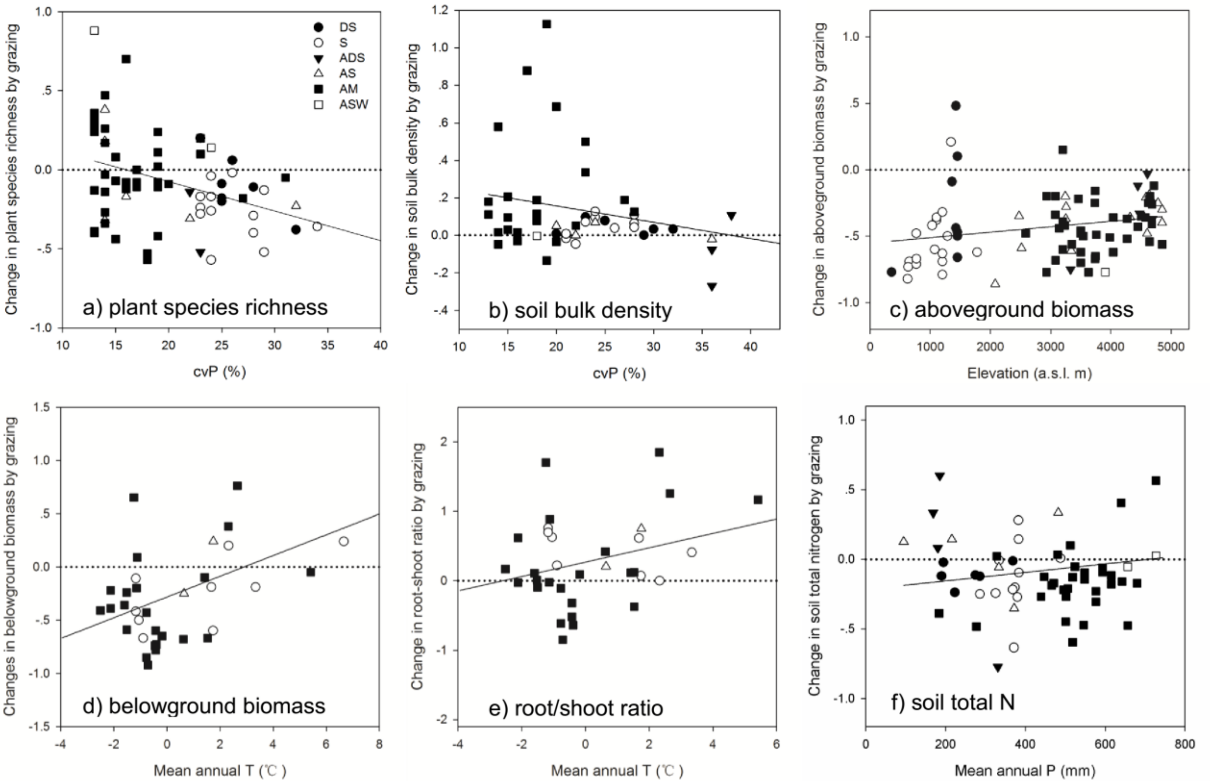

Fig. 4 Relative changes in a) plant species richness, b) soil bulk density, c) aboveground biomass, d) belowground biomass, e) root / shoot ratio and f) soil total N on heavily grazed sites compared to lightly grazed sites along dominant environmental gradients (in accordance with results from Table 3; abbreviations for vegetation types: DS=desert steppe, S=steppe, ADS=alpine desert steppe, AS=alpine steppe, AM=alpine meadow, ASW=alpine swamp).

Under heavy grazing, vegetation cover, soil pH, SOC, tP and aP did not respond to any environmental factors. Plant richness could be increased or decreased by grazing when cvP was low, but it was only decreased when cvP were high (Fig. 4a). Increase in soil BD was most when cvP was around 20%, and grazing effects were weaker when cvP increased (Fig. 4b). The negative grazing effects on AGB tended to be weaker at higher elevations (Fig. 4c) but stronger at wetter sites (Online Resource 4, Fig. S5). Responses in BGB changed from negative to positive with increasing temperature (Fig. 4d), which was in line with grazing responses of the rsRatio (Fig. 4e). Grazing responses of soil tN tended to be stronger when precipitation increased (Fig. 4f). Analysis for moderate grazing yielded qualitatively similar patterns of R, cover, BGB, SOC, pH and BD. But the effects of abiotic factors on grazing responses of tN disappeared, and precipitation patterns affected grazing responses of AGB, rsRatio and aP (Table 3).

Table 3 Summary of the minimum adequate linear models for environmental effects on relative grazing responses under heavy grazing (GE dataset) and moderate grazing (GE1 dataset) conditions. Abbreviations for vegetation, soil indicators and environmental factors are the same as in Table 1. Statistical estimates of coefficients and standard errors (se) were given for the significant environmental factors. Significance levels: † 0.1, * 0.05, ** 0.01, *** 0.001.

	Heavy grazing						Moderate grazing					
	Elev	T	P	cvP	Adjusted R^2	Df	Elev	T	P	cvP	Adjusted R^2	Df
Richness				-0.13**	0.12	65			0.09*	-0.09†	0.37	43
se				0.04					0.04	0.05		
Cover												
se												
AGB	0.11***		-0.06*		0.08	85				-0.05*	0.06	44
se	0.03		0.03							0.02		
BGB		0.28*			0.12	34		0.24*			0.14	20
se		0.12						0.11				
rsRatio		0.30†			0.06	31				0.28*	0.22	17
se		0.17								0.12		
pH												
BD				-0.08*	0.08	47			0.08†		0.08	25
se				0.03					0.05			
SOC												
se												
tN		0.12*	0.23**	0.18*	0.16	56						
se		0.05	0.07	0.07								
tP												
aP								0.17†	0.21*		0.15	22
se								0.1	0.09			

4. Discussion

Our results demonstrate strongly variable responses of vegetation and soil indicators to both the local environment and the intensity of livestock grazing in temperate Chinese grasslands. Only some grazing indicators showed generally negative responses, and even in these cases, environmental conditions still influenced the magnitudes of grazing effects.

4.1 Vegetation responses

Plant species richness is one of the most widely used grazing indicators as it reflects long-term responses, especially in grasslands dominated by perennial species such as those of Central

Asia (Lavrenko and Karamysheva, 1993; Wesche et al. 2010). We found both increased and decreased richness in relatively stable environments but mainly negative responses under highly variable (cvP) conditions, where the productivity is usually lower. This pattern partly confirms general trends: grazing tends to have no or slightly negative effects on richness at less productive sites, while at productive sites, moderate grazing may increase richness (Milchunas and Lauenroth 1993). However, we could not clearly distinguish whether richness responses were directly affected by cvP or indirectly controlled by productivity, because there is a positive linear correlation between richness and productivity for Chinese steppes (Bai et al. 2007).

Not surprisingly, heavy grazing reduced both overall plant cover and AGB (42% [95% Confidence Interval: 37%–47%]) and BGB (28 % [95% CI: 11%–45%]), which is in line with the results of a meta-analysis from similar regions (Yan et al. 2013). Observed changes of residue AGB did not support the grazing optimization hypothesis, which predicts the highest productivity at intermediate grazing intensity because of compensatory growth (McNaughton, 1979). Nevertheless, we highlight a commonly overlooked methodological problem: residual AGB harvested from grazed sites is not equal to the potential primary productivity, so reduced AGB and cover on grazed sites may only show the occurrence of grazing but do not necessarily indicate that grazing has negative effects on productivity. Interestingly, the grazing-induced reduction in AGB seemed to decrease with increasing elevation, especially in alpine grasslands. The difference in plant community properties might explain this pattern. From relatively low to higher elevations, grass-sedge mixed grasslands change to *Kobresia*-dominated alpine pastures, where most plant individuals are tiny in size, so very low AGB are accessible for livestock (Hafner et al. 2012). This idea is supported by the lower AGB at higher elevation sites in alpine grasslands (Online Resource 4, Fig. S6c). We also found that grazing effects on AGB become stronger under higher precipitation levels, indicating that herders may increase livestock numbers at more productive sites and thus the amount of forage consumption might be higher. Vegetation cover and soil nutrients were positively correlated under light and heavy grazing conditions, so reductions in vegetation cover may increase the loss of soil organic matter and speed up soil erosion (Trimble and Mendel 1995; Wang et al. 2003).

Negative grazing effects on BGB have been reported in the studied regions and other dry grasslands (Pandey and Singh 1992; Gao et al. 2008; Cheng et al. 2011a), but there are also positive examples (Milchunas and Lauenroth 1993; McNaughton et al. 1998). Grazing might increase BGB because higher BGB could facilitate nutrient uptake at humid sites, or water uptake at dry sites (Burke et al. 1998; Piñeiro et al. 2010). Higher biomass allocation to roots (Gao et al. 2008) or species composition shifts at community level (Derner et al. 2006) could both increase BGB. Grazing responses in BGB positively correlated with grazing effects on rsRatio and soil nutrients (Online Resource 4, Table S1), indicating that root systems play a crucial role in nutrient cycling in the studied grasslands. Moreover, heavy grazing resulted in notably high rsRatio with higher temperatures (Online Resource 4, Fig. S6e), suggesting that both aridity and grazing could favor species with high rsRatio (Coughenour 1985). Changes in BGB and rsRatio may therefore reflect long-lasting effects, and they are presumably more reliable grazing indicators than AGB or plant cover alone.

4.2 Soil responses

Soil indicators respond more slowly than AGB and cover to grazing, and are thus often seen as reliable indicators of grazing degradation. Our results showed complex response patterns for soil indicators. In many cases, soil BD increased under grazing. Under moderate moisture contents (i.e. intermediate cvP), trampling usually reduces soil pore volume (especially for big pores) and leads to higher BD. Increased BD might result in further nutrient loss, as showed by negative correlations of both SOC and tN with soil BD. In drier areas where cvP values were high, grazing could cause erosion of silt and small sand particles (He et al. 2011). The remaining soils with high proportions of bigger sand grains are not easily compacted by trampling, so soil BD is less affected by grazing. Grazing effects on soil pH were mostly positive and not sensitive to any climate variable. Higher pH values in areas of higher grazing pressure (Milchunas and Lauenroth 1993; Bardgett et al. 2001; Mikola et al. 2009) could be related to urine deposition (Haynes and Williams 1992) or changes in plant community composition (Semmartin et al. 2010).

SOC responses showed no clear pattern along abiotic gradients. Negative grazing effects on SOC are found in Central Asian grasslands where mean annual precipitation is less than 600 mm (reviewed in McSherry and Ritchie 2013; Xiong et al. 2014), but also in northwestern Sichuan where precipitation is higher than 600mm (Luan et al. 2014). Consumption of AGB by grazers and reduction of C pool in AGB and litter could lead to direct C loss (Bai et al. 2012). Reduced BGB may also reduce SOC, as suggested by the positive correlation between grazing responses of SOC and BGB. However, knowledge gaps on soil texture, plant functional type, soil microbe community composition and activity (Hassink 1994, Sankaran and Augustine 2004; Klumpp et al. 2009; McSherry and Ritchie 2013) confound clear explanations of the complex responses.

The amount of available N (NO_3^- and NH_4^+) changes quickly over time, and reliable measurements require standardized repeated sampling. Considering the available data, we only took soil tN as a crude indicator for potential N availability. The observed reductions of tN probably were caused by grazing management. Livestock take up nutrients across grasslands but release them in a few hotspots close to camps and overnight places (Holst et al. 2007). Moreover, local nomads collect dung as fuel for heating and cooking, which leads to further nutrient losses. The reductions in tN tended to become less severe or even changed to positive as precipitation increased (Fig. 4e), indicating climate variability and grazing intensity interactively impact on soil nutrient cycling (Giese et al. 2013). Similar to SOC, N dynamics involve complicated decomposition procedures and are influenced by plant community (Seagle et al. 1992; Knops et al. 2002), litter quality and quantity (Semmartin et al. 2004; Bai et al. 2012), soil microbes (Bardgett and Wardle 2003; Wardle and Bardgett 2004; Yang et al. 2013; Stark et al. 2015) and soil physical properties (Wang et al. 2010). Unfortunately, such information was limited in the studies reviewed.

The grazing response of soil P, especially aP, is less well studied, even though it may be a major limiting factor for plant growth, and especially in *Kobresia* meadows (Dong et al. 2012). The aP is usually low due to slow diffusion and high fixation in soil and the P dynamics in the soil/rhizosphere–plant continuum (Shen et al. 2011). We did not find any consistent grazing effects on soil tP or aP. There was only a slight trend for more negative responses at wetter sites compared to drier sites (Fig. 3f). However, the exceptionally strong increase of aP at the wettest site pointed out that grazing could also accelerate P cycling under certain conditions. We also found a positive correlation between relative grazing responses of aP and tN, indicating soil N and P dynamics are coupled, which holds true for many other terrestrial ecosystems (Marklein and Houlton 2011). The unclear pattern also reflects the difficulties in measuring the relatively low contents of aP in grassland soils. Again, further studies considering more relevant factors are required for better explanations.

5. Conclusions and Outlook

Our review revealed complex responses of vegetation and soil indicators to livestock grazing on the QTP and northern Chinese grasslands. Not surprisingly, grazing effects strongly depend on the indicators being evaluated and where and how the assessments take place. Sound and standardized methodologies should be adopted with respect to specific characteristics of different indicators. Although we already covered a wide range of published studies, a main shortcoming of our review is the lack of socio-economic aspects, which are also critical to grassland health (Yan and Wu, 2005; Yan et al. 2005; Cao et al. 2011; Fu et al. 2012; Cao et al. 2013b). We highlight that conclusions derived from vegetation cover and residue AGB should be treated with great care because they show prominent but not reliable signals, as they were largely collected from grazed sites without exclosures. Plant species richness should ideally be assessed with soil indicators; plant-soil-microbe interactions should be further studied to understand nutrient cyclings.

Local abiotic conditions must be considered together with grazing effects because environment, especially climate, interacts with grazing effects. In many cases, grazing effects shift from positive to negative along e.g. precipitation gradients. Grazing also modifies the correlations between vegetation and soil indicators. Although the observed patterns are not novel and are mostly well-rooted in theories of rangeland science, the apparent complexity and uncertainty are not always fully appreciated. Local-level management should therefore acknowledge spatio-temporal variations and traditional adaptations of pastoralists.

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Chapter 4 Responses of vegetation and soils

Combined effects of environment and livestock grazing on plant community and soil condition across Tibetan grasslands

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Abstract

Questions Inconsistent responses of plant communities and soil conditions to livestock grazing have been widely reported from various grassland systems. While abiotic factors such as climate and topography evidently influence resource availability for plants and affect soil nutrient cycling processes, the role of grazing-environment interactions on plants and soils has scarcely been studied. In order to test the hypothesis that grazing effects are stronger in more humid and productive regions, and to assess the role of climate in relation to grazing effects in semi-arid regions, we conducted a field study on Tibetan grasslands, as they are of global ecological importance and they exhibit broad climatic and elevational gradients.

Location Twenty-eight sites across the Tibetan Plateau

Methods We examined the effects of livestock activity (piospheres with excessive trampling and nutrient input, and heavy to light grazing) and habitat (meadow, steppe, steppe-meadow) and their interactions with respect to plants (species composition, richness, diversity, functional groups) and soils (organic carbon – SOC, total nitrogen–tN and other nutrient concentrations) by performing multivariate analyses and testing Generalized Mixed Linear Models (GLMM). Major environmental factors included precipitation, temperature and elevation. Plant indicator species sensitive to grazing were also indentified.

Results Livestock activity had significant effects on plant species composition and overall soil fertility across habitats. However, effects were only pronounced in piospheres directly adjacent to herders' camps, and were not related to grazing intensification. Increased annual species and reduced SOC and tN were found under heavy grazing in meadows. The environmental factors that control plant communities and soil conditions differed and varied among habitats. Plant-soil interactions were more pronounced in steppes and steppe-meadows than in alpine meadows.

Conclusions Livestock intensity has a strong effect on plants and soils in Tibetan grasslands, but effects are mainly confined to piospheres around herder camps. Among all tested vegetation characteristics, only annual species in meadows are responsive to intensified grazing, and several plant species are identified as being suitable for monitoring local mechanical disturbance. Across the grassland habitat as a whole, plant species compositions and soil condition are weakly affected by intensified grazing compared to that shaped by environmental conditions, which refutes the broadly held perception that increased grazing leads to grassland degradation. Such differing soil-plant relationships between similar habitat types highlight the importance of local nutrient cycling trends and emphasises the need to consider local abiotic factors in future grassland studies.

Keywords

Richness; composition; nutrients; alpine meadow; steppe; gradient; precipitation; elevation; organic carbon

Nomenclature

eFloras (2008) Missouri Botanical Garden, St. Louis, MO & Harvard University Herbaria, Cambridge, MA. [online] Available at: http://www.efloras.org (accessed Jan 2014)

1. Introduction

Grasslands cover approximately 40% of the Earth's terrestrial area (excluding Greenland and Antarctica) and support a large diversity of biota and human culture (White et al. 2013). Livestock grazing represents the dominant land use in grasslands across the world, where it forms the basis of local livelihoods (Bone et al. 2015; Kelaidis 2015). Several reviews have summarized grazing effects on vegetation and soil conditions and suggest that environmental factors (particularly climate and topography) and grazing histories interactively modify the effects of grazing on grasslands (Milchunas et al. 1988; Hobbs & Huenneke 1992; Milchunas & Lauenroth 1993; Greenwood & McKenzie 2001; McSherry & Ritchie 2013; Schrama et al. 2013). From the perspective of non-equilibrium theory (Illius & O'Connor 1999; Sullivan & Rohde 2002; Vetter 2005), climate factors (typically precipitation patterns) often override grazing impacts on plant communities, and especially where precipitation levels are low but highly variable, such as in Africa (Oba et al. 2003; Hanke et al. 2014) or Central Asia (Fernandez-Gimenez & Allen-Diaz 1999; von Wehrden et al. 2012). However, a long evolutionary history of grazing in arid grasslands can lead to grazing tolerance (Burke et al. 2008; Milchunas et al. 2008).

The main effects of grazing on soil condition arise from mechanical disturbance by livestock (Frank & Evans 1997; Schrama et al. 2013) and, indirectly, via grazing-induced changes in plant communities. Plants represent the main contributors of soil organic carbon (SOC) and they determine litter quality and quantity, both of which affect soil nitrogen (N) cycling (Piñeiro et al. 2010; McSherry & Ritchie 2013; Schrama et al. 2013). Moreover, soil-plant feedback processes trigger more complex responses and interactions between other biotic and abiotic factors (Soussana et al. 2004; Burke et al. 2008).

Grazing effects on plants and soils have been widely investigated in Tibetan grasslands, as local grassland degradation has been overwhelmingly attributed to overgrazing among all possible reasons (Akiyama & Kawamura 2007; Cao et al. 2013; Chen et al. 2013; Wang et al. 2015). As one of the world's largest grassland regions, Tibet hosts extensive elevational and climatic gradients along with an evolutionary history of grazing (Miehe et al. 2009; Miehe et al. 2014), the combination of which provide a unique platform for studying interactions between environmental factors and grazing intensity. Grassland vegetation is mainly constrained by stable and relatively low temperatures in the east, while low yet highly variable precipitation levels exert a stronger influence in the centre and western extents of the region (Chang 1983). A history of inconsistent methodologies, including in the definition of degradation and in the standards adopted for assessments, make the various estimates of degradation threat attributable to grazing questionable at best, while environmental influences have been largely overlooked (Harris 2010; Wang & Wesche 2016).

The interactive effects of grazing and environment can typically be studied by sampling along large-scale gradients, or through field experiments that control certain abiotic conditions. While several large-scale field investigations on vegetation and soils of Tibetan grasslands have revealed environmental impacts (Wang et al. 2008; Yang et al. 2008; Liu et al. 2012), such studies have rarely considered the influence of grazing. The few exceptions have been based on only single-site approaches (Wen et al. 2013; Dorji et al. 2014; Luan et al. 2014), and there is only one regional example from central Tibet (Wu et al. 2012). As an alternative to field studies, remote sensing or modelling can help disentangle grazing and climate effects (Gao et al. 2009; Chen et al. 2013; Chen et al. 2014), however, data have often not been properly calibrated with field data at the given scale (Lehnert et al. 2015; Xu & Guo 2015), resulting in greater uncertainty of results. With respect to smaller-scale or single-site studies, the majority of them overlooked abiotic influences (Wang & Wesche 2016), with only a few, i.e. those that simulated grazing and controlled the microclimate, having detected grazing and climate effects on plants (Klein et al. 2004, 2008) or soils (Rui et al. 2011). Unfortunately, the typically limited duration of such experiments (~4 years) brings into question whether slow responses of perennial plant species and soils could be detected. In addition, the oft-applied methodology of clipping without trampling or dung return might not well represent natural grazing conditions (Li et al. 2015). Finally, while indicator species identified in field (Sasaki et al. 2011; Mathar et al. 2015) are valuable from the perspective of applied ecological monitoring and grassland management, formal analyses of such on Tibetan pastures are scarcely available (Miehe et al. 2011).

To summarise, current knowledge on livestock grazing impacts on Tibetan grasslands is insufficient to form a reliable foundation for devising appropriate strategies for effective management and conservation. As such, for the present study we focused on plants, as they play a pivotal role in ecosystem functioning by producing forage and connecting different trophic levels, and soils, as they are fundamental to sustaining productivity and adjusting the nutrient cycling. We opted for the piosphere approach, which can represent both cumulative and historical grazing pressures (Adler & Hall 2005), because long-term grazing exclosures are scarce in our study region and maintaining ungrazed conditions within fenced off areas over the long term may be unrealistic in a region with such a long history of grazing as Tibet.

With respect to our study sites (Table S1), we stratified them into three habitat types in accordance with a published vegetation map (Hou 2001) and field observations: 1) Steppes, which include alpine steppes dominated by *Stipa* species in western Tibet along with more temperate steppes dominated by other grasses in parts of Qinghai (Sheehy et al. 2006); 2) (Sub-) alpine meadows (hereafter meadows), which typically comprise *Kobresia-Carex* species and prevail along the eastern plateau, and 3) Transitional steppe-meadows, which have similar environmental histories as meadows, but which host plant communities distinct to those found in the other two habitat types (Fig. S1). It should be noted that steppe-meadows are different from the typical Mongolian meadow steppes (Hilbig 1995).

The following hypotheses were specifically tested:

1) Grazing responses of plant communities vary among habitat types due to environmental interactions, with grazing effects being more pronounced in moist meadows than in steppes.

2) Intensified grazing reduces SOC and N contents (in accordance with our previous review: (Wang & Wesche 2016), while precipitation tends to interact with grazing effects as a result of positive plant-soil feedback.

2. Methods

2.1 Sampling strategy

The direct measuring of grazing intensity in the field is complex and time-consuming, and in any case the prevailing grazing intensity recorded at any point in time may not correspond to the conditions under which the extent vegetation became established. Livestock numbers from statistical reports, while valuable, fail to represent site-level grazing intensities, because they often originate from surveys covering larger administrative units, and data at the individual pasture level is consequently lacking. As such, for the present study we sampled along local grazing gradients (hereafter piospheres), which radiated in different directions from features identified as grazing hotspots, such as water sources, camps or settlements, in the assumption that grazing pressure decreases with increasing distance from the grazing hotspot. Distance from a grazing hotspot has been widely tested as a proxy for grazing intensity in various grassland systems with long pastoral histories (Fernandez-Gimenez & Allen-Diaz 2001; Manthey & Peper 2010; Haynes et al. 2012), although prevailing grazing intensities may not always be captured by this method (Dorji et al. 2013). Based on this concept, we identified 28 sites (grazing hotspots) and qualitatively established various plots at each site (173 plots in total) which delineated four levels of livestock activity with respect to the distance from the grazing hotspots (in our case camps): 1) P – piospheres with high levels of nutrient input and mechanical disturbance by trampling of (resting) livestock. Piospheres were distinguished from the other plots in that livestock did not freely move around to forage, and only grazed very lightly in place where possible; 2) H – heavily grazed plots relatively close to camps where livestock moved and foraged, but within a small area; 3) L – relatively lightly grazed plots where herds spread over a larger area relatively far from the camps; 4) M – moderately grazed plots were located between and roughly equidistant from heavily and lightly grazed plots.

At each of the sampling sites, each plot was sampled one to eight times depending on the local grazing range and field conditions, and at least one pair of heavily and lightly grazed plots was compared (Table S1). Plots were neither balanced among habitats nor among levels of livestock activity. We also counted yak, sheep, goat and horse droppings from three randomly placed quadrats (1x1 m^2) at each plot and calculated total dung cover (%) to validate recent livestock activity.

2.2 Sampling of vegetation and soil indicators

We estimated the cover of vascular plant species in 10x10 m^2 plots and assigned them to six plant functional groups (annual forb, perennial forb, grass, sedge, legume or shrub). Plant specimens were identified according to eFloras (2008) and related works, and cross-checked in the Herbarium (KIB, CAS). Difficult taxa were sent to specialists (see acknowledgements). Shannon diversity, dominance and evenness indices were also calculated using Past (Hammer et al. 2001).

Three samples of topsoil (0–5 cm) were collected from each plot and mixed, air-dried, sieved (2 mm) and separated from litter, roots and debris for lab analyses. Electrical conductivity (EC) and pH were measured with a pH/EC meter (water: soil volume=5:1). Total carbon (C) and nitrogen (tN) concentrations were analyzed using a CN-Analyser (Vario Pyro Cube Elementar, GmbH, Germany). Inorganic C ($CaCO_3$) content was determined with 10% HCl to correctly derive SOC. Plant available phosphorus (aP), calcium (aCa), magnesium (aMg) and potassium (aK) were extracted with an adopted Olsen–P method (22 °C, 200 r/min for 30 min, (Sims 2000)) and measured with ICP-OES (Varian 725-ES, Stadt, Australia). All results refer to oven-dried soil (75 °C, 18 h).

2.3 Extraction of environmental factors

Based on the coordinates of the lightly grazed plots, climate factors including mean total annual precipitation (P, mm), mean annual temperature (T, °C) and mean annual short-wave radiation (srad, w/m^2) were extracted from the China Meteorological Forcing Dataset (CMFD, spatial resolution 0.1 °, 1979.01.01-2012.12.31; (Chen et al. 2011; He & Yang 2011)). From the 3h-interval temperature data, we calculated average accumulated temperatures above 0 °C (acT0), 5 °C and 10 °C along with the corresponding number of days, the average temperature of the warmest and coldest months and the difference between these two temperatures (yearTdiff). The coefficient of interannual variation of precipitation (cvP, %) was also calculated. Plot-level temperature related variables were adjusted to elevation by assuming a lapse rate of 0.6 °C/100 m at a given site. Plot-level topographic conditions, including longitude (Lon), latitude (Lat), elevation (Elev), inclination (incli), relief conditions and aspect (expressed by northness=North and eastness=East), were also considered.

2.4 Statistical analyses

NMDS and PCA ordinations were separately performed to derive the potential explanatory variables for plant species composition and overall soil fertility (SOC, tN, aP, aCa, aMg, aK) based on Bray-Curtis dissimilarity and Euclidean distance respectively. Species cover values were log(x+1) transformed to down-weight the most abundant species. Soil chemical concentrations were log(x+1) transformed and standardized to zero mean/unit variance. Any redundancy of climate factors was defined by a correlation matrix PCA incorporating all continuous environmental variables, with 11 factors (P, cvP, acT0, yearTdiff, srad and Lon, Lat, Elev, East, North incli) being fitted into ordination axes by *post hoc* Pearson correlation and displayed where $P < 0.001$ (according to 9999 permutations). Similarity among plant species composition and soil fertility in multivariate spaces was compared using a Procrustes test. Effects of livestock activity, habitat and their interaction were then explored by way of multivariate permutation MANOVA. All multivariate analyses were performed across and within habitats.

Generalized Linear Mixed Models (GLMM) were fitted to test fixed effects of livestock activity, habitat and their interaction on specific plant and soil indicators; site was nested within habitat and treated as a random factor. A Poisson distribution was assumed for species richness (counts), while a Gaussian distribution was applied for other response variables (Crawley 2007). We progressively simplified full models by removing interactions as well as the main effects of habitat and livestock activity until the null model was achieved. We then compared these models with likelihood ratio tests to derive *P* values. Homoscedasticity was visually examined from residual plots. Multiple Tukey HSD tests were performed to compare differences among four levels of livestock activity within each habitat. We further checked Pearson correlations between the variables of vegetation, soil and environment. Finally, we investigated plant indicator species by way of Indicator Species Analysis (Dufrêne & Legendre 1997) within habitats.

Analyses were all made in R (R Core Team 2015) with the packages lme4 (Bates et al. 2015), vegan (Oksanen et al. 2010), multcomp (Hothorn et al. 2008) and indicspecies (De Caceres & Legendre 2009). We reported uncorrected *P* values throughout since our main goal was to initially screen for potential conservation problems (Roback & Askins 2005).

3. Results

We generated a total of 5,538 vascular plant records, corresponding to 626 taxa (185 genera/46 families). The distance-based livestock activity gradient was confirmed by estimates of total dung cover, which decreased with increasing distance from camps ($P = 0.03$, Kruskal-Wallis rank sum test).

3.1 Vegetation response

Livestock activity altered plant species compositions, but strong differences were only found within piospheres (Fig. 1a, Table 1) in both meadows and steppe-meadows (Fig. S3a-b). Commonly important environmental factors included srad, Lon and Elev across habitats, while some factors were only influential for certain habitats, namely P for meadows and steppes, inclination and acT0 for meadows and steppe-meadows, and latitude for steppe-meadows and steppes (Fig. S3a-c).

Table 1 Effects of grazing and main habitat class on plant species composition and soil fertility based on two-way multivariate significance tests (Permutation MANOVA) for the full dataset. Dissimilarity measurements and data transformation were adjusted according to data properties. Significance levels are indicated (*) $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ (No. of permutations=9999).

		Livestock activity	Habitat	Livestock activity*Habitat	Residuals	Total
Plant species composition *[Bray-Curtis, log(x+1)]*	Df	3	2	6	161	172
	F	2.21	11.72	0.96		
	R^2	0.03	0.12	0.03	0.82	1
	Pr (>F)	***	***	(*)		
Soil fertility *[Euclidean, log(x+1) then z-standardized]*	F	8.12	35.64	0.89		
	R^2	0.09	0.27	0.02	0.61	1
	Pr (>F)	***	*			

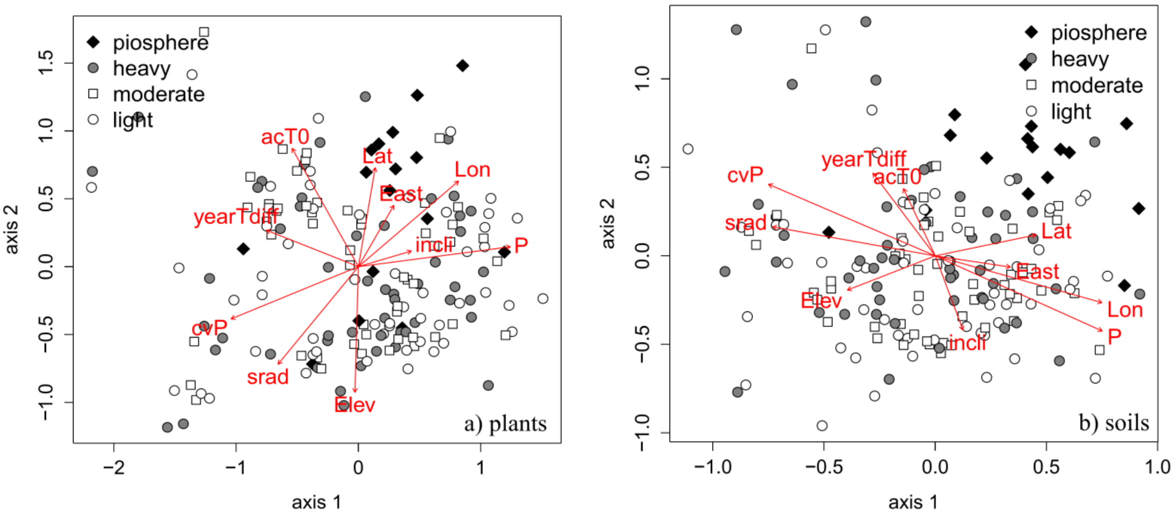


Fig. 1 Exploratory multivariate analyses across habitats: a) NMDS for plant species cover (173 plots, 626 species, log(x+1) transformed to down-weight the abundant species with Bray-Curtis dissimilarity, stress for 2D-solution=0.23), and b) PCA for soil fertility (SOC, tN, aP, aCa, aMg and aK, log(x+1) followed by centring and standardising, eigenvalue/explained variance: PC1=3.82/63.7%, PC2=1.03/17.1%). Environmental vectors were-best fitted by *post hoc* correlation to the first two ordination axes (No. of permutations=9999, threshold for plotting $P < 0.001$).

Strong effects of livestock activity on richness and cover of most functional groups were confirmed by GLMM (Table 2). However, multiple comparisons (Fig. 2) showed that these effects were again mainly restricted to piospheres; meadows showed negative effects on total richness, vegetation cover, and richness of perennial forbs but positive effects on richness and cover of annual forbs; steppe-meadows showed negative effects on Shannon diversity, relative cover of grasses (Fig. 2a) and sedges. Heavy grazing increased both richness and cover of annual forbs compared to that of light grazing. The highest cover of sedges was found under moderate grazing.

3.2 Soil responses

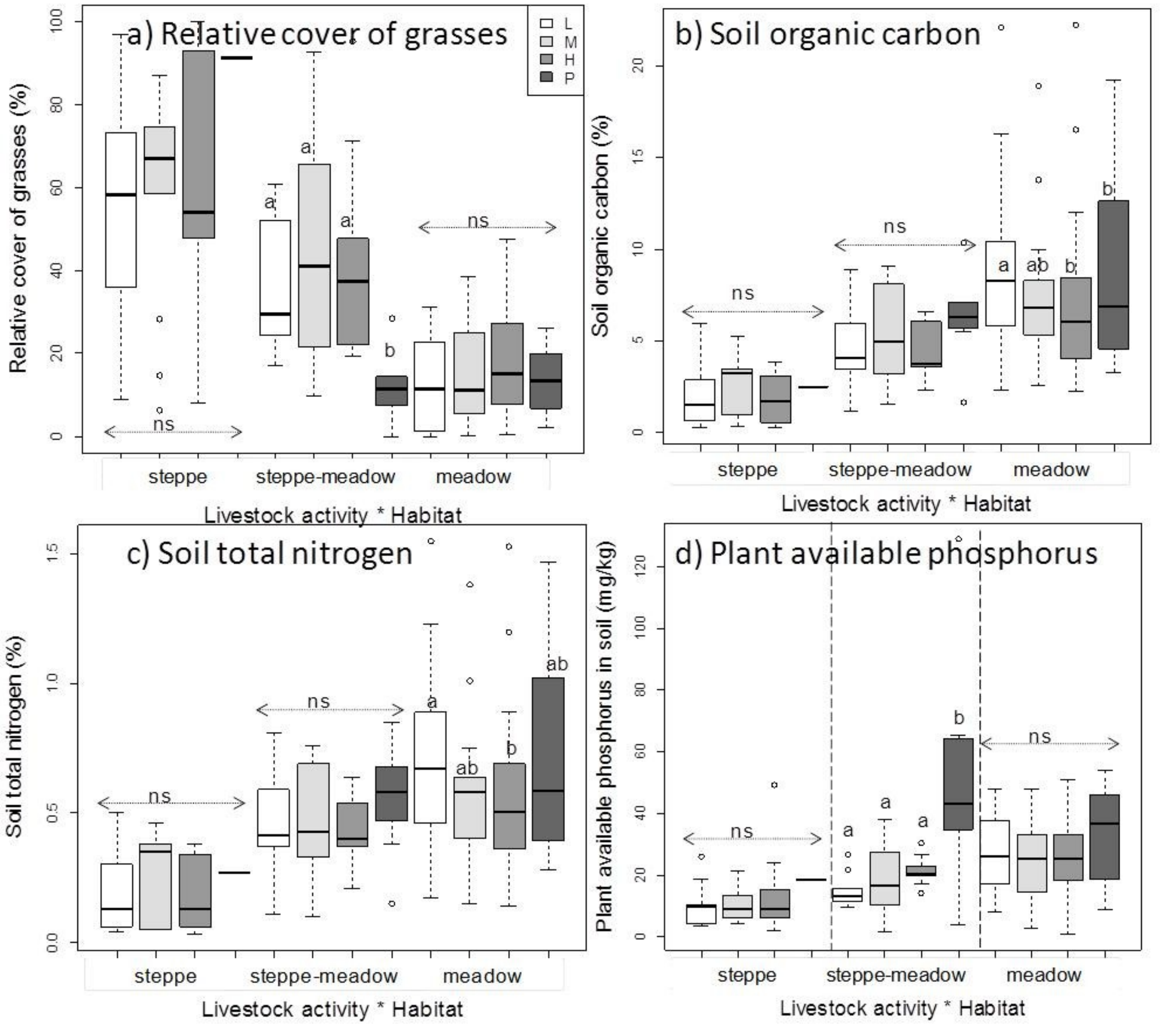
Both livestock activity and habitat showed independent effects on the overall soil fertility (Table 1), and piospheres were again the most distinct areas. Across habitats, abiotic controls were similar to those for all plant species compositions (Fig. 1b). However, within habitats, environmental influences were much stronger in steppes than in the two other habitat types; Lon and srad were important for meadows, while East, North and yearTdiff mattered in steppe-meadows and steppes (Fig. S3d-f).

Table 2 Effects of livestock activity, habitat and their interaction on plant and soil indicators according to GLMM results (Poisson model for counts, otherwise Gaussian). Significance levels were obtained by performing likelihood ratio tests and comparing progressively simplified models by removing the effects in question until the null model was achieved; levels indicated by (*) $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Indicators with both significant effects of livestock activity and their interaction are underlined and shown in Fig. 2 (except soil EC because of the non-normal distribution of original data) along with results of Tukey HSD multiple comparisons among the four levels of livestock activity.

		Livestock activity		Habitat		Livestock activity *Habitat	
Indicators	Transformation	*P*-value		*P*-value		*P*-value	
Total vegetation cover (%)		.	.	<0.001	***	<0.001	***
Relative cover of							
annual forbs (%)	rank	<0.001	***	.	.	0.038	*
perennial forbs (%)		0.002	**	0.039	*	.	.
grasses (%)		0.030	*	0.006	**	0.022	*
sedges (%)		<0.001	***	0.022	*	.	.
legumes (%)		.	.	.	.	.	.
shrubs (%)		0.004	**	.	.	0.019	*
Richness of							
all species	Poisson	<0.001	***	0.004	**	.	.
annual forbs	Poisson	<0.001	***	0.080	(*)	.	.
perennial forbs	Poisson	<0.001	***	0.003	**	.	.
grasses	Poisson	0.076	(*)	0.022	*	.	.
sedges	Poisson	0.009	**	0.005	**	.	.
legumes	Poisson	0.054	*	0.048	*	.	.
shrubs	Poisson	0.01	*	.	.	.	.
Shannon diversity		<0.001	***	0.009	**	.	.
Dominance	rank	0.007	**	0.012	*	.	.
Eveness		.	.	0.097	(*)	.	.
Soil pH		.	.	0.011	*	0.083	(*)
EC	rank	0.009	**	.	.	0.026	*
SOC (%)		0.057	(*)	0.016	*	0.012	*
total N (%)	z-transform	0.058	(*)	0.013	*	0.026	*
aP (mg/kg)		<0.001	***	0.020	*	<0.001	***
aCa (mg/kg)		0.016	*	0.004	**	.	.
aMg(mg/kg)		<0.001	***	.	.	.	.
aK (mg/kg)	lg(x+1)	<0.001	***	.	.	.	.

Although multivariate analysis did not indicate any interaction between livestock activity and habitat, soil pH, EC, SOC, tN and aP all showed different response patterns among habitats according to the GLMM results (Table 2). Within piospheres, SOC and tN were lower than that under light grazing conditions in meadows (Fig. 2b–c), while aP (Fig. 2d) and EC were highest among all levels of livestock activity in steppe-meadows, and soil Mg and K were highest in all habitats. Strict effects of heavy grazing on SOC and tN were only confined to meadows.

Fig. 2 Comparisons of vegetation and soil indicators among three habitat types (meadow, steppe-meadow and steppe) and four livestock activity levels (P=piospheres, H=heavy grazing, M=moderate grazing, L=light grazing) according to GLMM results from Table 2. Only variables showing significant effects of livestock activity and their interaction are shown (except the highly abnormally distributed data). Raw data are plotted without transformation. Lower case letters indicate significant differences ($P < 0.05$) based on results of post hoc Tukey HSD tests between four levels of livestock activity within habitats: a) relative cover of grasses; b) soil organic carbon; c) soil total nitrogen, d) plant available phosphorus in soil. Sample size of piosphere plots in steppes was too small to calculate the standard errors thus are not shown here.



3.3 Vegetation and soil relationships

Plant species composition and soil fertility were closely correlated in multivariate spaces across habitats (Procrustes correlation of the first two axes of the ordination plots, r=0.50, Fig. S4). Within habitats, correlation was strongest in steppes and lowest in meadows (Procrustes r_{steppe}=0.73, $r_{steppe\text{-}meadow}$=0.47, r_{meadow}=0.17). Plant species richness, SOC and tN were mostly positively correlated in steppes and steppe-meadows, irrespective of grazing intensities (Table S2).

3.4 Indicator species

As with the responses of plant species compositions, plant indicator species were largely confined to piospheres (Table 3). Common species from meadows and steppe-meadows included *Capsella bursa-pastoris*, *Artemisia hedinii*, *Cirsium souliei*, *Hypecoum leptocarpum, Poa pratensis, Polygonum sibiricum* and *Potentilla anserina*. Indicator species from steppes were distinct from the other two habitats. Elsewhere, *Thalictrum alpinum* was present at all grazing intensity levels except in piospheres, while in meadows, *Kobresia pusilla* and *Leontopodium leontopodioides* showed a similar pattern to that found in steppes- meadows.

4. Discussion

Our results reveal clear effects of livestock activity on both plant species composition and soil fertility; however, effects were mainly constrained to piospheres. Strong effects in piospheres confirm the widely held notion that heavy mechanical disturbance results in grassland degradation, irrespective of the prevailing abiotic conditions (von Wehrden et al. 2012), since trampling and livestock excreta both affect vegetation structure (Hobbs & Huenneke 1992; Schnoor & Olsson 2010; Sasaki et al. 2011). However, the effects of grazing intensification on plant and soil indicators were limited compared to strong environmental impacts, highlighting the complexity of ecological processes on Tibetan grasslands.

Table 3 List of plant indicator species for different levels of livestock activity within habitats. Indicator values of specificity (A) and fidelity (B) for each species are given (Dufrêne & Legendre 1997). Specificity refers to the frequency of species under a particular level of livestock activity while fidelity is the probability of finding a species at a particular site. Cases of A=1 and B > 0.5 are shaded. Significance levels refer to Indval values (A x B) and are indicated after species names (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, No. of permutations=999).

Meadows			Steppe-meadows			Steppes		
(82 plots, 516 species)			(42 plots, 222 species)			(49 plots, 178 species)		
Species name	A	B	Species name	A	B	Species name	A	B
Piospheres: 16 species			**Piospheres: 16 species**			**Piospheres: 7 species**		
Hypecoum leptocarpum***	0.98	0.75	_Poa pratensis***_	0.99	0.86	_Achnatherum splendens*_	0.87	1.00
Poa pratensis***	0.89	0.75	_Artemisia hedinii***_	1.00	0.71	_Anthriscus sylvestris*_	0.93	1.00
Capsella bursa-pastoris***	1.00	0.63	_Capsella bursa-pastoris***_	1.00	0.71	_Artemisia roxburghiana*_	1.00	1.00
Potentilla anserina**	0.74	0.63	_Hypecoum leptocarpum**_	0.85	0.71	_Asperugo procumbens*_	0.94	1.00
Axyris prostrata***	0.95	0.50	_Polygonum sibiricum***_	1.00	0.71	_Lepidium densiflorum*_	0.99	1.00
Cirsium souliei***	0.97	0.50	_Potentilla anserina***_	0.99	0.71	_Leymus paboanus*_	0.91	1.00
Elymus nutans*	0.67	0.50	_Lepidium apetalum**_	0.87	0.57	_Plantago depressa*_	1.00	1.00
Glaux maritima***	0.99	0.50	_Microgynoecium tibeticum**_	1.00	0.57			
Lagotis brachystachya**	0.71	0.50	_Plantago depressa*_	0.85	0.57			
Polygonum sibiricum***	0.79	0.50	_Carex scabriostris*_	0.98	0.43			
Artemisia hedinii***	1.00	0.38	_Anisodus tanguticus*_	1.00	0.29			
Carex kansuensis*	0.65	0.38	_Avena fatua*_	1.00	0.29			
Carum carvi*	0.83	0.25	_Cirsium souliei*_	1.00	0.29			
Draba ellipsoidea*	1.00	0.25	_Descurainia sophia*_	1.00	0.29			
Plantago asiatica*	0.87	0.25	_Lepidium capitatum*_	1.00	0.29			
Smelowskia tibetica*	0.59	0.25	_Polygonum aviculare*_	0.95	0.29			
light-moderate-heavy grazing plots: 1 species			**light-moderate-heavy grazing plots: 2 species**			**moderate grazing plots: 1 species**		
Thalictrum alpinum*	1.00	0.73	_Kobresia pusilla*_	0.99	0.66	_Dracocephalum heterophyllum*_	0.91	0.71
			Leontopodium leontopodioides*	1.00	0.54			

4.1 Vegetation responses

Strong environmental controls were confirmed by the presence of interaction of habitat and livestock activity, and the overwhelming controls of cvP in steppes and steppe-meadows. This is in line with non-equilibrium theories (Illius & O'Connor 1999) and studies from (Inner) Mongolia (Fernandez-Gimenez & Allen-Diaz 1999; Ma et al. 2010; Wesche et al. 2010) and central Tibet (Wu et al. 2014). Moreover, plant communities in semi-arid steppes tend to be grazing-tolerant because selective pressures of drought and grazing usually converge (Milchunas et al. 1988; Milchunas et al. 2008; DeMalach et al. 2014). However, it is surprising that plant communities in meadows were also insensitive to intensified grazing, which challenges the perception of widespread grazing-caused degradation on Tibetan grasslands (Akiyama & Kawamura 2007; Harris 2010; Cao et al. 2013) as well as results from several single-site studies in meadows (Wang & Wesche 2016). Such strong negative effects found from short-term fenced-off grazing exclusion experiments may reflect the consequences of excluding mechanical disturbance, such as that experienced in piospheres, as fences precluded the effect of trampling and nutrient input via livestock excreta.

The only significant change due to heavy grazing was the increase of annual species in meadows. This corresponds with previous studies (Osem et al. 2002; Pakeman 2004) and suggests that grazing does cause physical disturbance to extremely dense *Kobresia* turf and provides opportunities for annuals to establish. In contrast, no pronounced effects were found for perennials that are well adapted to both harsh alpine climate conditions (Körner 2003) and a long history of grazing pressure. Typical examples are *Kobresia–Carex* species, which can benefit from moderate grazing and are thus dominant in meadows and even distributed across parts of steppes (Miehe et al. 2011). Given that former site-level studies showed significant interactions between climate and grazing on other functional groups (Klein et al. 2004, 2007), more in-depth investigations into plant traits are needed.

Of particular note in our study, within steppe-meadows, plant species composition was affected by cvP independently of P (Fig. S3b), implying that under intermediate P levels, plant communities are strongly controlled by interannual variability of moisture supply (Knapp & Smith 2001). This is especially important because such transitional habitats are affected by both livestock activity (particularly in piospheres) and variability of climate, making them potentially sensitive to the combined pressure of overgrazing and climate change.

4.2 Soil responses

We found strong effects of livestock activity on overall soil fertility across all habitats, but particularly so in piospheres. However, intensified grazing only reduced SOC and tN in meadows. Soil responses tend to be slower than vegetation responses and thus represent more long-term effects (Milchunas & Lauenroth 1993). As a global review suggested, grazing effects on SOC tend to shift from positive to negative with increasing precipitation (McSherry & Ritchie 2013), and the observed negative effects in wet meadows partly support this hypothesis. Reductions of SOC in meadows may be attributed to reductions in carbon input from plants, including litter (Semmartin & Ghersa 2006) and roots (Giese et al. 2009; Smith et al. 2014), as we found an average decline in litter cover of 0.8% under heavy grazing compared to light grazing (*P*=0.08, Kruskal-Wallis rank test). Root biomass in alpine meadows is mostly reported to decline following heavy grazing, as suggested in a recent review (Wang & Wesche 2016). Our study indicates that grazing responses in steppe-meadows and steppes are not significant, with roughly an equal number of negative and positive cases (Fig S5), which again implies the high contextual dependence of C dynamics. Finer scale studies that consider further abiotic and biotic factors are therefore required.

Heavy grazing also reduced soil tN in meadows in our study, which supports the hypothesis that grazing tends to reduce soil N in more productive habitats (Schrama et al. 2013). Changes of soil N can be caused by: 1) Redistribution by livestock, which tends to result in nutrient hotspots due to dung and urine deposition near camps (Holst et al. 2007), albeit in our study area local Tibetan herders frequently collect yak dung as a fuel resource, which may remove N inputs into soils (Miller 2005); 2) Side effects of changing SOC. Changes of soil C and N from heavy to light grazing were mostly consistent (Fig. S5), indicating C and N cycling are coupled (Piñeiro et al. 2010); or 3) Changes of soil physical conditions, plant quantity or quality due to grazing, which can also affect soil N cycling (Schrama et al. 2013).

Phosphorus is crucial for plant growth and is usually a limiting factor due to its high fixation in soils and low availability to plants. In line with our review (Wang & Wesche 2016), no evidence was found for grazing effects on aP except for an increase in piospheres, where phosphorus is frequently excreted via livestock excreta and thus concentrated near camps. However, P cycling is extremely complex and might be distinct from C or N processes because both biological factors (e.g. root architecture, rhizosphere interaction and mycorrhizal association) and geochemical conditions (e.g. soil age, mineral and weathering) are influential (Shen et al. 2011).

4.3 Links between vegetation and soil

Plant-soil links were inconsistent across habitats, with strong positive correlations being recorded between richness and SOC, tN in steppe-meadows and steppes, but no linear correlation in meadows, irrespective of grazing intensity. Instead, we found a unimodal response between soil tN and richness (r^2=0.38, Fig. S6), suggesting there are nutrient limitations in less productive sites but competition exclusion in more productive sites (Fraser et al. 2015).

Possible explanations for the apparent uncoupling in meadows include: 1) Plant communities are more controlled by macroclimatic conditions, grazing and their interactions, while soil conditions are not, as shown from the overall weak environmental controls for meadows and steppe-meadows; 2) Soils and plants may respond at different temporal scales. The dominant perennial species did not respond to grazing in our study areas, while biological processes in the soil may be more sensitive to grazing as inputs from the aboveground plant layer may vary quickly. In addition, soil fauna, fungi and microbes operate at small spatial scales and are highly dynamic over time (Hamilton III & Frank 2001; Klumpp et al. 2009; Li et al. 2013). In steppes, vegetation is often discontinuous and islands of fertility are formed under perennial bunchgrasses (Allington & Valone 2014), resulting in tight plant–soil interactions.

5. Conclusion and outlook

While the effects of grazing and climate are strong in piospheres within Tibetan grasslands, increasing grazing intensities on lightly to heavily grazed grassland habitat other than piosphere do not cause changes in the plant communities or soil condition. Our study confirms that livestock effects are often overridden by environmental controls. The most pronounced grazing responses were found for meadows, which showed increased annual forb cover and richness and reduced SOC and tN. The impact of local climate conditions varied among habitats and it differed for plants and soils. Plant communities were primarily controlled by cvP across habitats, indicating the importance of water variability.

In terms of grazing management, our data unequivocally highlight the strong effects of mechanical disturbance by livestock. At present, piospheres are largely spatially restricted, but they may increase in size over time, especially given the current trend toward reduced mobility of local herders, which brings into question national sedentarization policies (Ptackova 2011). The listed plant indicator species are therefore of practical importance for monitoring piosphere expansion. Monitoring is also needed in the steppe-meadows, where piosphere effects were strongest and grazing responses were pronounced and at least partly negative (deteriorated soil conditions in heavily grazed sites). Soil nutrient contents thus deserve attention in any future monitoring programme.

Further studies recommended to contribute to a better understanding of grazing responses should focus on: 1) the effects of herd composition (Cincotta et al. 1991), grazing regime and local implementation of governmental policies on vegetation and soils (Yan et al. 2005); and 2) how links between vegetation/soil conditions and environment change under grazing. Such studies would be appropriate to Tibetan grasslands given the vast gradients in vegetation, physical environmental conditions and prevailing grazing regimes.

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Chapter 5 Responses of multiple indicators

Multiple indicators yield diverging results on grazing degradation assessment across Tibetan pastures

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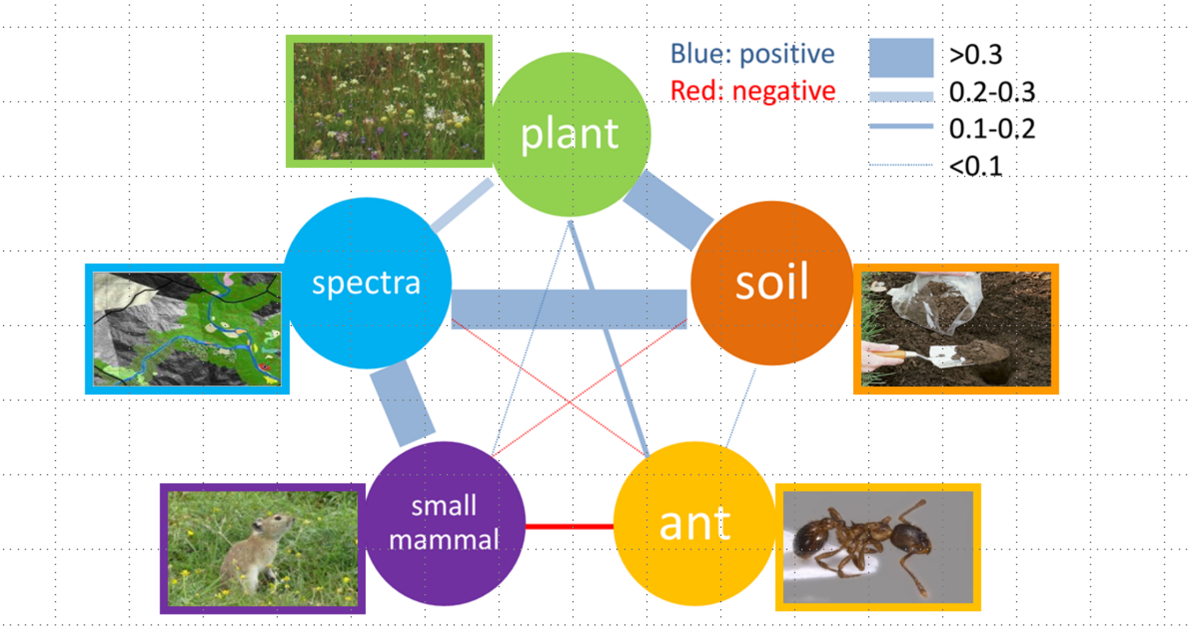

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Supplementary figures and tables are on the CD version of the dissertatio

Grazing is more than just defoliation of plants.
Large grazing herbivores change energy balance at the soil surface,
create different levels of system disturbance,
impact colonization of plants,
remove and redistribute nutrients
and influence interactions with other kinds of animals.

Trlica et al. 1993

Abstract

1. Understanding the impacts of livestock grazing on grasslands is crucial to rangeland management and conservation. Numerous indicators are employed to detect changes caused by grazing but yield widely different results among single studies. Across Tibetan pastures which have evolved with long grazing history and harbor large biodiversity, we tested: (1) whether grazing effects are pronounce in moist pastures and environmental impacts overrule in dry habitat, and (2) the relative importance of grazing and abiotic factors differs between indicator groups.

2. We compared species compositions of plants, small mammals, ants, as well as the overall soil fertility condition and field hyperspectra by multivariate analyses between two levels of grazing intensity (heavily vs. lightly grazed) from 18 sites across two main habitat types (steppe and meadow). Effects of grazing, habitat and their interaction on richness and abundance of biotic groups and key soil and hyperspectra properties were explored by Generalized Linear models. Environmental factors included temperature, precipitation, elevation, relief, exposure and inclination.

3. Few indicators responded to increase of grazing, as shown by reduced vegetation cover, soil organic carbon, total nitrogen concentration and corresponding hyperspectral indices. Grazing effects were significant in moist meadows, while environmental impacts overruled in drier steppes. Precipitation patterns were of most influence for plant communities, soil nutrients and hyperspectra, while elevation and temperature controlled ant and small mammal communities.

4. Our results do not support the widely held notion that increase of grazing broadly causes degradation across Tibetan pastures. Reliable assessments should select appropriate indicators and carefully consider local climate and topographic conditions. Different response patterns between habitat types must be acknowledged in future grassland conservation and management.

Keywords

ant, field spectrometry, vegetation, small mammal, soil nutrient, organic carbon, steppe, rangeland

1 Introduction

Grasslands cover up to 40% of the terrestrial surface and are grazed by domestic and wild ungulates (White et al., 2000). Central Asia hosts the most extensive grazing systems comprising semi-nomadic (Mongolia, parts of Tibet) and sedentary (northern China, Tibet) pastoralism. The region covers large climatic and elevational gradients and shows huge variations of productivity in space and time (Wesche and Treiber, 2012; Yang et al., 2010). Grassland degradation on the Tibetan Plateau is of major concern to ecologists and policy makers because health condition of these grasslands is primarily important for local livelihoods and also affects environment of surrounding Asia. Different methodologies and standards employed in assessments (Akiyama and Kawamura, 2007; Reed et al., 2011) result in varying estimates of degradation extent from 10% to >50% of the whole grassland area in this region (Harris, 2010). Overgrazing has been blamed as the main cause of degradation and governmental policies mainly focus on reducing livestock numbers and restricting mobility of herders. However, these strategies are still controversial as they might conflict with traditional nomadic grazing managements (Ptackova, 2011; Shang et al., 2014).

A comprehensive understanding of grazing effects with respect to the local environmental contexts is urgently needed. The relative importance of biotic and abiotic factors in driving vegetation dynamics has been discussed in conceptual models (Vetter, 2005). Classic equilibrium models strengthen plant-herbivore interactions and are suitable for rangelands subject to relatively stable climate and productivity. State-transition models (Noy-Meir, 1975; Westoby et al., 1989) and non-equilibrium models suggest that there is no single stable state for vegetation dynamics, and climatic perturbations may have stronger influence, particularly in dry rangelands (Ellis and Swift, 1988). Few reviews have confirmed that grazing responses vary among ecosystems due to the prevailing environmental and resource conditions (Milchunas and Lauenroth, 1993; von Wehrden et al., 2012). Surprisingly, field studies comparing different habitat types are lacking, and most assessments from Tibet fail to consider the local environmental context.

Fauna groups are also influenced by livestock grazing indirectly through the changes of vegetation structure, such as species composition and heterogeneity (Joern, 2005; Zhu et al., 2012), Especially, small mammals, typically rodents have been regarded as pests to grasslands due to their foraging and digging activities (Fan et al., 1999; Harris, 2010; Liu et al., 2013), but how they respond to livestock grazing and plant community changes is still unclear. Insects are also sensitive to livestock grazing since the shifts in plant communities will change their habitat and food conditions. As one of the suitable land-use change indicators, ants have been widely investigated because of their high diversity, abundance and sensitivity to environmental changes (Andersen et al., 2002; Rosenberg et al., 1986). Ants also adjust soil nutrient cycling (de Bruyn, 1999) then link various trophic levels (Read, 1999). However, grazing responses of ant communities are inconsistent from various grasslands (Hoffmann, 2010; Underwood and Fisher, 2006) and no study is available in Tibetan context.

Besides biotic groups, grazing impacts on soils are slower, long-lasting and even irreversible (Milton et al., 1994; Whisenant, 1999). Grazing often directly alter soil physical-chemical condition by trampling and nutrient redistribution from livestock (Augustine, 2003; McSherry and Ritchie, 2013; Schrama et al., 2013) Furthermore, grazing-mediated changes in plant communities might also feedback on soils and *vise versa* (Milchunas and Lauenroth, 1993). Soil properties are related to macroclimate (Mosier, 1998) and topography (O'Geen et al., 2007), with which impacts of grazing interact. Remote sensing approach offers an alternative to laborious field studies to assess grassland conditions at large spatial scale (Gao et al., 2010; Guerschman et al., 2009; Zhou et al., 2014). The normalized difference vegetation index (NDVI, Tucker, 1979) estimates vegetation cover and is related to productivity and the normalized difference nitrogen index (NDNI, Serrano et al., 2002) indicates bulk canopy nitrogen. Novel index, such as the red-edge position through linear extrapolation (REP_LE, Cho and Skidmore, 2006) is related to foliage chlorophyll content (Lehnert et al., 2014). However, most remote sensing studies have not been validated with field-derived spectral data at given grazing intensities.

Only few grazing assessments have employed multiple indicators, and those that do, point to a limited consistency of responses (Grandin et al., 2013; Milchunas et al., 1998; Whitford et al., 1998). Here we present the first study to assess grazing effects on multiple indicator groups from multiple sites across large environmental gradients in Central Asian grasslands. We focus on five indicator groups, i.e. vascular plants (hereafter plants), small mammals, ants, soils and field hyperspectra, comparing their changes to increased grazing and abiotic factors in two main habitat types (meadow and steppe) in Tibetan pastures (Yu et al., 2010). We consider grazing has effects when heavy grazing changes key characteristics of indicator groups compared to light grazing, and test the following hypotheses: 1) Local precipitation patterns override grazing effects in dry steppes, while grazing effects should be strong in moist meadows; 2) Indicators differ in their sensitivity to grazing and abiotic factors (e.g. climate and topography) due to their specific attributes.

2 Materials and Methods

2.1 Study area and sampling strategy

The Tibetan Plateau presents an elevational gradient from below 2000 m to above 5000 m a.s.l. and a mean annual precipitation range of < 80 mm in the west to > 800 mm in the east. Tiny sedges of the genus *Kobresia* form dense mats (alpine meadow) and dominate in the east while open alpine steppes prevail in the west (Miehe et al., 2011a; Miehe et al., 2011b). In 2011 and 2012, we assembled multi-indicator datasets from 18 sites along extensive climatic gradients across Tibetan pastures (Table 1, Fig. 1). We compared at least one pair of light vs. heavy grazing plots at each site, in the assumption that grazing intensity decreases as the distance from a camp increases. Immediate surroundings of camps were excluded because trampling and excessive nutrient inputs often completely alter vegetation (Sasaki et al., 2008). This distance-based local grazing gradient has been applied in many studies from dry or alpine grasslands (Qian and Shimono, 2012; Stumpp et al., 2005), and can present the cumulative grazing effects (Adler and Hall, 2005). Moreover, long-term grazing exclosures are insufficient to cover our study area, and short-term experiments cannot detect slow responses in soils and perennial plants. All sites were mainly grazed by yaks and/or sheep/goats.

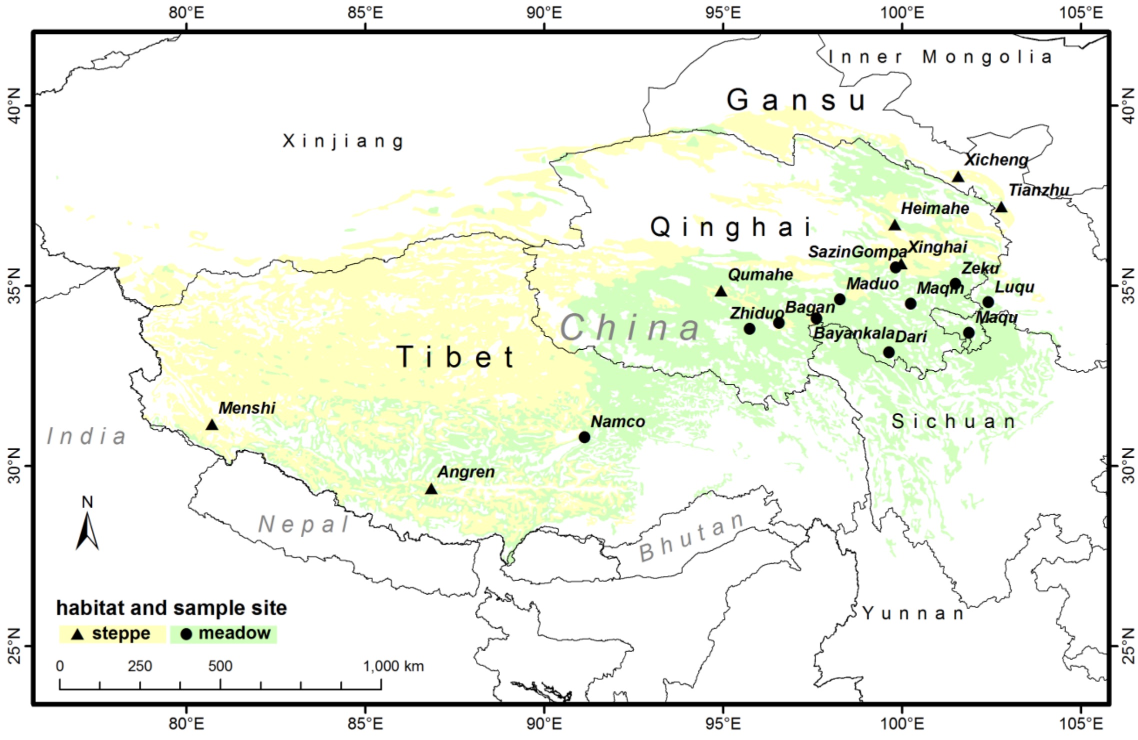

Fig. 1 Locations of study sites. The habitat type was based on the Atlas of the Tibetan Plateau. Site name abbreviations refer to Table 1.

Table 1 List of study sites, coordinates, elevations, key climatic parameters (P=mean annual precipitation, cvP=coefficient of interannual variation of precipitation, T=mean annual temperature) and number of sampled plots for each indicator group (vp=vascular plants, an=ants, sm=small mammals, so=soil, fs=field hyperspectral data)

	Geographic information			Climate			Sample Size				
Site name	North (°)	East (°)	Elevation (m a.s.l.)	P (mm)	cvP (%)	T (°C)	vp	an	sm	so	fs
Meadow							*46*	*40*	*29*	*45*	*37*
Bagan	33.966	96.561	4362	536	19	-1.6	6	6	2	6	5
Bayankala	34.091	97.604	4679	510	13	-3.9	2	2	2	2	2
Dari	33.147	99.631	4427	570	12	-1.9	2	2	2	2	2
Luqu	34.538	102.413	3365	608	15	2	4	2	2	3	2
Maduo	34.619	98.263	4260	352	19	-2.9	4	4	2	4	4
Maqin	34.496	100.239	3870	530	15	-0.9	2	2	2	2	2
Maqu	33.693	101.871	3628	620	10	1.1	8	6	6	8	6
Namco	30.793	91.129	4872	420	30	-1	6	6	2	6	6
SazinGompa	35.501	99.823	3530	475	23	-1	4	2	3	4	4
Zeku	35.049	101.496	3679	564	17	-0.1	2	2	2	2	0
Zhiduo	33.797	95.741	4322	460	17	-1.9	6	6	4	6	4
Steppe							*34*	*22*	*15*	*33*	*31*
Angren	29.379	86.846	4595	263	34	1.3	2	0	0	2	2
Heimahe	36.692	99.800	3335	392	21	0.6	4	4	3	4	3
Menshi	31.152	80.723	4392	78	36	1	6	6	2	6	6
Qumahe	34.859	94.941	4335	360	24	-2.9	6	6	4	5	6
Tianzhu	37.201	102.780	2965	428	16	1.5	6	2	2	6	6
Xicheng	38.040	101.573	2850	193	20	1.8	4	2	2	4	4
Xinghai	35.614	99.979	3302	412	22	0.5	6	2	2	6	4

We counted livestock droppings in three randomly located quadrats (1 x 1 m^2) within each vegetation plot and calculated the total dung cover (%) as a proxy for current grazing intensity. Sampling of vegetation and soil were repeated one to four times for both light and heavy grazing plots per site to capture variance within site, while ants, small mammals and hyperspectral signals were only sampled at one pair of plots per site due to limited investigation time (Table 1).

2.2 Vegetation sampling

We recorded all plant species and estimated their ocular canopy covers from 10 x 10 m^2 plot. We also noted which functional groups, i.e. shrubs, grasses, sedges, perennial forbs, annual forbs and legumes, they belong to. We identified most specimens according to eFloras (2008) and related works, and cross-checked in the Herbarium of the Kunming Institute of Botany, CAS. Difficult taxa were determined by specialists (see acknowledgements).

2.3. Small mammal sampling

We placed traps in 100 x 100 m^2 sampling grids along with the vegetation plots and left open for at least three consecutive days and nights. We checked traps three times per day and identified small mammal individuals captured, color-marked and released them. We determined species following Smith *et al*. (2008) and calculated the abundance as the number of captured individuals per 100 trap-nights (or days) at each plot (Gurnell and Flowerdew, 2006).

2.4 Ant sampling

We sampled ant species richness and abundance (nest density) with a two level sampling strategy (Seifert, 1986) which compared well with results from excavation of all ant colonies (Gallé, 1980; Nocke, 1999). We examined various hypo- and epigaeic microsites by turning rocks and following foraging workers. Species were considered present when a nest (with broods or gynes) was found or at least one adult worker with a relatively small foraging range was observed. We investigated nest density/100 m^2 by turning over soils for intense screening in a small area (at least 40 m^2), and also coarsely screened in a larger area (50–150 m^2) for large and populous species, which usually have a larger home range and lower nest densities. The size of screening area was decided by site conditions and expert experience. We identified species based on collections from Senckenberg Natural History Museum, Görlitz, Germany which houses one of the worlds' most comprehensive ant collections. We especially distinguished cryptic species by Exploratory Data Analysis (EDA) on morphometric measurements (Seifert et al., 2013) and compared type specimens and DNA sequences.

2.5 *Soil sampling*

We collected three samples of topsoil (0–5 cm) from each plot and mixed, air-dried, sieved (2 mm) and separated from roots, stones and litter for lab analyses. We measured electrical conductivity (EC) and pH with a pH/EC meter (water: soil=5:1) and analyzed total carbon (C) and nitrogen (N) contents using a CN-Analyser (Vario Pyro Cube Elementar, GmbH, Germany). Inorganic C ($CaCO_3$) content was determined with 10% HCl to correctly derive soil organic carbon. We also extracted plant available phosphorus (P), calcium (Ca), magnesium (Mg) and potassium (K) by the adopted Olsen-P method (Sims, 2000) and measured with ICP-OES (Varian 725-ES, Stadt, Australia). All results refer to oven-dried soil (75 °C, 18 h).

2.6 *Hyperspectra sampling*

We used a HandySpec spectrometer (Tec5 AG, Oberursel, Germany) to measure hyperspectral signals from three randomly located quadrats (50 x 50 cm^2) from each plot. Five replicates of measurement were averaged for each quadrat and spectra of three quadrats were averaged to derive the plot spectra. The hyperspectral differences between plots were compared with the Spectral Angle Mapper dissimilarity (SAM, Kruse et al., 1993):

$$SAM = \cos^{-1}\left(\frac{\sum_{i=1}^{nb} t_i r_i}{\left(\sum_{i=1}^{nb} t_i^2\right)^{1/2} \left(\sum_{i=1}^{nb} r_i^2\right)^{1/2}} \right)$$

Here, t_i and r_i denote the reflectance values of the target (t) and reference spectrum (r) in band i, and nb is the number of bands available. Thus, a SAM value of 0 means equal hyperspectra, or t is a linear combination of r. Larger SAM value means greater dissimilarity between t and r.

2.7 Environmental factors

We extracted site-level macroclimate variables, including mean annual temperature (T), as a crude proxy for growing season temperature, from Worldclim (Hijmans et al., 2005) based on site coordinates, then cross-checked with available data from the China Meteorological Administration (CMA; http://data.cma.cn/). We obtained mean annual precipitation (P) from CMA datasets and complemented with institutional data (personal communication) and calculated the interannual variability in precipitation (cvP) based on a recent High-Asia refined analysis (Maussion et al., 2014), in which cvP values were more comprehensive than CMA datasets. We also included plot-level topographic variables such as relief (sediment, gravel terrace, lower slope, middle slope, upper slope, top of the hill), inclination and aspect. The latter two were combined as incident radiation (McCune and Keon, 2002, eq. 1).

2.8 Statistics

To test the relative importance of all explanatory variables on spatial patterns of each indicator group, we employed Principal Coordinates Analysis (PCoA) based on Bray-Curtis, SAM and Euclidean dissimilarity matrices for plants, field hyperspectra and other indicator groups, respectively. We log-transformed abundance data to down-weight the abundant species and log- and standardised soil data (C, N, P, Ca, K and Mg concentration) to keep zero mean/unit variance. Continuous environmental predictors (P, cvP, T, Elev and incident radiation) were graphically fitted to ordination axes by *post hoc* Pearson correlation. Separate redundancy analyses (dbRDAs) based on the same dissimilarity matrices as in PCoA were calculated for each explanatory variable and the variance explained by the first (and only) canonical axis was recorded. We further stratified datasets by two habitat types and repeated the analyses for each habitat. This a priori classification corresponded well to our field vegetation records from lightly grazed plots, and captured large differences in P and T (Fig. S1. Supporting information). The similarity of overall spatial patterns of all indicator groups was compared by Mantel correlations using the same dissimilarity matrices as in PCoAs.

We tested effects of grazing, habitat and their interaction on richness and abundance of biotic indicator groups and selected soil properties and field hyperspectral indices by Generalized Linear Mixed Models (GLMM). Site nested in habitat was treated as a random factor. A Poisson distribution was assumed for species richness (counts) and the Gaussian model was for other variables. We compared the full model and the subsequently simplified models without grazing or habitat effect against a null model with likelihood ratio tests to derive *P* values (Crawley, 2007).

As the study was of an exploratory nature, we reported uncorrected *P* values (Roback and Askins, 2005). All analyses were made in R (R Core Team, 2015) using the packages lme 4 (Bates and Maechler, 2009), vegan (Oksanen et al., 2010) and hsdar (Lehnert et al., 2015).

3 Results

3.1 Multivariate responses of each indicator group

Dung cover estimates confirmed that intensity of livestock activity differed among plots, and the elevation–temperature gradient was the most important (Fig. 2a). Increased grazing also explained a large share of the overall variance in dung composition compared to other tested variables (Table 2).

Among 500 vascular plant species (see Table S1) encountered in 80 plots, 373 occurred at least twice and were chosen for multivariate analysis. Grazing effects on compositions of species (Fig. 2b) and functional groups (Fig. 2c) were limited across and within habitats. Precipitation and cvP explained most of the variance in species composition, while relief and elevation explained most variance in functional groups from steppes and meadows respectively (Table 2).

We found fifteen small mammal species from 44 plots, and 34 plots had at least one species sampled. Grazing effects on small mammal species composition were generally negligible (Table 2). The overall environmental controls across habitats were mainly due to the strong influences of elevation and temperature in steppes (Fig. 2d, Table 2).

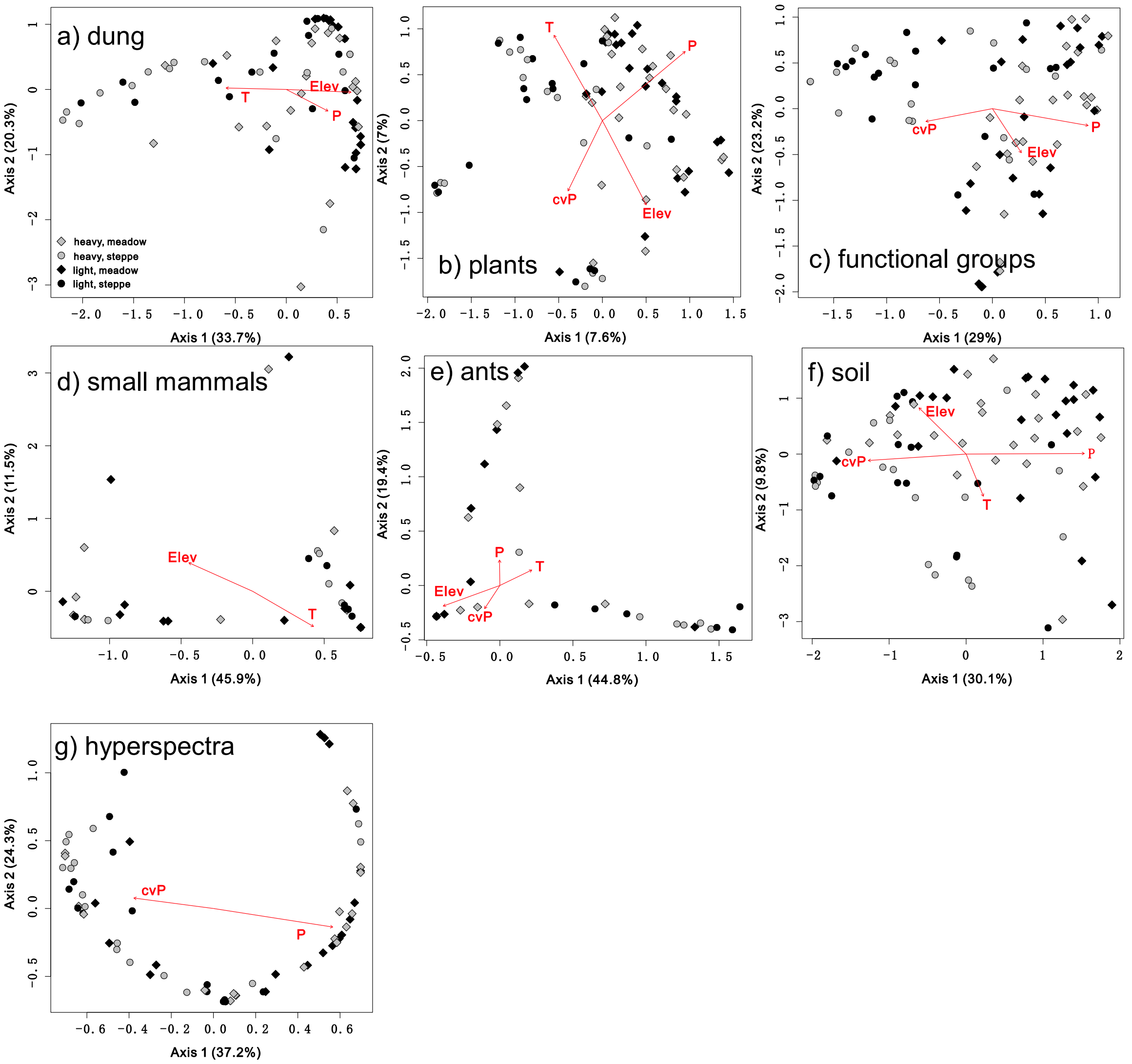

Fig. 2 Grazing and environmental effects on each indicator in multivariate space summarized by PCoAs (details of dissimilarity matrices and transformations see Table 2): a) dung cover (goat/sheep and yak); b) plants; c) relative cover for different functional groups (annuals forbs, grasses, sedges, perennial forbs, shrubs); d) small mammals; e) ants; f) soil nutrient concentrations (C, N, P, Ca, Mg, K), and g) hyperspectral data. Abiotic variables including elevation (Elev), precipitation (P), interannual variability of precipitation (cvP) and temperature (T) were fitted with post hoc correlation (significance threshold 0.01, 1000 permutations).

Table 2 Responses to grazing intensity and abiotic conditions for indicator groups based on multivariate regression analysis. Explained variance (%) of total variance for each predictor was calculated from separate dbRDAs in the full and habitat-wised (meadow vs. steppe) dataset. Dissimilarity matrices and transformations were adjusted to dataset specifics. Abbreviations for environmental factors are the same as in Table 1. The largest portion of the explained variance is in bold and underlined.

	Grazing intensity	P	cvP	T	Elevation	Radiation	Relief	Habitat
Dung cover [Euclidean]								
Full	2.9	5.0	1.9	6.6	7.6	1.3	**11.6**	7.5
Steppe	4.8	4.5	7.0	10.7	17.1	2.1	**25.6**	
Meadow	3.7	2.1	4.2	1.0	1.4	3.5	**5.4**	
Vascular plants [Bray-Curtis (freq>2) (log(x+1))]								
Full	0.7	**5.7**	4.9	4.6	5.4	2.0	4.4	5.3
Steppe	1.5	**14.0**	**14.0**	10.5	12.9	3.3	11.1	
Meadow	1.3	8.0	**8.1**	6.6	7.2	3.8	3.2	
Functional groups [Euclidean]								
Full	0.9	11.1	6.3	2.8	4.4	0.8	6.8	**14.2**
Steppe	1.5	6.1	4.6	2.9	3.3	2.1	**15.7**	
Meadow	2.2	5.1	10.6	1.7	**12.1**	1.7	4.7	
Small mammals [Euclidean (log(x+1))]								
Full	1.3	4.5	2.9	8.2	**8.9**	2.6	6.4	5.2
Steppe	3.2	12.7	14.4	**28.3**	23.2	4.8	19.7	
Meadow	1.9	3.5	3.8	7.3	6.1	**8.8**	5.8	
Ants [Euclidean]								
Full	0.6	3.4	4.3	7.9	**22.0**	1.0	10.7	11.3
Steppe	2.5	19.5	27.8	4.4	31.9	2.3	**33.4**	
Meadow	1.0	11.2	7.7	15.5	**23.7**	2.4	6.9	
Soil nutrients [Euclidean (z-transformed)]								
Full	1.1	**17.7**	12.4	3.2	6.2	3.8	6.0	10.3
Steppe	2.2	18.8	**21.4**	6.4	18.1	6.6	12.3	
Meadow	2.4	**12.9**	6.2	8.7	10.7	7.2	5.7	
Field hyperspectra [SAM]								
Full	1.1	**22.3**	10.6	2.6	1.3	0.4	8.3	10.8
Steppe	3.0	**18.8**	10.7	3.1	4.4	2.3	12.2	
Meadow	1.8	**17.7**	6.6	8.3	10.3	1.6	6.3	

Fifteen ant species were found from 29 of the total 62 plots and other plots were without any ants. Grazing effects on ant species composition were negligible, but elevation played the major role (Fig. 2e), regardless of the habitat (Table 2). Relief and temperature were similarly important in steppes and meadows respectively. Estimates of incident radiation showed little effect.

The overall soil nutrient condition (including C, N, P, Ca, K and Mg concentration) were largely controlled by precipitation across habitats (Fig. 2f). Elevation was also important in the habitat-wise analysis (Table 2). Hyperspectral signals were largely controlled by precipitation and cvP (Fig. 2g). Relief and elevation were additionally important for steppes and meadows separately (Table 2).

Small values of the standardized Mantel coefficient (Table 3) indicated that the dissimilarity matrices between light and heavy grazing of each indicator group were weakly correlated. Grazing-caused changes in plants species composition, plant functional group composition and the overall soil nutrient conditions were positively correlated. Changes in hyperspectral data were correlated to small mammal species composition and the overall soil nutrient condition.

Table 3 Pair-wise Mantel-correlations between the main indicator groups (distance matrices are the same as in Table 2, but no log-transformation performed for vascular plants or small mammals).

	vp	gf	sm	an	so
Vascular plants (vp)					
Functional groups (fg)	0.30				
Small mammals (sm)	0.09	0.06			
Ants (an)	0.16	0.04	-0.15		
Soil nutrients (so)	0.31	0.11	-0.02	0.01	
Field hyperspectra	0.23	0.15	0.63	-0.01	0.32

3.2 Grazing response and interactions with habitat conditions

GLMM results confirmed limited grazing effects and revealed few interactions of habitat (Table 4). Total dung cover, however, significantly decreased with distance to settlements, with a median of 1.1% for heavy grazing and 0.7% for light grazing plots (Fig. 3a).

Grazing had a negative effect on vegetation cover (Fig. 3b), but had varying impacts on plant richness (Fig. S2). Annual forb richness in meadows increased by grazing but decreased in steppes (Fig. 3c), while other functional groups did not respond (data not shown). Similarly, grazing reduced soil C and N mainly in meadows, while responses in steppes were insignificant (Fig. 3d & e). Available P increased under heavy grazing, especially in meadows (Fig. 3f). NDVI and REP_LE (Fig. 3g & h) declined by heavy grazing, while NDNI only marginally increased (Fig. S2). Other indicators from ants and small mammals were not affected by grazing, but habitat remained always important, even when site was taken as a block factor.

Table 4 Effects of grazing intensity, habitat and their interaction according to GLMM results (site treated as random block factor, Poisson model for counts; otherwise Gaussian). Significance refers to comparison of full model against null model, and values are bold and underlined if $P < 0.05$. Marginal significance ($P < 0.1$) is underlined with medium dash. Estimates were taken from the full models.

	Grazing intensity light		Habitat steppe		Grazing intensity*habitat		Transformation
	Estimate	*P*	Estimate	*P*	Estimate	*P*	
Dung cover	-0.088	**0.004**	0.075	0.128	-0.005	0.930	log(x+1)
Plant richness	-0.016	0.111	-0.569	**0.017**	0.102	0.207	Poisson
Plant cover	8.904	**0.010**	-24.825	**0.013**	-3.124	0.676	
Annual forb richness	-0.332	0.286	-0.393	0.284	0.436	**0.046**	Poisson
Relative cover annual forbs	0.581	0.937	2.126	0.144	-0.676	0.683	
Small mammal richness	-0.184	0.997	0.124	0.365	0.399	0.467	Poisson
Small mammal density	-4.435	0.558	-9.025	0.087	3.372	0.598	
Ant richness	-0.182	1.000	0.810	0.237	0.377	0.453	Poisson
Ant abundance	-0.062	0.468	0.561	**0.043**	0.086	0.186	
Soil organic carbon	0.112	**0.048**	-0.157	**0.038**	-0.157	**0.011**	log(x+1)
Soil total nitrogen	0.146	0.058	-0.112	0.057	-0.168	**0.008**	
Plant available phosphorus in soil	0.006	**0.008**	-0.288	**0.009**	-0.116	0.093	log(x+1)
Hyperspectral NDVI	0.076	**0.046**	-0.168	0.051	-0.038	0.423	
Hyperspectral NDNI	-0.012	0.079	0.024	0.078	0.003	0.738	
Hyperspectral REP_LE	0.001	**0.019**	-0.001	0.546	0.001	0.597	log(x+1)

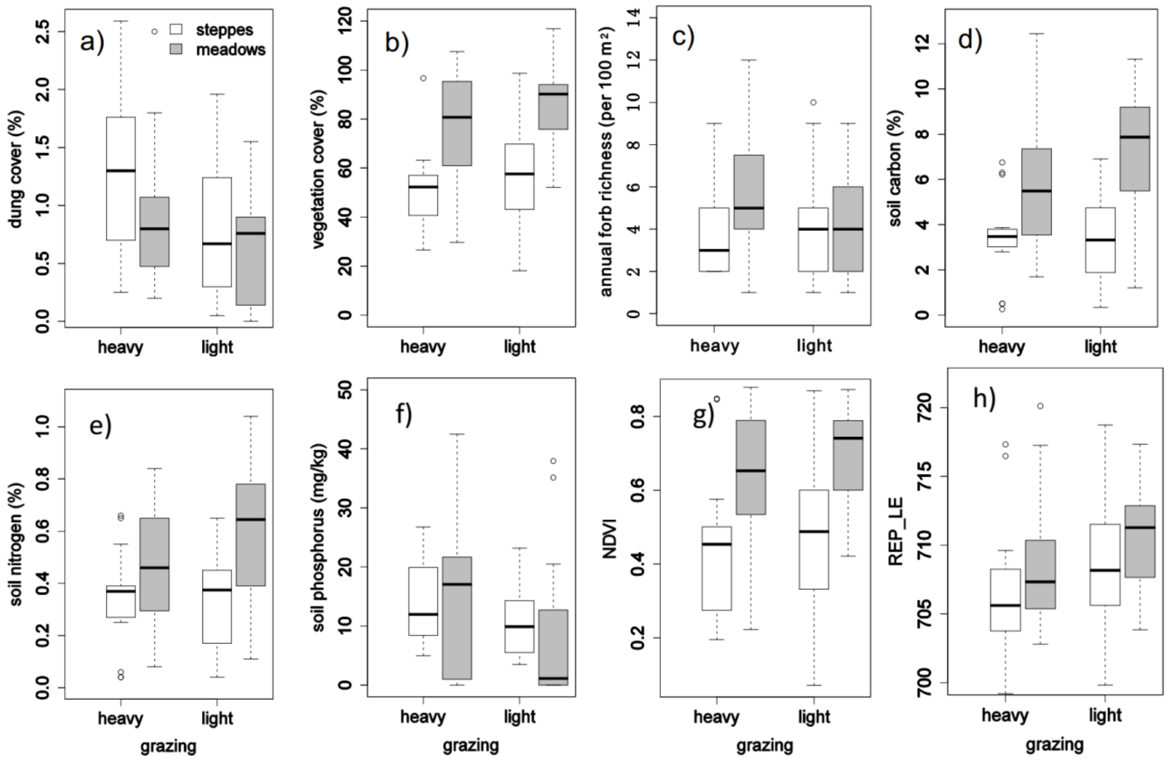

Fig. 3 Grazing responses of key indicators for steppes and meadows: a) dung cover; b) vegetation cover; c) annual forb richness; d) soil organic carbon; e) soil total nitrogen; f) plant available phosphorus in soil; g) hyperspectral NDVI; h) hyperspectral REP_LE. Only those with significant grazing effect or interaction of grazing and habitat (according to Table 4) are shown.

The strong controls of environment on indicator groups were supported by univariate correlations from lightly grazed plots (Table S1, lower diagonal). Vegetation, soil and hyperspectral data were positively associated with precipitation, while ants were more responsive to temperature and elevation. Climate impacts on plant cover, soil C, N, and hyperspectral variables became weaker under heavy grazing condition (Table S1, upper diagonal). Precipitation was positively related to plant species richness, total cover, soil nutrients, NDVI and NDNI, while small mammal richness was negatively correlated with precipitation. Elevation/coldness had negative effects on ant richness and abundance.

Variables within each indicator group were mostly positively correlated, except that soil pH was negatively correlated to soil nutrients (Table S1). Plant richness and cover were positively correlated to soil nutrients. Small mammal richness increased with reduced vegetation cover and NDVI, but positively correlated with NDNI under light grazing. Richness of ants and small mammals were negative correlated under heavy grazing. NDVI was positively correlated with vegetation (cover, richness) and soil nutrients, while NDNI showed an opposite pattern. Correlations were generally weaker under heavy grazing.

4 Discussion

Our multi-site study indicates that intensified grazing do not severely change plant, ant, small mammal communities, neither affect the overall soil nutrient conditions across the Tibetan pastures. However, environments strongly modified or even overruled grazing effects. Few indicators showed significant grazing responses and environmental controls differed among indicators and habitats. Although distance-based grazing gradient might be constrained by a lack of experimental controls and might only capture a small share of the current grazing intensity (Dorji et al., 2013a), we confirmed higher dung cover of livestock near settlements.

4.1 Grazing responses and environmental impacts

Vegetation cover declined by heavy grazing in meadows, indirectly reflecting forage removal. However, overall cover change should be treated carefully with consideration of plant species composition shift because if poisonous or unpalatable weeds increase under grazing, the vegetation cover will still increase at the cost of decrease in grassland quality. The strong controls of P and cvP for plant communities are in line with non-equilibrium theories, and results from other grassland systems (Cingolani et al., 2003; Fensham et al., 2010). The only significant change was an increase of annual forb richness in moist meadows, suggesting that frequently mechanical disturbance on dense *Kobresia* turf might create open soils and allow annuals to grow (Olff and Ritchie, 1998). The trivial responses in steppes might indicate grazing tolerance of species in drylands (Fensham et al., 2014) and perennials from meadows might be well adapted to grazing by different growth forms (Miehe et al., 2009). Therefore, further studies on plant functional traits (Díaz et al., 2007), such as life form, forage quality and palatability (Klein et al., 2007, 2008) might help to better understand plant responses to grazing.

Small mammals did not respond to grazing except for marginally higher abundances with lower vegetation cover under heavy grazing conditions (Fig. S2). Similar results have been reported in other regions of the plateau, indicating livestock grazing might lead to soil degradation and support higher density of small mammals (Delibes-Mateos et al., 2011; Pech et al., 2007). However, small mammal richness is related to litter amount and vegetation heterogeneity (Eccard et al., 2000; Giuliano and Homyack, 2004) and thus should be further investigated. Moreover, different species might show varying responses to livestock grazing (Root-Bernstein and Ebensperger, 2013). In steppes, temperature and relief explained a large share of the variance in small mammal communities, thereby reflecting a combination of heat and intensive radiation could exert pressures on small mammal survival in drylands (Walsberg, 2000). In meadows, climatic conditions are relatively more suitable throughout, so abiotic controls were less pronounced.

Ant richness did not respond to grazing, habitat or their interaction, but ant abundance tended to be higher at lower elevations (Fig. S2). Similarly, limited grazing responses were found in other arid grasslands (Read and Andersen, 2000; Whitford et al., 1999), implying the overruling abiotic controls on ants (Hoffmann and James, 2011). Strong effects of elevation and relief point to the importance of surface runoff, infiltration, soil moisture and heat gain for ant communities (O'Geen et al., 2007). Further fine-scale studies on specific species (Hoffmann and James, 2011), functional groups (Andersen, 1995) or foraging characteristics (Milton et al., 1994) would aid the understanding of ant responses to grazing and abiotic conditions.

Soils are crucial because changes of nutrients affect productivity and may cause slow but lasting degradation (Breman and de Wit, 1983; Milchunas and Lauenroth, 1993). Strong correlations between soil C, N, P and vegetation cover suggested nutrient limitation, which has been reported from fertilization experiments in alpine meadows (Li et al., 2014) and dry steppes (Wesche and Ronnenberg, 2010). We found an overall reduction in soil C and N, but an increase in available P by heavy grazing. In line with the global patterns (McSherry and Ritchie, 2013; Schrama et al., 2013), grazing effects on soil C and N were negative in productive meadows but minor or even slightly positive in drier steppes (Fig. S2). Livestock triggers nutrient translocation towards settlements in dry grasslands (Augustine, 2003; Stumpp et al., 2005). Plant available P is higher near the settlements because P is released in faeces that are largely deposited at night.

Hyperspectral indicators provided reliable information for grazing intensity. NDVI is closely connected to vegetation cover and related to soil nutrients. NDNI and REP_LE are responsive to grazing through the connection of biomass (Cho and Skidmore, 2006), foliar nitrogen content (Feng et al., 2008) and chlorophyll content (Lehnert et al., 2014). Hyperspectral data also associate to small mammal communities because of the connection to bare soils. Those connections demonstrate that remote sensing techniques could detect important biophysical properties of ecosystems (Kerr and Ostrovsky, 2003).

Within biotic indicator groups, richness and abundance were typically correlated, suggesting biodiversity and biomass respond to similar drivers (Bai et al., 2007; Ma et al., 2010). Across indicator groups, plant richness, vegetation cover, soil nutrients and hyperspectral data were correlated to each other. However, indicator groups differed in sensitivity to grazing and environmental factors, and therefore displayed generally low correlations in multivariate spaces. Grazing assessments should therefore consider a comprehensive range of biotic and abiotic attributes within the systems.

4.2 Grazing degradation threat on the Tibetan Plateau

Given that differences between light and heavy grazing were generally limited, the widely held notion of widespread threat of grazing degradation on the Tibetan Plateau seems to be too simplistic. Most previous studies of grazing effects on plant and soil have been only based on single sites and thus show varying results in different parts of the plateau (e.g. Luan et al., 2014; Wu et al., 2009). However, interactions of grazing effects and environmental factors have never been explored within a single multi-site field study on multiple trophic groups, although few field studies separately indicated abiotic controls varied among sites (Qian and Shimono, 2012; Wen et al., 2013; Wu et al., 2012) and manipulated grazing and warming interactively affected plant richness, productivity (Klein et al., 2004, 2007), soil nutrient availability (Wang et al., 2012) and plant-insect interaction (Cao et al., 2015) on plot level.

Small mammals are often considered as a cause of grassland degradation, so most studies focus on the effects of burrow density on plant/soil properties (Guo et al., 2012; Sun et al., 2015). Few studies, however, have linked small mammal communities to livestock grazing levels. The few exceptions indeed show varying responses to increased grazing (Raoul et al., 2006). Grasshoppers have been reported to respond to increased grazing (Kang et al., 2007; Zhong et al., 2013; Zhu et al., 2012), but no study on ants is available across Tibetan pastures.

5 Conclusion and outlook

Our study reveals the importance of selecting appropriate indicators for grazing assessments . Among those tested, plants and soils were responsive to increased grazing, and the correlations with NDVI and REP_LE indicate that response patterns can be upscaled by remote sensing. Spectral indicators were also correlated with small mammal abundance and community composition, yet more data are needed to check how these relate to grazing.

Even for potential grazing indicators, effects were only significant after filtering local environmental impacts. Responses of soils, and hyperspectral indicators tended to be stronger in the moister parts of our study region, while grazing effects on vegetation cover and annual forb species were smaller at drier sites. The strong climatic controls are in line with general theories in rangeland ecology that predict relatively weak grazing effects in less productive environments (Cingolani 2005). While mean values of precipitation and - to a lesser extent - temperature clearly were important, we did not find evidence for an additional effect of interannual climatic variability (cvP). Non-equilibrium theory with its focus on variability (Swift et al) may thus not apply in Tibet. Indeed, the coefficient of interannual variation mostly is below 30%, a threshold commonly applied to invoke non-equilibrium dynamics (Ellis & Swift, von Wehrden et al. 2012)

In addition, cvP values could not reflect the climatic variability in terms of snow events, which can reduce the number of livestock and strongly affect local livelihoods, particularly in regions with sufficient summer rainfall (Shang et al., 2012). Heavy snowfall can also promote plant growth in the following season (Dorji et al., 2013b), but how do the amount and variability of snow influence grassland health is still poorly understood on the Tibetan Plateau.

Moreover, we acknowledge the local grazing management practices and policy implementations might differ among sites and affect the grazing effects although the evolutionary grazing history across Tibetan pastures is long (Miehe et al., 2014). Thus grassland managements and policies should avoid *one-size-fits-all* strategies. Fixing stocking rates by estimated carrying capacities may be reasonable for productive regions, but climate variability should be taken into account across Tibetan pastures. Traditional managements relying on seasonal mobility and local-site adjustment are likely to be more effective for conservation and the sustainable use of dry or cold rangelands.

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Chapter 6 Responses of hyperspectral data

Retrieval of grassland plant coverage on the Tibetan Plateau based on a multi-scale, multi-sensor and multi-method approach

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Abstract

Plant coverage is a basic indicator of the biomass production in ecosystems. On the Tibetan Plateau, the biomass of grasslands provides major ecosystem services with regard to the predominant transhumance economy. The pastures, however, are threatened by progressive degradation, resulting in a substantial reduction in plant coverage with currently unknown consequences for the hydrological/climate regulation function of the plateau and the major river systems of SE Asia that depend on it and provide water for the adjacent lowlands. Thus, monitoring of changes in plant coverage is of utmost importance, but no reliable tools have been available to date to monitor the changes on the entire plateau. Due to the wide extent and remoteness of the Tibetan Plateau, remote sensing is the only tool that can recurrently provide area-wide data for monitoring purposes. In this study, we develop and present a grassland-cover product based on multi-sensor satellite data that is applicable for monitoring at three spatial resolutions (WorldView type at 2-5 m, Landsat type at 30 m, MODIS at 500 m), where the data of the latter resolution cover the entire plateau. Four different retrieval techniques to derive plant coverage from satellite data in boreal summer (JJA) were tested. The underlying statistical models are derived with the help of field observations of the cover at 640 plots and 14 locations, considering the main grassland vegetation types of the Tibetan Plateau. To provide a product for the entire Tibetan Plateau, plant coverage estimates derived by means of the higher-resolution data were upscaled to MODIS composites acquired between 2011 and 2013. An accuracy assessment of the retrieval methods revealed best results for the retrieval using support vector machine regressions (RMSE: 9.97%, 7.13% and 5.51% from the WorldView to the MODIS scale). The retrieved values coincide well with published coverage data on the different grassland vegetation types.

Keywords

Tibetan Plateau, plant coverage, degradation monitoring, MODIS, SVM regression, partial least squares regression, linear spectral unmixing, spectral angle mapper, vegetation indices

1. Introduction

Plant coverage is a key proxy used to estimate and monitor important ecosystem parameters and functions by remote sensing, particularly for such expanses as the grasslands on the Tibetan Plateau. Important cover-related parameters and functions are primary production (PP; Seaquist et al. 2003), evapotranspiration (ET; Mu et al. 2007) and leaf area index (LAI; Soudani et al. 2006), where PP is commonly used as a proxy of CO_2 fluxes (Wylie et al. 2003) and ET is used to investigate interactions among vegetation, hydrology and climate (Murray et al. 2013). In addition, plant coverage and its changes over time have been directly used as an indicator for grassland degradation in several studies (e.g., Gao et al. 2010). The Tibetan Plateau hosts the world's largest high-mountain grassland ecosystem, and it significantly influences the hydrology of East and South-East Asia (Piao et al. 2010). The plateau, with its extended pastures, serves as a globally important "water tower", providing water for nearly 40% of the world's population (Barnett et al. 2005, Xu et al. 2008), and it plays an important role in monsoon generation (Ding & Chan 2005; Mölg et al. 2014). Despite their great importance, the pastures of the plateau are threatened by environmental change. To date, there is strong evidence that degradation of the grassland due to climate change and overgrazing may alter the phenology of the vegetation, thus adversely affecting ecosystem stability on the plateau (Harris 2010; Zhang et al. 2013). Consequently, monitoring the state changes of the Tibetan grasslands under conditions of global environmental change is of utmost importance.

Information about plant coverage of the grasslands on the Tibetan Plateau is important for various stakeholders. On the local scale (covered by WorldView-type satellite data), a plant coverage monitoring product would improve the early detection of over-grazing and would allow adjustment of the carrying capacities of the spacious rangeland ecosystems (Cao et al. 2013). On the regional scale (covered by Landsat-type satellite data), knowledge of changes in plant coverage is essential for county administrators who assign rangeland to the farmers (Banks et al. 2003). On the plateau scale (MODIS data), detailed knowledge on pasture degradation is particularly interesting for scientists, e.g., to simulate the effect of land-use changes on hydrological and atmospheric processes (Cui & Graf 2009).

Because of the enormous spatial extent and remoteness of the Tibetan pastures, it is obvious that remote sensing is the only tool for assessing and monitoring the plateau's plant coverage. To be suitable for the different stakeholders mentioned above, a remotely sensed plant coverage product for the grasslands of the Tibetan Plateau must have a spatial resolution fine enough to cover local terrain effects and to differentiate the pastures belonging to a village.

To warrant its suitability for monitoring purposes, the temporal resolution must be high enough to allow comparisons between seasons and to investigate differences among years. Thus, satellite systems offering continuous and consistent data over a long time are a precondition for an operational monitoring product.

Previous attempts at plant coverage monitoring on the Tibetan grasslands using remote sensing have mainly been based on the analysis of normalized difference vegetation index (NDVI) data, either by inspecting NDVI time-series (Zhang et al. 2013) or conducting change-detection analysis (Gao et al. 2010). However, the link between plant coverage and NDVI is sometimes ambiguous because the index is highly sensitive to the soil background signal, particularly in arid (and/or degraded) environments with low vegetation cover (Huete et al. 1997). Thus, to make the plant coverage product suitable for estimation and monitoring purposes regarding, e.g., the provisioning of ecosystem services by pastures, the satellite reflectance values must be transformed into plant coverage. This transformation can be achieved using field-derived transfer functions, which have been established for single sites (e.g., Liu et al. 2014) but not for the entire plateau. Other possibilities to derive plant coverage from remotely sensed images are the application of linear spectral unmixing (LSU, Göttlicher et al. 2009) and spectral angle mapper (SAM; Yang & Everitt 2012) techniques. One simple and fast method to translate reflectance values or SAM distances into plant coverage values is linear-regression analysis. This method has been applied in a variety of studies (Meyer et al. 2013; Psomas et al. 2011; Zha et al. 2003). More advanced multivariate methods used to retrieve plant coverage from satellite data encompass partial least squares regressions (PLSR) and machine-learning algorithms such as support vector machines (SVM), which have been evaluated as a valuable tool to cope with non-linear relations and highly correlated predictor variables. Thus, SVM might be advantageous in studies of complex interacting systems. For instance, Schwieder et al. (2014) recently highlighted the high potential of SVM for the determination of fractions of land cover types in satellite images.

However, none of the previous studies have answered the question of which method is most suitable for deriving plant coverage, particularly on the Tibetan Plateau. Consequently, reliable and area-wide information on plant coverage and its changes over time is lacking to date. Therefore, the paper has two objectives:

- Objective one is to compare different methods to derive the summer plant coverage of the grasslands on the Tibetan Plateau. In this context, plant coverage information is derived along a cascade of satellite data with three spatial resolutions. This allows for a direct link between locally observed plant coverage and satellite-derived values. The methods to be compared are (i) LSU, (ii) SAM in combination with linear regression, (iii) PLSR and (iv) SVM regression based on the same feature space comprised by vegetation indices (VI) and normalized difference indices (NDI).

- Objective two is to apply the method with the highest accuracy to generate a summer (JJA) plant coverage dataset for the grasslands of the Tibetan Plateau for the years with field data at hand (2011 – 2013), based on Moderate Resolution Imaging Spectroradiometer (MODIS) imagery.

First, a short overview of the considered grassland vegetation types on the Tibetan Plateau is given. Then, the upscaling methodology to compare the different estimation methods to derive plant coverage on three spatial scales is described. In the third part, we present and discuss the results, including the finally generated grassland cover data set.

2. Grasslands on the Tibetan Plateau

Plant coverage on the Tibetan Plateau is calculated for the most widespread and grazed grassland vegetation types. For further processing, grassland areas were pre-assigned to the five major grassland vegetation types on the Tibetan Plateau as proposed by Hou (2001): (1) *Kobresia pygmaea* pastures, (2) *K. humilis* pastures, (3) swamps and salt marshes, (4) montane and (5) alpine steppes. The distribution of the grassland vegetation types under investigation is shown in Fig. 1.

Kobresia humilis pastures (Fig. 2a) are widespread in the north-eastern Tibetan Plateau between 3300 and 3600 m, and they grow under 400-600 mm of mainly summer precipitation. The plant cover normally exceeds 80%, and a typical *Kobresia* pasture is composed of 30 to 40 species. In less-grazed areas, grasses up to 40 cm of height overgrow the widespread Cyperaceae, which reach 10 to 20 cm in height. If pastures are intensively grazed, grazing weeds (*Stellera chamaejasme*, *Ligularia tangutica*, *Iris* spp., *Cryptothladia kokonorica*), which are generally taller than the Cyperaceae, may cover up to 30% of the area. Since the mid-Holocene optimum (8,000 BP), these grasslands have replaced forests of *Picea crassifolia* and *Juniperus przewalskii* due to human impact (Miehe et al. 2014).

Montane steppe is also a secondary grassland vegetation type. It occurs in areas with lower rainfall and terrain altitude. Tussocks of *Stipa splendens* and the poisonous bunch grass *Achnatherum inebrians* grow up to 80 cm tall in a grazing lawn of 2–5 cm consisting of matted *Sibbaldianthe adpressa*, *Potentilla bifurca*, *Heteropappus* spp., and annual *Artemisia* spp. The total cover of the steppe, with its approximately 20 species, ranges between 30 and 60%. The number and cover of matted and rosette grazing weeds are highest in comparison to the other grassland vegetation types considered in this study.

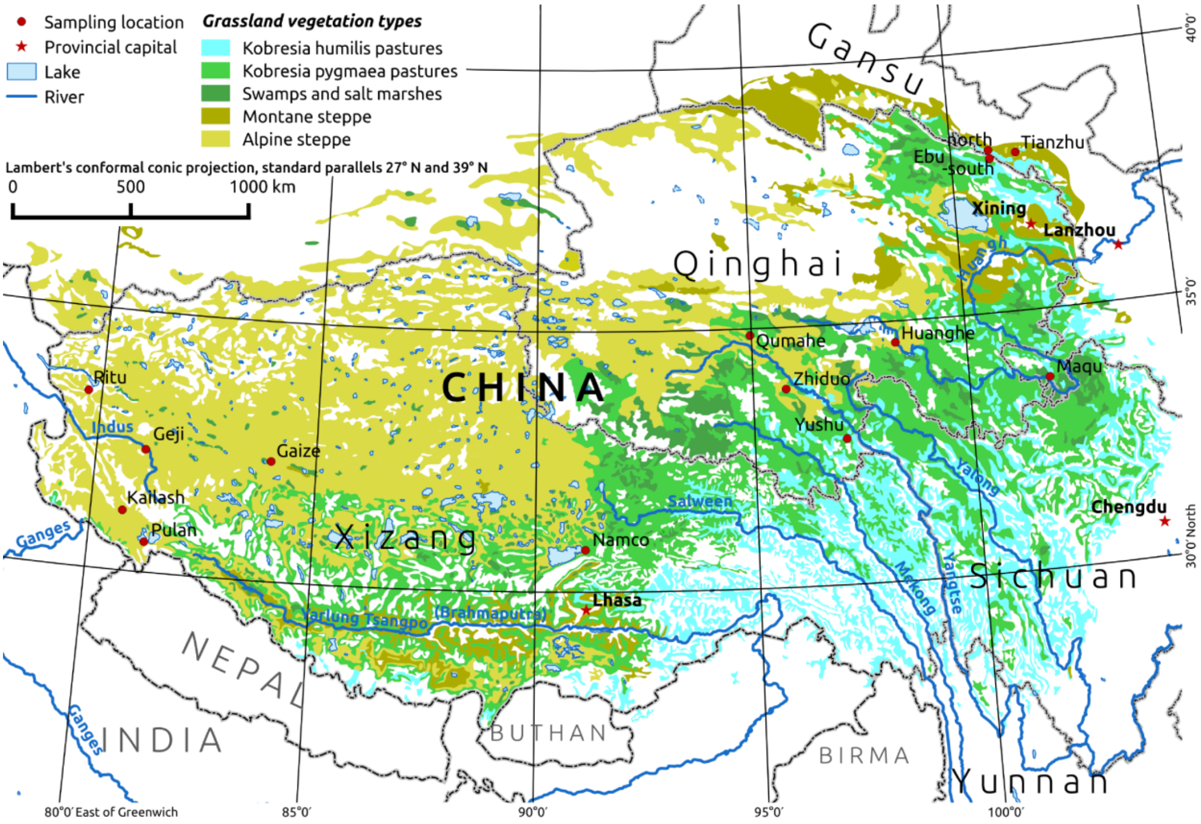

Fig. 1 Distribution of grassland vegetation types. The extent of *Kobresia pygmaea* pastures is taken from Miehe et al. (2008a), with other vegetation types taken from Hou (2001). Sampling locations are shown as red points.

Kobresia pygmaea pastures cover the humid south-eastern quarter of the Tibetan Plateau (450,000 km²; Fig. 2b). The altitudinal range of this alpine plant community is globally unique, forming the world's highest alpine vegetation (up to 5960 m) on sunny slopes. In the core area, the tiny sedge *Kobresia pygmaea* (2–4 cm in height, Fig. 2c) forms a nearly monotypic pasture on a felty turf with up to 98% cover, dominating the plant composition by 90% abundance. The closed grasslands are generally species-poor (average 10 species). In areas of *Kobresia pygmaea* pastures with higher disturbance and in the ecotone towards the Alpine steppe (Fig. 2d), the mosaics of *Kobresia pygmaea* turfs are surrounded by a vegetation on open sands and gravels composed of rosette plants and alpine cushions (average 24 species).

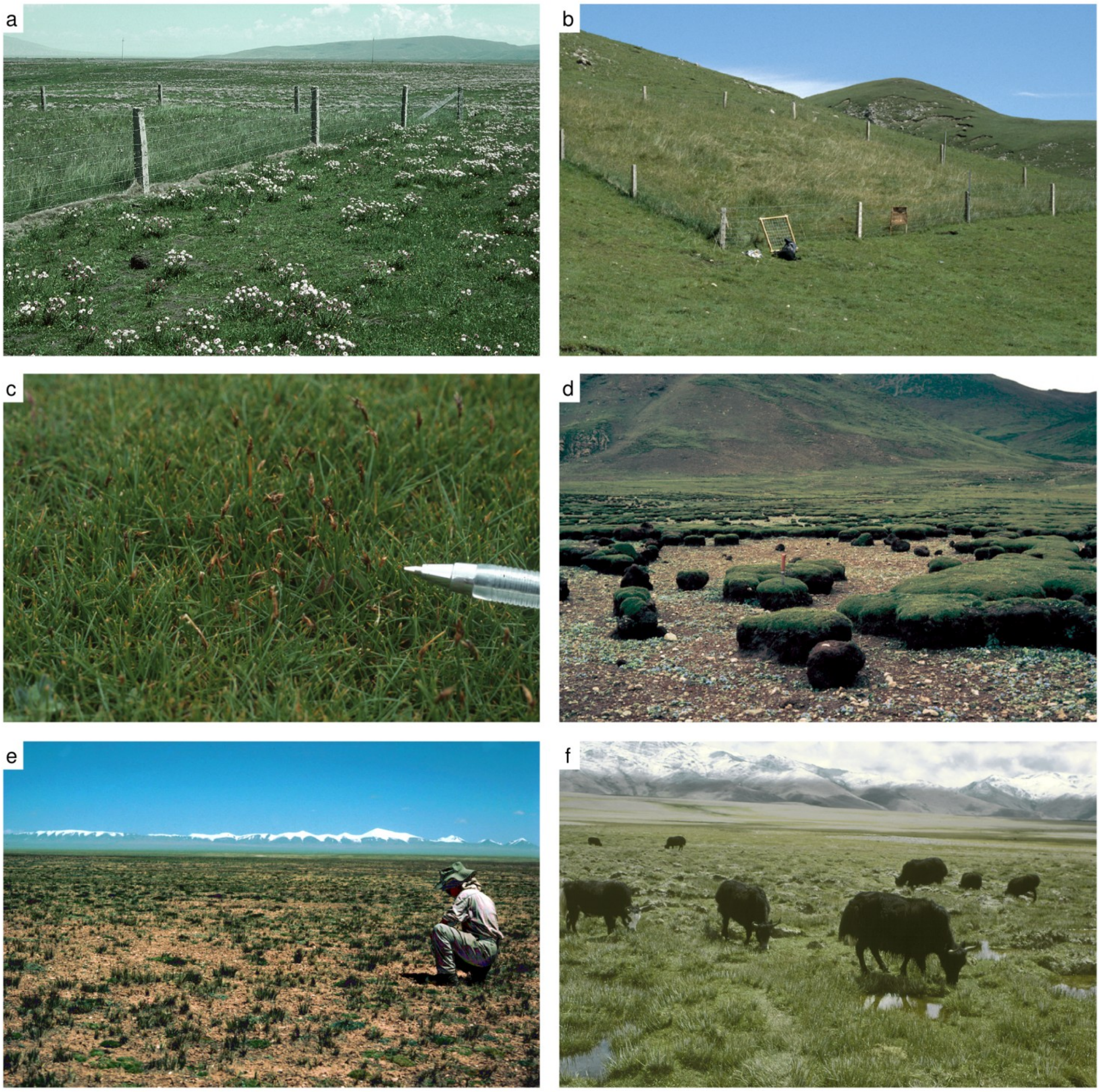

Fig. 2 Photographs of the investigated grassland vegetation types on the Tibetan Plateau. *Kobresia humilis* pastures are widespread in the montane belt of the north-eastern highlands. Selective free-range, which is the traditional livestock management practice, results in high abundances of grazing weeds such as *Stellera* (white flowers) (a). *K. pygmaea* (b-d) pastures cover a huge altitudinal range between the montane belt, probably replacing former forest (b), and build firm felty grazing lawns in the alpine belt (c). The disintegration process of those felty root mats (d) is poorly understood but is widespread in the ecotone between both major ecosystems. The alpine steppe (e) is a Central Asian short grass steppe with cushion plants, which is widely grazing resilient. *Kobresia schoenoides* swamps (f) are the most important grazing reserves and are under great grazing pressure. The steppes' vulnerability is the bottleneck of the pastoral system of the entire plateau.

Alpine steppes are Central Asian short-grass steppes in the arid northwest of the Tibetan Plateau associated with alpine cushions plants. This grassland vegetation type covers an area of approx. 800,000 km². The less diverse *Carex moorcroftii* desert steppe normally consists of 2–8 species. Cushion plants dominate at 50–100 mm of summer precipitation at elevations between 4500 and 5400 m in the remote north of the Tibetan Plateau (Fig. 2e). The moister eastern region with 100–400 mm of rainfall is characterized by a mean cover of 35% and an average of 25 species. *Carex montis everestii* is common in the south, while *Stipa purpurea* is found throughout the area. The majority of the species are resistant against grazing.

The swamps of the Tibetan Plateau are largely dominated by felty hummocks of *Kobresia schoenoides*, a plant forming tussocks up to 30 cm high (Fig. 2f). They cover approximately 80,000 km^2 on the Tibetan Plateau. Intact swamps not containing too much salt in the water have a closed vegetation cover.

3. Data and Methods

In this paper, plant coverage is derived along a cross-scale set of satellite data with three spatial resolutions (scales) using RGB and hyperspectral field surveys as references. At each scale, four methods (SAM, LSU, PLSR, and SVM) were applied to retrieve plant coverage from the satellite data. First, we briefly outline the field-sampling methods. The second and main part of this section describes the upscaling methodology, the four methods used to derive plant coverage at each scale and the error propagation and validation approaches.

3.1 Field methods and data

Field data were taken during the growing seasons in 2011, 2012 and 2013. Overall, the field studies of grassland vegetation at 14 locations covered all major grassland vegetation types of the Tibetan Plateau (Fig. 1). At all sampling locations, plant coverage was recorded by analyzing digital photographs and visual estimations. Previous field studies on the Tibetan Plateau have demonstrated a positive correlation between plant coverage and distance to settlements (Dorji et al. 2013; Lehnert et al. 2013; Lehnert et al. 2014; Meyer et al. 2013). Consequently, we applied a unified transect design for the field surveys to cover the entire range of vegetation-degradation stages at each location. Transects started at villages or camp sites. Transect length was kept variable depending on the distance to neighboring settlements and the land-use rights of the village under investigation. Digital photos/visual plant coverage estimates were taken/conducted along transects with a constant distance. The geographic locations of the sampling sites were recorded by using a GPS-device. The digital photos with a vertical field of view were taken with a common digital camera. The height and the focal length of the camera were always kept constant. To calculate the ground size of each photo, a measuring tape was arranged at the edge of the photos. Additionally, plant coverage estimates were visually conducted by an experienced observer on 10x10-m plots at the starting and ending points of each transect.

The definitions of pure reference spectra (spectral endmember) of the surface types of interest (e.g., pasture species, soil) are generally required to apply LSU and SAM. These reference spectra can be either extracted directly from satellite images or measured *in situ* with a spectrometer or a hyperspectral camera. A common problem when reference spectra are extracted from satellite images is the mixed pixel effect, with increasing pixel resolution preventing the capture of pure spectral endmember information. This is especially problematic in arid areas, where vegetation is usually characterized by very small-scale patches in subpixel resolution. To avoid this problem, we used endmember spectra measured *in situ* at each sampling location using a HandySpec field spectrometer. This instrument provides reflectance values between 305 and 1705 nm with a spectral resolution of 1 nm. Soil spectra were measured with different soil water contents (soil endmember spectra). Vegetation spectra were taken from single plants (species endmember spectra). To this end, leaves were cut and arranged to achieve a leaf area index of one. For noise reduction in the captured data, all spectra were filtered with a Savitzky-Golay filter (filter length=15 nm). To generate endmember spectra for the grassland vegetation types, all species endmember spectra from each grassland vegetation type were averaged (vegetation endmember).

3.2 Calculation of plant coverage from digital images

Using the digital photographs taken from each measuring plot, we derived the plant coverage within the footprint of the digital photo. We calculated an image (*e*) from the RGB values in which green vegetation was enhanced using the following formula (Woebbecke et al. 1995):

$$e = 2g - r - b \tag{1}$$

where g, r, and b are the digital values in the green, red, and blue channels. By applying a manual threshold, we selected green vegetation pixels and calculated the plant coverage of the green vegetation in the images.

3.3 Satellite and auxiliary data

We used satellite data with three spatial resolution levels: (i) WorldView-2 (2 m nominal spatial resolution), Quickbird (2 m) and RapidEye (5 m) at the local scale; (ii) Landsat 7 (30 m) and Landsat 8 data (30 m) at the regional scale; and (iii) MODIS BRDF-corrected composites (MCD43A4; Schaaf et al. 2002; 500 m) at the plateau scale.

Data at the WorldView scale were ordered prior to field surveys to minimize the time lag between field and satellite observations. For the regional-scale analysis, Landsat scenes were downloaded from United States Geological Survey (USGS) website (http://earthexplorer.usgs.gov). All Landsat data used are taken at a time-span of one month around the acquisition time of the corresponding WorldView-scale imagery. For a summary of satellite data used at the WorldView and Landsat scales, see Table 1 in the supplementary material. MODIS 16-day composites were downloaded from the Atmosphere Archive and Distribution System (LAADS) FTP server for summer months between 2011 and 2013.

The Aster digital elevation model data (GDEM, Tachikawa et al., 2011) were used to generate altitude data for the topographic correction of satellite data. On the MODIS scale, the MODIS MCD43A2 quality product data was used to exclude pixels for further processing contaminated by snow. An important step is the pre-selection of MODIS pixels on the plateau that are covered by grassland vegetation for which MODIS data was principally masked. This step was performed with the help of the digital and co-located map presented in Fig. 1 (Hou 2001). Because of the pre-assignment of the pixels based on only one GIS map, land-use changes potentially appearing over the time span of the MODIS time series might blur the pre-assignment. Thus, MODIS pixels affected by land-cover changes (mostly to croplands and urban/built-up areas) were eliminated from later plant coverage retrieval based on land use information in the annually available MODIS land-cover product (MCD12Q1, Friedl et al. 2010), which is used to mask each MODIS composite of the same year. For the calculation of the final plant coverage map, only pixels were included and were classified as grasslands in all years. However, it should be stressed that pixels affected by changes from grassland to the classes “barren or sparsely vegetated” were not removed from further processing because the change may contain important information regarding the usage of the product for pasture degradation monitoring.

3.4 Preprocessing of satellite data of the WorldView and Landsat scales

Preprocessing of satellite data of the WorldView and Landsat scales encompassed three steps: (i) geometric, (ii) atmospheric and (iii) topographic correction.

Geometric correction was performed to ensure that spatially corresponding pixels from the two scales overlapped. The WorldView scale was used as the reference where Landsat scale data was co-registered to the WorldView-scale by selecting corresponding ground control points (GCPs) in both images. For each image pair, at least six GCPs were identified. A first-order polynomial was used for transformation.

Atmospheric correction was conducted to ensure the spectral comparability of reflectance values in different satellite scenes of the same sensor. To match satellite-retrieved reflectances, a proper atmospheric correction is required, particularly for the SAM and LSU methods, which rely on reference spectra measured on the ground. To cope with the huge volume of image data in atmospheric correction, a modified and fully automatic version of the 6S radiative transfer code extended for spatial raster applications was developed and applied (for the 6S code, refer to Vermote et al. 1997; for the modifications, see Curatola Fernández et al., 2015). The atmosphere at the time of image acquisition was approximated by using the pressure, temperature and humidity profiles from NCEP reanalysis data (Kalnay et al. 1996). Ozone and aerosol contents were taken from Aura OMI data (Dobber et al. 2006; Levelt et al. 2006). To properly process the state-of-the-art sensor data, WorldView-2, RapidEye, Quickbird, and Landsat-8 sensors with their respective spectral-response functions and acquisition geometries were included in the 6S code.

To remove the effects of topography and illumination on reflectance values of the satellite data, the statistical-correction method of Teillet et al. (1982) was applied to the data at the Landsat scale. Therefore, the digital elevation data model was bilinearly resampled to the resolution of the satellite data.

At the Landsat scale, cloud-free image composites covering the respective field transects were compiled. In the first step, clouds and cloud shadows were classified manually. Then, if only Landsat 7 data were available, the pixels affected by scanner errors were excluded and added to the cloud masks. For further processing, only pixels without errors and clouds were selected. If two or more scenes could provide the same pixel for the composite, the pixels with the greatest proximity of acquisition time between the Landsat and WorldView-scale imagery were used. A statistical radiometric normalization was applied to inter-calibrate the different scenes in each composite (Elvidge et al. 1995). For this purpose, the Landsat scale image in closest temporal proximity to the spatially corresponding WorldView scale image was selected as a reference. Pairwise linear regression models were fitted between the reflectance values of the Landsat scale reference image and each other Landsat scale image by only considering pixels not affected by clouds or scanner errors in both images. The derived regression model was afterward applied to all other reflectance values of the images to be normalized.

3.5 Upscaling of plant coverage from ground transects to MODIS scale

3.5.1 Concept and overview

The general processing scheme for upscaling grassland plant coverage is depicted in Fig. 3 and encompasses the following steps:

- At the WorldView scale, the plant coverage values were only estimated for pixels that are covered by field observations and the surroundings of those pixels inside the spatially collocated Landsat pixel. To transform pixel reflectance values into plant coverage, several methods (SAM, LSU, PLSR, and SVM) were applied as described in the following sections in more detail. The plant coverage values derived from the in-depth analysis of digital photographs taken during field work at the locations of Worldview scale pixels were used to derive statistical regression models between satellite and *in-situ* values. An exception is the LSU method, where the endmember fractions of vegetation were directly used as plant coverage values. Afterward, the plant coverage values determined at the WorldView scale were spatially aggregated to the Landsat scale (30-m nominal pixel resolution) by averaging all pixel values from the WorldView scale spatially belonging to each respective and co-located Landsat pixel.
- At the Landsat scale, all Landsat pixels were selected that covered at least one sampling site and the surroundings of those pixels inside the spatially collocated MODIS pixel. Their spectral information was then used to train new regression models. As reference data to train the linear (SAM), PLSR and SVM regression models, the co-located and spatially aggregated values previously calculated from the WorldView scale were used. The resulting models were then applied to the entire Landsat dataset to estimate plant coverage values for all Landsat pixels. Afterward, the plant coverage values were spatially aggregated to the MODIS scale by spatially averaging all Landsat-derived plant coverage values belonging to each respective and co-located MODIS pixel.
- At the MODIS scale, the same model training and validation approach described for the Landsat scale was used to estimate plant coverage values for all relevant MODIS pixels. Thus, the spatially aggregated plant coverage estimates from the Landsat scale were used accordingly.

After validation of the entire model cascade (see 3.5.3), the approach with the highest accuracy was selected. Its associated regression model was then applied to all MODIS scenes (see http://pademos.org for data access). Finally, the mean plant coverage of grasslands on the Tibetan Plateau was calculated from the estimation maps using the MODIS land-cover products and the grassland vegetation types from Hou (2001) for the selection of grassland pixels.

3.5.2 Methods to derive plant coverage

Because the first aim of the article is to compare different methods to derive plant coverage on the Tibetan Plateau (Fig. 3), these methods will be outlined below in more detail.

3.5.2.1 Linear spectral unmixing and spectral angle mapper

LSU was applied to directly calculate the percentage of each of land-cover type (endmember) in mixed pixels (Sohn & McCoy 1997, Lehnert et al. 2014). Because we aim to estimate plant coverage across large scales, it must be noted that our knowledge of the spectral properties of the vegetation and soil over the grasslands of the entire plateau is certainly limited to our transect areas. Thus, we presume that the mean of all dry-soil spectra acquired in the field can be taken as a first guess for a representative average soil endmember for the whole plateau. Regarding vegetation analysis with LSU, we used different green vegetation spectra for each vegetation type (vegetation endmember). All endmember spectra taken in the field were spectrally resampled to the spectral bands of the respective sensor using the band-specific spectral response functions.

SAM is a frequently used measurement of distance between a known reference spectrum, e.g., ground measurement, and the reflectance values taken from satellite images (Kruse et al. 1993). We used the green vegetation endmember spectra as calculated for LSU as reference data.

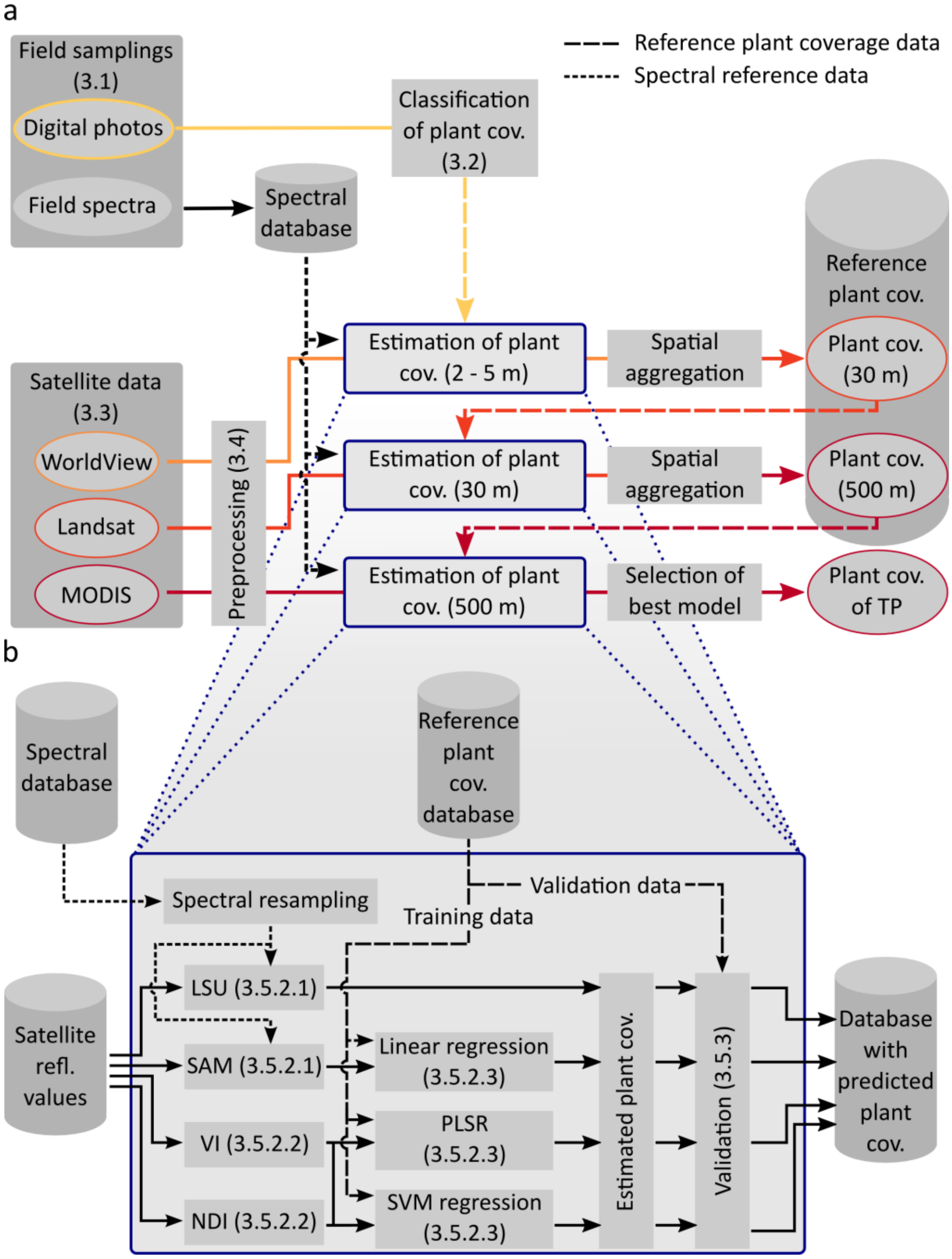

Fig. 3 Flow chart of the methodology: overall upscaling approach (a) and plant coverage estimation performed at each scale (b). The blue boxes in (a) correspond to the blue box in (b). Scales of satellite and in situ data are indicated by colors of lines and ellipses in (a). Numbers in brackets indicate the relevant section in the text.

3.5.2.2 Calculation of vegetation indices and normalized band indices

To derive plant coverage values from the satellite data without using spectral reference data taken at the ground, we extracted a feature space from the reflectance values encompassing a set of previously defined vegetation indices (enhanced vegetation index, EVI, Huete et al., 1997; soil-adjusted vegetation index, SAVI, Qi et al., 1994; modified SAVI, MSAVI, Huete 1988) (Table 2 in the supplementary material) and all NDVI-like normalized difference indices for each satellite sensor (NDI; Thenkabail et al. 2000) as predictors used for PLSR and SVM based plant coverage estimates (next section). The vegetation indices selected were required to be derivable from all sensors in our study.

3.5.2.3 Prediction of plant coverage using linear regression, partial least squares regression and support vector machines

Regression techniques are required to convert the SAM distances and the feature space into plant coverage values. Here, we applied three different approaches: (i) linear regression, (ii) partial least squares regression and (iii) support vector machine regression.

(i) In the linear-regression model, the SAM distances were fitted against the reference plant coverage values. We did not take non-linear relationships into account because the initial tests did not indicate any non-linearity between SAM distances and plant coverage.

(ii) PLSR was applied to estimate plant coverage values using the feature space comprised by the vegetation indices and the NDI values as predictors. To build PLSR models, one free parameter, the number of components used for the regression model, has to be defined. Therefore, the entire range of possible values (from 1 to the number of predictor variables) was tested and the optimum number of components was selected comparing the R^2 values from the cross validation.

(iii) SVM regression was the second approach to estimate plant coverage values using the same feature space as for PLSR as predictors. One of the important benefits of SVM regression models is the very good balance between estimation accuracy and overfitting (Mountrakis et al. 2011). We selected SVM regression for two additional reasons: (1) the indices must not be linearly dependent on plant coverage values, and (2) correlated predictors do not have an effect on the performance of the resulting SVM model. In general, there are three parameters that must be well defined to fit SVM models with high predictive performance: the cost value (C), the threshold for residuals that do not contribute to the regression fit (ε) and the Parzen window width (γ) for the radial basis function used as kernel. To define γ, C and ε, we tested exponential ranges of parameter values in a grid search as proposed by Schwieder et al. (2014). SVM regression models to estimate plant coverage were fitted for all possible combinations of the three parameters. The cross-validation of the derived models is described in the following section. The model resulting in the highest R^2 from cross-validation was chosen for further analyses.

3.5.3 Error propagation and validation of plant coverage predictions

Each approach in the model cascade at each scale was validated with a test dataset that was not used for model training at the same scale. If the dataset comprised more than 40 samples/pixels, one-third of the samples were used as test data to validate the predictive performance of the resulting model. If the number of samples was below 40, a leave-one-out cross-validation was performed. As error measurement, the root-mean-square error, the cross-validation correlation coefficient (r_{cv}) and the R^2-value of the linear relationship between predicted and observed plant coverage values were calculated.

The 30-m-resolution training samples used to fit the regression models at the MODIS scale encompass estimation errors at the Landsat scale model output. To quantify this error, we used Monte-Carlo simulations as proposed by, e.g., Gessner et al. (2013).

- The pixel estimates of plant coverage from the WorldView scale model were spatially aggregated to the MODIS scale resolution and assigned to the geographically corresponding MODIS pixels. Note that this aggregation was only possible if the MODIS pixel was completely covered by the respective satellite dataset at the WorldView scale.
- Then, the estimates of plant coverage derived from the Landsat scale model were spatially aggregated to MODIS pixels and then subtracted from the estimates of the WorldView scale data spatially aggregated to the MODIS pixels.
- Several distribution density functions (exponential, gamma, log normal, normal, Weibull) were fitted to the frequency distribution of the pixel differences, and the best-fitting ones regarding the PLSR and SVM regressions were selected. The success of the fitting was assessed by Kolmogorov-Smirnov tests and visual interpretation, respectively. In both cases, the normal distribution was selected as the best-fitting distribution density function.
- In Monte-Carlo simulations, the training samples at the MODIS scale were manipulated using random values from the respective error distribution functions. Afterward, the PLSR and SVM regression models were fitted with the manipulated training data and validated against the original data as described above. This step was performed 10,000 times.

4. Results

4.1 Accuracy of models to estimate plant coverage

Regarding the performances of the four different methods (LSU, SAM, PLSR, and SVM) used to estimate plant coverage on the Tibetan Plateau on three different scales, we found large differences in their estimation accuracies (Table 1). Regardless of the scale of the satellite data used for estimation, the highest error rates were observed in plant coverage values estimated by LSU, followed by those estimated by SAM. Higher accuracies were observed using NDI and vegetation indices in combination with PLSR. The best results were obtained for SVM regression.

Table 1 Accuracy of plant coverage estimations for sensors and methods applied in the approach. Underlined values are the method with the highest accuracy comparing RMSE values. Italic font symbolizes the method with the lowest accuracy.

Method	WorldView scale				Landsat scale				MODIS scale			
	Sensor	RMSE	r_{cv}	R^2	Sensor	RMSE	r_{cv}	R^2	Sensor	RMSE	r_{cv}	R^2
SAM	Quickbird	15.88	0.70	0.49	Landsat7	10.26	0.75	0.56	MODIS	8.00	0.77	0.59
	RapidEye	8.15	0.83	0.70	Landsat8	14.80	0.75	0.56				
	WorldView2-8	11.00	0.82	0.67								
LSU	Quickbird	*17.16*	*0.63*	*0.40*	Landsat7	*15.87*	*0.67*	*0.45*	MODIS	*12.65*	*0.94*	*0.88*
	RapidEye	*24.59*	*0.72*	*0.51*	Landsat8	*56.95*	*0.65*	*0.43*				
	WorldView2-8	*29.97*	*0.49*	*0.24*								
PLSR	Quickbird	13.28	0.78	0.60	Landsat7	8.05	0.92	0.84	MODIS	8.20	0.93	0.86
	RapidEye	13.28	0.78	0.60	Landsat8	5.38	0.98	0.95				
	WorldView2-8	6.45	0.90	0.81								
SVM	Quickbird	12.28	0.81	0.66	Landsat7	7.01	0.94	0.88	MODIS	5.59	0.95	0.91
	RapidEye	6.17	0.91	0.83	Landsat8	3.95	0.99	0.98				
	WorldView2-8	7.01	0.93	0.87								

In the approach for plant coverage estimation, six different sensors with three classes of spatial resolutions were used. At the WorldView scale, we found low accuracies in estimations based on Quickbird imagery. If RapidEye or WorldView-2 imageries were available, the error rates were much lower. This ranking was inverted for LSU, where the lowest errors were observed if the Quickbird data were unmixed. By comparing the two Landsat sensors, Landsat 7 revealed higher error rates than Landsat 8, except for LSU and SAM.

Regarding the estimation accuracies at the three scales of the cascade, we found the highest error rates at the local scale. Intermediate accuracies were observed at the Landsat scale, while the best results (RMSE below 6%) were yielded with MODIS at the plateau scale. Fig. 4 shows the predictions of the validation data at each scale using the SVM regression models. In general, no bias, and thus, no evidence for systematic under- or overestimation, was observed. However, scatter (and thus RMSE) is obviously decreasing toward lower-resolution imagery. Here, it must be stressed that the number of samples is declining with decreasing pixel resolution because several plots of the WorldView and Landsat scales are covered by only one co-located pixel in the Landsat- and MODIS-scale imagery, respectively. For PLSR, the pattern was similar to the results obtained from SVM regression (Fig. 1 in the supplementary material). However, the variation around the 1:1 line was far higher, especially at the WorldView scale. The largest variation was found for LSU estimates at all three scales. For LSU, a considerable overestimation of low plant coverage values was observed at the WorldView and Landsat scales.

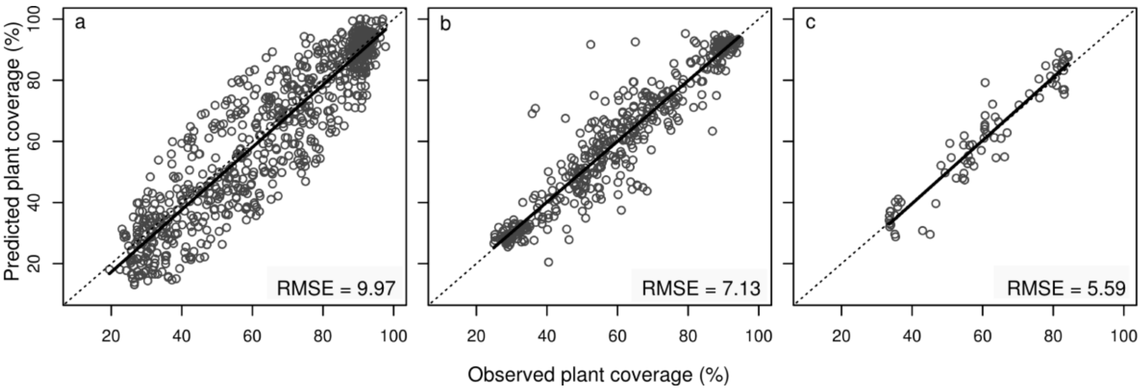

Fig. 4 Predicted vs. observed plant coverage for all sensors at the WorldView (a), Landsat (b) and MODIS scales (c) using SVM regression. The dotted lines are the 1:1 lines, and solid lines are linear regressions between observed and predicted plant coverage values.

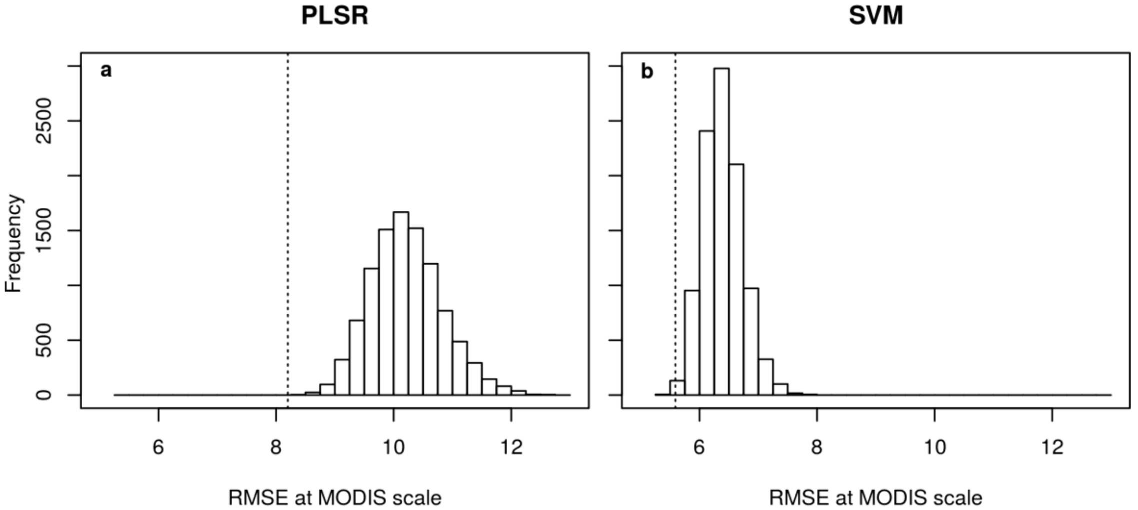

Fig. 5 Histograms of RMSE values from 10,000 Monte-Carlo simulations of plant coverage estimates at the MODIS scale with training samples randomly manipulated by the error distribution. The dashed vertical line is the RMSE obtained without manipulation.

4.2 Cross-scale error propagation

Although the accuracies regarding each single estimation model were promising, the cross-scale error had to be assessed, which was performed using Monte-Carlo simulations. Fig. 5 shows the results of the error propagation analysis for PLSR and SVM regression from the Landsat to the MODIS scale. The errors at the MODIS scale are partly the result of errors already introduced in the Landsat training samples used for training of PLSR and SVM regression models to derive plant coverage at the MODIS scale. The sensitivity to the error committed at the Landsat scale was much higher in PLSR than SVM. In the PLSR regression, RMSE values up to 13% were observed, whereas the maximum RMSE values of the SVM regressions were still below the RMSE value of the PLSR model trained on the original data (dashed line in Fig. 5a).

4.3 Spatial configuration of estimation errors

The spatial distribution of the estimation errors is shown in Fig. 6 for the SVM regression models. The highest errors at the local scale were observed in the central and northeastern region of the plateau, whereas error rates at sampling locations in the western and eastern region of the plateau were lower. At the Landsat scale, no clear geographical pattern of accuracies was observed. At the MODIS scale, a remarkably high error was found at Ebu North.

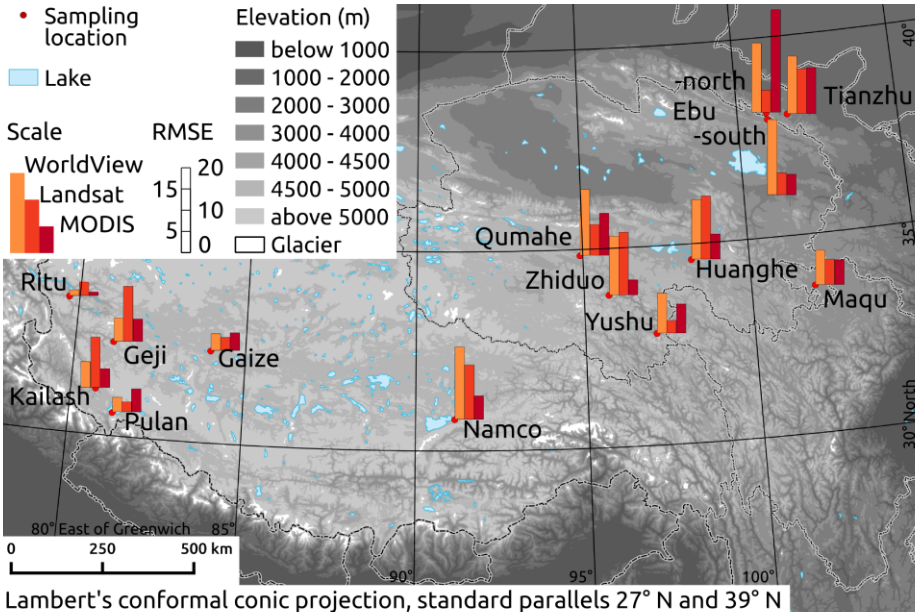

Fig. 6 Prediction errors of SVM regression at all sampling locations. The bar colors indicate the scale of plant coverage prediction. The bar heights correspond to the RMSE at the sampling location.

4.4 Application of the best performing model to estimate plant coverage of Tibetan grasslands

Fig. 7a shows the mean summer plant coverage of the grasslands on the Tibetan Plateau between 2011 and 2013 as calculated by the best-performing method (SVM regression) on the plateau scale based on MODIS data. In the western and north-western regions of the map, the mean plant coverage during the summer months was approximately 30%. In the eastern and south-eastern regions, values up to 95% were observed. The transition zone between both areas was approximately along the headwater regions of the large East Asian rivers. The histograms and boxplots in Fig. 7b depict the distribution of plant coverage estimates for all important grassland vegetation types. They show that the part covered by *Kobresia pygmaea* pastures had the largest numerical range of plant coverage values (9% and 84%), with higher values in the south-eastern region. Approximately 40% plant coverage was observed in the transition zone between *K. pygmaea* pastures and Alpine steppe vegetation. The highest mean plant coverage was observed in areas covered by *K. humilis* pastures (63%). The alpine-steppe vegetation is characterized by a low spatial variability and a small range of plant coverage values (30 – 44%).

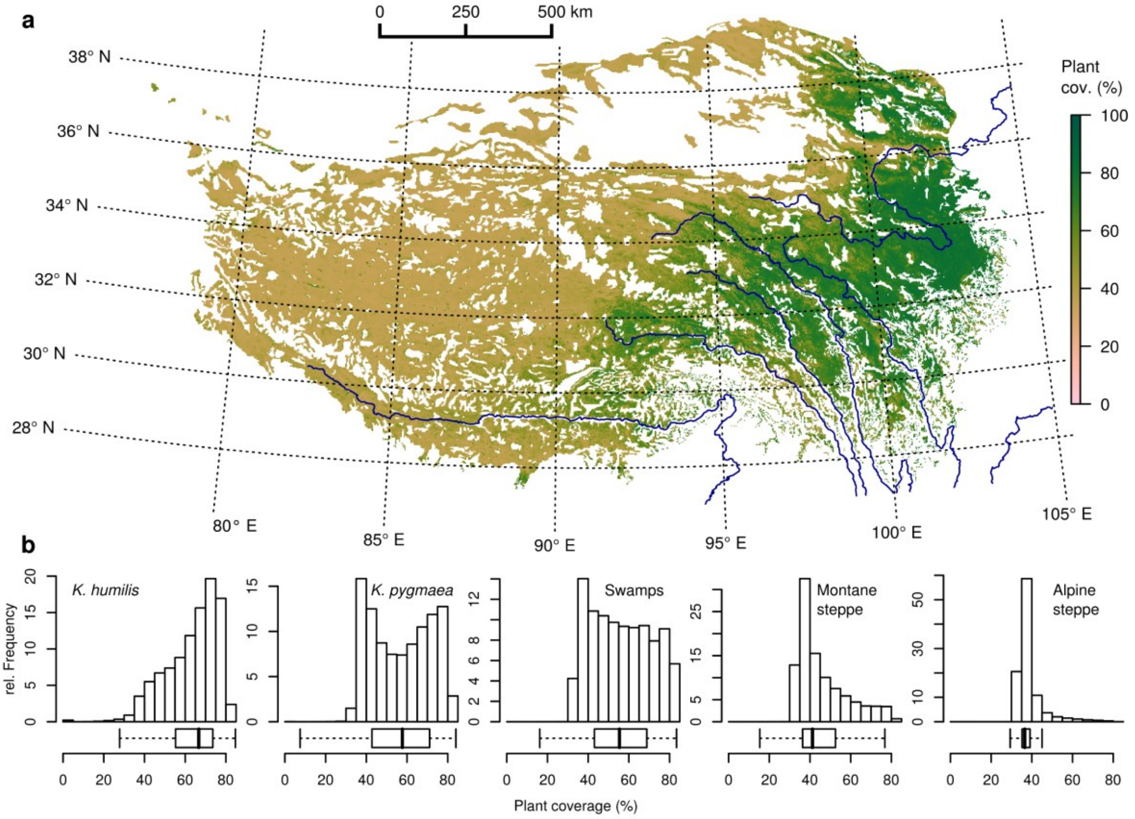

Fig. 7 Plant coverage (%) of the grasslands on the Tibetan Plateau. Colors indicate the mean values of all MODIS scenes acquired between 2011 and 2013 in June, July and August (summer period; **a**). White areas are not covered by grasslands of any of the investigated types. Histograms (rel. frequencies) and boxplots in (**b**) show the distribution of plant-cover values within grassland vegetation types (outliers are omitted in the boxplots; lines and boxes correspond to extreme values, the first quartile, third quartile, and the median).

5. Discussion

In this study, plant coverage was estimated along a cross-scale model cascade based on satellite data with decreasing spatial resolution. Although the accuracy of the estimations differed among the four methods applied, the quality of the estimations of the vegetation indices and normalized difference indices in combination with PLSR and SVM regressions was promising. The predictions using SVM regression were in particularly good agreement with the reference data of plant coverage.

According to a comparison of the estimation accuracies of the different approaches, the methods based on *in situ* spectral data (SAM, LSU) provided by a spectrometer at ground generally produced higher error rates than the methods using only the feature space derived from the reflectance values of the satellite imagery as predictors for plant coverage (PLSR, SVM). Comparing the two methods requiring spectral ground information, we found that LSU was unable to predict plant coverage on larger scales for the whole Tibetan Plateau. This finding shows that the great potential of LSU to estimate plant coverage for small areas on the Tibetan Plateau (Somers et al. 2011, Lehnert et al. 2014) might not extend to the plateau scale. The reason might be that LSU requires spectral knowledge (endmembers) of all major land-cover types and their variations over space and time. These requirements were difficult to meet for two reasons: (i) First, the area of our analysis encompasses all grazed grasslands on the Tibetan Plateau, so there are substantial knowledge gaps regarding the spectral properties of soils and non-organic components in areas not covered by field measurements. This inherent uncertainty led us to include only soil and vegetation as endmembers in the LSU analysis. A better result might be achievable if more endmembers, such as stones, would be included in LSU as shown in a previous study (Lehnert et al. 2014). However, the spectral properties of the stones depend on various factors, such as mineral composition, that greatly vary across the plateau and whose variation is largely unknown. (ii) Second, the spectral properties of soil within the spectral range of our sensors depend largely on the soil moisture content (Nagler et al. 2000). Therefore, the soils are spectrally highly variable in space and time, even between the time of our measurements and the acquisition of the satellite images. In general, it might be possible that the high LSU error also arises from an improper spectral description of the vegetation endmembers. For instance, the change in chlorophyll content at the end of the vegetation period may cause that *in situ* measured vegetation endmembers do not represent the vegetation in the satellite data. If so, the finding that the error rates of SAM were far lower than those of LSU would not be explainable. Therefore, we conclude that the vegetation endmember is not the primary source of error in our LSU analysis.

The accuracies of the PLSR and SVM regressions were higher than those for LSU and SAM. Because neither method depended on the *in situ* measured spectral data, this finding implies that our results were in better agreement with reference data when we relied only on the feature space calculated from reflectance values than when spectral properties of plants measured *in situ* were incorporated into the analysis. This may be explained by the time lag between the sampling of the vegetation spectra and the acquisition of the satellite data. Alternatively, the atmosphere may cause the satellite surface-reflectance values to differ from those measured *in situ,* or the choice of reference spectra in the SAM analysis may not reflect the spatial variability of the spectral properties of vegetation. The best method to derive plant coverage of pastures on the Tibetan Plateau was the combination of NDI values and vegetation indices in SVM regression. This finding underlines the great potential of SVM regression to analyze satellite imagery, as previously documented in several studies (Camps-Valls et al. 2006; Schwieder et al. 2014; Sun et al. 2009).

Irrespective of the method applied, the error rates decreased at lower spatial resolutions of the satellite data, a pattern that has already been addressed by previous studies deriving vegetation cover along satellite data of multiple scales (Gessner et al. 2013, Hansen et al. 2002). At the WorldView scale, where the highest error was observed, the most likely reason is that *in situ* observations were compared to satellite data only at this scale. The comparison of *in situ* observations with satellite data may cause higher error rates because of the unavoidable time lags between the acquisition of the reference and the high-resolution satellite data. At the Landsat and the MODIS scales, the differences in accuracies were lower than those between the WorldView and the Landsat scales. Although the overall lowest error rate was observed for Landsat 8, the total error of Landsat 7 and 8 was higher than at the MODIS scale. This occurred because the number of samples in Landsat 8 was considerably lower than that in Landsat 7. The reason is that the data from Landsat 8 were only available for the year 2013.

The spatial analysis of the accuracy of plant coverage estimates showed that SVM regression produced higher error rates in the central part of the Tibetan Plateau, where plant coverage is intermediate, than in areas with low or high plant coverage. The reason for this pattern was that the range of observed plant coverage values was highest at locations in the *Kobresia pygmaea* ecosystem in central Tibet. Here, cover values below 10% were observed in extremely degraded areas, while the cover values reached 90% at non-degraded plots.

Because the landscape is extremely patchy, often with less than 10 m distance between degraded and non-degraded plots, a spatial uncertainty of a few meters may cause high error rates at the WorldView scale. Subsequently, even if our field measurements indicated heavy degradation, the signal at the satellite sensor may be a mixture of degraded and less degraded vegetation because the spatial extent (< 1 m) of heavily degraded areas is frequently below the spatial resolution of the satellite data available at the WorldView scale. This may also explain why the error rates decreased at the Landsat and MODIS scales for locations in the *Kobresia pygmaea* ecosystem.

The geographical pattern in the configuration of error rates may also explain the large differences among sensors at the WorldView scale. Here, we found remarkably lower accuracies using Quickbird than RapidEye or WorldView-2 data. We had only three Quickbird images (Kailash, Namco and Qmarrhexiang) at our disposal. Thus, two of three scenes were located in the *Kobresia pygmaea* ecosystem. We compared the results of the plant coverage estimates using Quickbird and WorldView-2 imagery at the Kailash location and found nearly equal error rates. Thus, the accuracies of the estimations based on the Quickbird imagery were lower than for the RapidEye or WorldView-2 data because of the location of the Quickbird scenes in the transition zone between *K. pygmaea* and Alpine Steppe rather than the spectral resolution or spectral configuration of the Quickbird sensor.

The results of the plant coverage estimations at MODIS scale are affected by the estimation errors committed at the Landsat scale. In particular, we found a low sensitivity at MODIS scale on this estimation error if plant coverage was estimated with SVM regression. If PLSR was used, the error at the Landsat scale had a far greater effect on the accuracy of the estimations at the MODIS scale. Thus, we conclude that the error committed at the Landsat scale only slightly influences the total accuracy of the product.

The second objective of the article was to create the first plant coverage product for the grasslands of the Tibetan Plateau. Here, the mean plant coverage of the Tibetan grasslands ranges from 30% in the western and north-western regions to 95% in the eastern and south-eastern regions. Care must be taken in comparing the values to other ground data derived at other scales published in the literature. The values predicted from our model are generalized due to the coarse spatial resolution of our product, and most of the available sources from on-site observations report sums of species cover rather than plant coverage. Compared to field samples of previous studies in the area, the model tends to overestimate plant coverage in the western region by approx. 10% (Miehe et al. 2011a). This overestimation results from the low number of ground samplings in the far western region, which is the most remote area and the most difficult to access. The central region, including the transition between *Kobresia* pastures and Alpine steppe, has a plant coverage of 40% to 60%, which is very close to published data based on field samplings in the area (Babel et al. 2014; Miehe et al. 2008b, 2011b). A cover of approximately 85% is reported for non-degraded grasslands in the hydrologically important headwaters of the Yangtze and Huang Rivers (Zhou et al. 2005), which is slightly above the mean plant coverage predicted by our model.

6. Conclusions

In this study, we presented the first plant coverage product for the grasslands of the Tibetan Plateau to be fully validated against ground data sampled in the field. We tested four different methods (SAM, LSU, PLSR and SVM regression) in a cross-scale cascade of satellite data (WorldView-2, Landsat, MODIS) with decreasing pixel resolution and found that the methods using only satellite reflectance values (PLSR, SVM regression) yielded better results than those based on spectral endmembers (SAM, LSU). Because the error rates of the SVM regression models were low, the final product may help stakeholders at local and regional scales to define livestock storage capacities or redistribute pastures to villages and families. Furthermore, the plant coverage data may serve as data sources for future estimations of LAI, biomass and primary production. Such datasets are urgently required to improve the simulation of vegetation dynamics and vegetation-climate interactions on the Tibetan Plateau.

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Chapter 7 Synthesis–lessons for different indicator groups

The main results from investigations on plant communities, soils and other indicator groups indeed indicate significant livestock grazing effects, but these effects are solely in alpine meadows and are shown by few indicators. Various environmental factors interactively shape Tibetan grasslands. This study not only contributes to a better understanding of complicated biotic-abiotic interactions and several basic rangeland theories, but also challenges the widely held notion that grassland degradation on the TP is broadly caused by intensified grazing. Great caution should be taken for future grassland management and conservation based on the following aspects.

7.1 Responses of vegetation

Insensitive grazing responses in steppes are in line with non-equilibrium theories and several studies from lowland steppes in other regions (Chapter 1 and 3). However, it's contrary to the expectation that plant communities in alpine meadows are also not sensitive to increased grazing (Chapter 4–5), from both the theoretical perspective and results of the review (Chapter 3). Grazing effects on plant communities in moist and productive grasslands are assumed to be strong because livestock density and plant population growth should be in equilibrium. This concept gets supports from a large amount of single site studies which are based on short-term grazing manipulating experiments and indeed overwhelmingly suggest negative grazing effects on vegetation cover, plant richness, AGB and BGB (Chapter 3). In the transitional steppe-meadows, strong grazing effects on plant communities tended to be constrained to piospheres in the direct vicinity of grazing hotspots, which were totally distinct from plots under other grazing intensities (Chapter 4).

Long grazing histories and strong environmental controls are two possible reasons for the observed pattern. First, Tibetan grasslands have been evolved under relatively long grazing histories across all three habitat types (Miller 1990; Miller 2005; Sheehy et al. 2006; Miehe et al. 2009; Miehe et al. 2014) no matter what the specific local-scale grazing regime and herd composition are (Chapter 2). Most plant species, especially perennials, are well-adapted and tolerant to grazing in both steppes and meadows (Miehe et al. 2011a; Miehe et al. 2011b). In steppes where selective forces of aridity and grazing operate in the same direction, most species are grazing resistant, such as cushion plants (Milchunas et al. 2008; Miehe et al. 2011b). Second, environmental controls from precipitation, elevation and incident radiation were primarily common and strong across habitat types (Chapter 3–5), while inclination and temperature (both T and acT0) additionally influenced plant species composition in meadows and steppe-meadows, and yearTdiff was of significant impact in steppes (Chapter 4–5). Therefore, great care must be taken if assessments on plant community are without consideration of environmental interactions. Specifically, although richness and relative cover of annual species (Chapter 4) and total vegetation cover (Chapter 5) were shown to be sensitive to intensified grazing in alpine meadows, it should be noticed that the growth of annual species might also be attributed to interannual variability of P or acT0. The diagnostic value of vegetation cover suffers from its potential relatively fast recovery (e.g. 3–5 years) by grazing exclosures and the cover change alone often fails to detect forage quality changes (Shang et al. 2014).

7.2 Responses of soil conditions

Similar to vegetation, intensified grazing only reduced SOC and tN in meadows and the overall changes in soil fertility were restricted to piospheres (Chapter 4–5). Unlike vegetation, environmental controls on soils were generally weak in meadows and steppe-meadows, but were obvious in steppes, suggesting that direct positive plant–soil feedback processes are kept in steppes. Grazing could directly modify soil physical (e.g. increase of BD, Chapter 3) and chemical conditions (increase of aP, Chapter 4) by mechanical disturbance from livestock including trampling and nutrient translocations (Augustine 2003; Stumpp et al. 2005). However, further modifications are through indirect alterations of vegetation. Basically, vegetation retains surface water, improves soil structure by physically binding soils and protects soil against erosion from wind (van de Koppel et al. 1997). Moreover, grazing-induced changes in plant inputs (Kuzyakov & Domanski 2000; Fang et al. 2013; McSherry & Ritchie 2013; Schrama et al. 2013) including BGB (Chapter 3), litter (Chapter 4), and plant species composition (increased annual species, Chapter 4) are likely to affect soil C and N cycling.

Great care should be taken for interpreting the reduced SOC, because roots within the *Kobresia* turf layer in meadows have been demonstrated as the main sink for the recently assimilated C (Babel et al. 2014), indicating more C might be stored in roots, so the C storage at ecosystem level might not necessarily decrease. Additionally, with global warming, N mineralization (Rustad et al. 2001) and soil respiration might speed up and change soil biochemistry processes (Kirschbaum 1995; Schlesinger & Andrews 2000).

7.3 Responses of fauna indicators

Although small mammals have been widely blamed for grassland degradation (Guo et al. 2012; Sun et al. 2015), no changes of richness, abundance and composition were detected in response to intensified grazing. However, our results still indirectly suggest that small mammals may be responsible for soil degradation because there were negative correlations between small mammal richness and both vegetation cover and SOC (Chapter 5). This indicates that small mammals most likely prefer microhabitat with open soils and might cause further soil degradation when vegetation cover is reduced by livestock grazing (Arthur 2007). In line with previous studies (Walsberg 2000; Li et al. 2003), elevation and temperature had strong controls on small mammal species composition (Chapter 5). However, these influences are likely to be confounded with food availability, soil property and vegetation structure (Stapp et al. 2008), and thus should be further investigated in detail. Moreover, the potentially various response patterns among small mammal species (Raoul et al. 2006; Yarnell et al. 2007) should also be awared of and specially analyzed given that current policies unequivocally consider effects of small mammals on grassland health are negative.

Likewise, ants did not respond to intensified grazing in species richness, composition and nest density (Chapter 5) despite studies from other grassland systems show their great potential for land-use monitoring (Andersen et al. 2002; Andersen & Majer 2004). There are two possible reasons for the non-sensibility to grazing in ant communities. First, soil and vegetation properties are primary determinants for ant communities (Bestelmeyer & Wiens 2001; Hoffmann 2010), so weak responses in plant communities and soils could lead to similar weak response in ant communities. However, this explanation might not hold true on Tibetan grasslands because ant species composition showed weak correlation to soil conditions and plant species composition in our study region (Chapter 5). The other reason is the overriding environmental influences and the context dependency (Hoffmann 2010). Elevation and relief conditions were indeed found to be most important for ant communities (Chapter 5), implying that the local-scale habitat features such as surface runoff, infiltration, soil moisture and heat gain might account more for ant species composition (Bestelmeyer & Wiens 1996).

7.4 Responses of hyperspectral data

The value of including hyperspectral data lies in the emphasis of proper field calibrations for remote sensing studies (Chapter 3). Only in this way, the bottom-up upscaling approach will be reliable. Traditional and relatively novel indices indeed produced good results for assessing grassland conditions in this region (Chapter 5–6). Not surprisingly, NDVI was reduced by heavy grazing as it is an indicator of green vegetation cover (Chapter 5). Nevertheless, although NDVI has been widely used to evaluate grassland degradation, there is still considerable uncertainty with regard to the fast recovery of vegetation cover and the mixed effects of climate changes (Chapter 3–5). Increase of NDNI (Chapter 5) under heavy grazing conditions might indicate positive grazing effects on N cycling. However, whether this signal is corresponding to the measurements of N contents from plant tissues is still unclear since both positive (Bai et al. 2012) and negative (Wang et al. 2005; Niu et al. 2015) grazing effects on plant N contents have been reported.

The most intriguing point from hyperspectral data is the correlations with small mammals. First, NDNI increased with small mammal richness (Chapter 5), suggesting diverse small mammal species might indicate rich nutrient contents, so positive roles of small mammals on grassland nutrient supply should be better acknowledged (Wesche et al. 2007; Arthur et al. 2008). Moreover, overall hyperspectral signals were also more correlated to species composition of small mammals than to plants (Chapter 5), suggesting that hyperspectral data might provide more information on changes in vegetation structure other than plant species composition and thus are potentially worthwhile for monitoring. Moreover, vegetation cover might be used as the first step towards estimation of leaf area index, biomass and primary productivity (Chapter 6), and properly field-calibrated remote sensing products may be helpful to understand large-scale vegetation dynamics and the interactions with climate.

7.5 Lessons from interdisciplinary approach

The diverging responses of multiple indicators underline the basic and fundamental ecological concept that different biotic groups have unique niches and play distinct roles, but all correlated to each other and the physical environmental factors in grassland systems (Whitford et al. 1998; Kruess & Tscharntke 2002; Grandin et al. 2013). As primary producers, plants are central for energy and material cycling by providing food sources and shelters for various fauna groups, adjusting soil conditions and linking soils and other trophic levels. Fauna groups are interacting with each other and by prey–predator relationships. Moreover, abiotic indicators, such as soil properties and spectral data, are often affected by grazing through the indirect impacts on plants and other biota.

However, to assess grassland health condition in an ecosystem view with consideration of the food chain concept is undoubtedly necessary but has been mostly omitted because of the difficulties of combining expertise from several disciplines, especially on the TP which holds large biodiversity and extensive environmental gradients (Chapter 2). A better understanding of the observed diverging responses still requires further thoroughly detailed investigations on each indicator group and interdisciplinary data analyses (Chapter 9).

7.6 Management implications

First, non-equilibrium theories, especially interannual variability of climate conditions should be considered for future grassland management and pastoral planning programmes on the TP. Although cvP has been identified as the main driver of the changes in plant communities from steppes (Chapter 1 and 3), it's surprising that grassland ecologists working in ecosystems with cold winters rarely paid attention on it (Behnke 2000; Ho 2001). Therefore, most of the current policies have been based only on equilibrium concept and predominantly try to reduce livestock numbers and mobility patterns of local nomads for grassland restoration (Goldstein & Beall 1989; Cao et al. 2013a; Shang et al. 2014; Nyima 2015). However, these strategies might not be effective considering the overall low productivity of the prevalent grazing-resistant plant communities. Furthermore, the current concept of cvP does not consider the winter precipitation, i.e. snow, which has obvious effects on plant communities (Dorji et al. 2013; Wang et al. 2015) and livestock population (Shang et al. 2012). Thus traditional grassland management with high mobility and even emergency aid systems (Fu et al. 2012) might be more effective across the plateau.

Plant species that are indicators of piospheres can provide a direct warning for the frequent and intensive livestock activity (Chapter 5). They could be helpful in monitoring early stages of grassland degradation to prevent further negative changes, especially under the condition that changes of plant species compositions are not easily to be perceived. Soil properties are reliable and should necessarily be included into grassland assessments at least in alpine meadows of Tibet because even when plant communities do not respond to intensified grazing, the long-term effects may still be accumulated in soils. The transitional ecotone should get more attentions and be monitored, especially under the background of climate changes.

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Chapter 8 Conclusion

The overall threat from intensified grazing for grassland degradation is not as serious or as widely distributed across main habitat types on the TP as expected. Plant species composition and soil fertility changed by livestock grazing, but not in steppes, and could not be attributed exclusively to grazing intensification. Only few indicators were generally sensitive to grazing, such as increased richness and cover of annual forbs and reduced SOC and tN in meadows, although overwhelming negative effects may still be found from single sites. Small mammals and ants were not sensitive to increased grazing pressure but controlled by temperature and elevation. Hyperspectral data have potentials to upscale responses of vegetation and small mammals.

Non-equilibrium concept may apply not only in steppes, but also in alpine meadows as the uncoupled responses of plant species composition and soil fertility suggested. The convergent evolution under grazing, aridity and coldness might explain the resistance of plant species composition and should be acknowledged. Assessments on grassland health should first select appropriate indicators and incorporate a comprehensive ecosystem view. An interdisciplinary approach can assist the understanding of interactions among various biotic and abiotic factors and explore underlying mechanisms in grassland systems.

Chapter 9 Outlook–the way ahead for further studies

From the vegetation perspective, plant functional (especially leaf) traits are crucial to understand the general grazing reponses across various grassland systems (Díaz et al. 2001; Díaz et al. 2007; Zheng et al. 2009) and might help to explain the complicated patterns which have been demonstrated from plant species compositions and plant richness. Various studies revealed environmental impacts on leaf traits and forage quality from single-site (Wang et al. 2014; Li et al. 2015) to regional (He et al. 2006; Gao et al. 2013; Shi et al. 2013) and global scales (Ordoñez et al. 2009). However, how do grazing and climate interactively shape plant functional traits has rarely been investigated (Pakeman 2004; Dainese et al. 2015). We are currently in the process of analyzing responses of plant growth forms, life forms, canopy height, plant nutrients and SLA to environmental and grazing gradients. Additionally, in terms of ecological monitoring, other classification methods for plant indicator species, such as increaser vs. decreaser in response to grazing (Fensham et al. 2010; Sasaki et al. 2011) might give further information for monitoring the increase of grazing intensity or preferable environmental conditions for certain species.

Given that a large share of the variance in soil fertility was not captured by the tested environmental factors, other factors might play important roles and should be included to explore the underlying mechanisms of soil biochemistry. Specifically, soil physical properties such as soil texture, temperature, infiltration and hardness (Hassink 1994; Burke et al. 2008; McSherry & Ritchie 2013), and biotic interactions which affect litter decomposition, such as soil microbes (Hamilton III & Frank 2001; Frank et al. 2003; Liu et al. 2015) should be inspected.

Considering plant–soil feedbacks, relationships among environment, plant and soil properties are fundamental questions for ecologists to understand spatial patterns and ecological niches of species with or without disturbance. Although several studies have revealed how specific characteristics of plant community change along environmental gradients on the TP (Song et al. 2008; Wang et al. 2008; Shimono et al. 2010; Wang et al. 2012), the following questions are still not fully understood: 1) Are abiotic effects on plant communities and soils consistent across habitats or do they still hold when grazing intensity changes? 2) For those sites with several grazing intensity levels available, could the intermediate disturbance hypothesis apply at different spatial scales? 3) How do soil properties change along continuous abiotic gradients and whether theses relationships vary between grazing intensities?

With respect to small mammals, potentially interesting questions include: 1) How do small mammal communities respond to changes of plant canopy height, relative cover of different plant functional groups (e.g. palatable species) or soil conditions (Bagchi et al. 2006; Bösing et al. 2014)? 2) How do small mammals change plant communities through their foraging on certain plant species, or particular parts of a plant individual, or do they indirectly change plant communities by changing soil physical properties and fertility due to their burrowing activity (Howe & Brown 1999; Liu et al. 2013; Pearson et al. 2014)? 3) What are the relationships between plant species from their diets and the richness and abundance of small mammals (Root-Bernstein & Ebensperger 2013)?

For ants, it would be interesting to ask 1) If ants are not sensitive to grazing, and how do they respond to specific abiotic conditions such as radiation, accumulative temperature and slope exposure (Bale 1991; Abril et al. 2010)? 2) Do functional groups of ants (Bestelmeyer & Wiens 1996; Underwood & Fisher 2006) respond to grazing and are they related to properties of any other biotic groups?

Further studies on hyperspectral indices, especially on REP_LE and NDNI, will be valuable to link vegetation characteristics, such as cover and richness of different functional groups, life forms and growth forms, as well as to nutrient concentration from soils and plant tissues and other functional traits (Mansour et al. 2012; Higginbottom & Symeonakis 2014).

The social science perspective is another important topic for further studies. As reviewed in Chapter 2, herd species (Cincotta et al. 1991), grazing regimes including grazing season (summer, winter, all-year-round), length of the grazing period (Cao et al. 2011) and local management strategies such as size of the grazing radius and extent of mobility as well as implementations of governmental policies (Yan et al. 2005) all might potentially affect grazing intensity at local level.

Given the importance of climate changes, the potential impact of snow disasters certainly requires more attention. In contrast to other, particularly warmer, semi-arid grasslands where drought causes non-equilibrium relationships between plant and livestock populations, heavy snow not only directly reduces livestock number and affects local livelihoods (Shang et al. 2012; Dorji et al. 2013b; Yeh et al. 2013), but also influences plant growth (Chen et al. 2015; Wang et al. 2015). Remote sensing is a convinient tool to detect variablity of snow amounts and events on the TP (Immerzeel et al. 2009; Maussion et al. 2014; Yang et al. 2015), while filed-based meteorological observations should also consider this aspect to fully understand the water availability besides summer precipitation patterns.

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Erklärung über den persöhnlichen Anteil an den Publikationen

Chapter 3:

Wang, Y., Wesche, K. (2016) Vegetation and soil responses to livestock grazing in Central Asian grasslands: a review of Chinese literature. *Biodiversity and Conservation*. (In press)

Data collection	Yun Wang (100%)
Analysis	Yun Wang (90%); Karsten Wesche (advisory 10%)
Writing	Yun Wang (60%); Karsten Wesche (40%)

Chapter 4:

Wang, Y., Heberling, G., Görzen, E., Miehe, G., Seeber, E., Wesche, K., Combined effects of environment and livestock grazing on plant community and soil condition across Tibetan grasslands. *Applied Vegetation Science* (major revision)

Data collection	Yun Wang (60%); other coauthors (40%)
Analysis	Yun Wang (80%); Karsten Wesche (advisory 20%)
Writing	Yun Wang (80%); other coauthors (20%)

Chapter 5:

Wang, Y., Lehnert, W.L., Holzapfel, M., Schultz, R., Heberling, G., Görzen, E. Meyer, H., Seeber, E., Pinkert, S., Ritz, M. Ansorge, H., Bendix, J., Seifert, B., Miehe, G., Long, R.J., Yang, Y.P., Wesche, K. Multiple indicators yield diverging results on grazing degradation assessment across Tibetan pastures. *Ecological Indicators* (in preparation of resubmission)

Data collection	Yun Wang (40%); other coauthors (60%)
Analysis	Yun Wang (data preparing, 40%, other coauthors, 60%); Karsten Wesche (statistic analysis, 100%)
Writing	Yun Wang (30%); Karsten Wesche (50%); other coauthors (20%)

Chapter 6:

Lehnert, L.W., Meyer, H., **Wang, Y**., Miehe, G., Thies, B., Reudenbach, C., Bendix, J., 2015. Retrieval of grassland plant coverage on the Tibetan Plateau based on a multi-scale, multi-sensor and multi-method approach. *Remote Sensing of Environment* 164, 197-207.

Data collection	Yun Wang (20%); other coauthors (80%)
Analysis	coauthors (100%)
Writing	Yun Wang (10%); other coauthors (90%)

Halle (Saale), den

Unterschrif

Additional publications during PhD study period:

- Dissertation related

Meyer, H., Lehnert, L.W., **Wang, Y**., Reudenbach, C., Bendix, J., Lehnert, W.L., 2013. Measuring pasture degradation on the Qinghai-Tibet Plateau using hyperspectral dissimilarities and indices, In SPIE Remote Sensing, at Dresden. eds U. Michel, D.L. Civco, K. Schulz, M. Ehlers, K.G. Nikolakopoulos, p. 88931F. International Society for Optics and Photonics.

- Not related to dissertation

Fu, Y., **Wang, Y**., Yang, Y.P., Yang, X.F., 2015. Indigenous knowledge and use of *Anisodus tanguticus* in pastoral communities of Eastern Tibet, China, and its implications for local adaptation. *Plant Diversity and Resources* 37, 1-10.

Meng, L.H., **Wang, Y**., Luo, J., Yang, Y.P. & Duan, Y.W. (2014) The trade-off and altitudinal variations in seed weight-number in *Sinopodophyllum hexandrum* (Royle) Ying (Berberidaceae) populations from the Hengduan Mountains. *Polish Journal of Ecology*, 62, 413–419.

Meng, L.H., **Wang, Y**., Luo, J., Liu, C.Y., Yang, Y.P. & Duan, Y.W. (2012) Pollination ecology and its implication for conservation of an endangered perennial herb native to the East-Himalaya, *Megacodon stylophorus*. *Plant Ecology and Evolution*, 145, 356–362.

Fu, Y., Grumbine, R.E., Wilkes, A., **Wang, Y.,** Xu, J.C. & Yang, Y.P. (2012) Climate change adaptation among Tibetan pastoralists: challenges in enhancing local adaptation through policy support. *Environmental Management*, 50, 607–621.

Zhang, L., Luo, T., Liu, X. & **Wang, Y**. (2012) Altitudinal variation in leaf construction cost and energy content of *Bergenia purpurascens*. *Acta Oecologica*, 43, 72–79

Curriculum Vitae

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EDUCATION

2012-now	Martin-Luther-University Halle -Wittenberg, Institute for Biology, Geobotany and Botanical Garden PhD study
2006-2009	Kunming Institute of Botany, CAS, Kunming, Yunnan, China **Master of Natural Science**, "Pollination mechanism and ecological adaptation of *Anisodus luridus* and *A. carniolicoides* (Solanaceae)" Supervised by Prof. Yongping Yang, Prof. Jianchu Xu
2002-2006	Sichuan University, Chengdu, China **Bachelor of Science**, Biology

WORK EXPERIENCE

2011-2015	Botany Department, Senckenberg Museum of Natural History Görlitz **Scientific assistant** in BMBF project - PaDeMoS (Pasture Development Monitoring System) *Focus on plant biodiversity and soil nutrients, working on plant determination, soil analysis and data analysis*
2009-2011	Kunming Institute of Botany, CAS **Scientific assistant** in "Evolutionary ecology of alpine plants" group *Focus on pollination ecology of alpine plants*

PRESENTATIONS

15.04. 2015	"*Testing congruence among multiple grazing indicators: a multi-site study across the Tibetan plateau*" (Poster, EGU2015-324), Vienna, Austria, EGU General Assembly
12.04. 2014	"*Grazing and environmental effects on vegetation structure: a view from Tibet*", Erfurt, Germany, Internationales Symposium "Biodiversität und Naturausstattung im Himalaya"
08.06. 2012	"*Effects of grazing on plant biodiversity in climatically different parts of Tibet*", Bozen, Itaty, Annual meeting of the "Arbeitsgemeinschaft für Vergleichende Hochgebirgsforschung"
16.01. 2012	"*Plant biodiversity change along the grazing gradient on Tibet Plateau*", Oberjoch, Germany, Tip-BMBF PhD Meeting

SEMINARS

03.02. 2015	“*Recent formed allopolypoid systems as natural genetic laboratories*” Lectured by Dr. Aleš Kovařík, Institute of Biophysics, Department of Molecular Epigenetics, Academy of Sciences of the Czech Republic
02.12. 2014	“*Scaling of energy use, abundance and biomass of forest soil in vertebrates in the biodiversity exploratories*” Lectured by Dr. Roswitha Ehnes, University of Göttingen
02.04. 2013	“*Grassland Research in the Jizera Mountains*” Lectured by Dr. Vilém Pavlů from the Leibniz Institute of Plant Genetics and Crop Plant Research (IPK), Liberec, Czech Republic

PUBLICATIONS (before 2012)

Wang, L.L., Zhao, M.F., **Wang, Y.**, Duan, Y.W. & Yang, Y.P. (2011) A preliminary study on geographical variations in floral traits of *Halenia elliptica* (Gentianaceae) based on herbaria. Plant Diversity and Resources, 33, 503–508.

Zhang, C., Hu, L.J., **Wang, Y.**, Duan, Y.W. & Yang, Y.P. (2011a) Effects of the position on floral traits and reproductive success of *Comastoma pulmonarium* (Gentianaceae). Plant Diversity and Resources, 33, 495–502

Zhang, C., Irwin, R.E., **Wang, Y.**, He, Y., Yang, Y. & Duan, Y.W. (2011b) Selective seed abortion induced by nectar robbing in the selfing plant *Comastoma pulmonarium*. New Phytologist, 192, 249–255.

Wang, Y., Meng, L.H., Yang, Y.P. & Duan, Y.W. (2010a) Change in floral orientation in *Anisodus luridus* (Solanaceae) protects pollen grains and facilitates development of fertilized ovules. American Journal of Botany, 97, 1618–1624.

Wang, Y., Hu, L.J., Duan, Y.W. & Yang, Y.P. (2010b) Altitudinal Variations in Reproductive Allocation of *Bergenia purpurascens* (Saxifragaceae). Acta Botanica Yunnanica, 32, 270–280.

Xu, J.C., Grumbine, R.E., Shrestha, A., Eriksson, M., Yang, X.F., **Wang, Y.** & Wilkes, A. (2009) The melting Himalayas: Cascading effects of climate change on water, biodiversity, and livelihoods. Conservation Biology, 23, 520–530.

Wang, Y., Luo, J. & Xu, J.C. (2009) A Comparative Study on the Pollination Mechanism of *Anisodus luridus* and *A. carniolicoides* (Solanaceae). Acta Botanica Yunnanica, 31, 211–218.

Eigenständigkeitserklärung

Hiermit erkläre ich, dass die Arbeit mit dem Titel „Combined effects of livestock grazing and environment on Tibetan grasslands: a multi-site, interdisciplinary study“ bisher weder der Naturwissenschaftlichen Fakultät I Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt wurde.

Ferner erkläre ich, dass ich die vorliegende Arbeit selbstständig und ohne fremde Hilfe verfasst sowie keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe. Die den benutzten Werken wörtlich oder inhaltlich entnommenen Stellen wurden als solche von mir kenntlich gemacht.

Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe.

Halle (Saale), den

Unterschrift:

Yun Wang