LEUPHANA
UNIVERSITÄT LÜNEBURG

Climate-grazing interactions in Mongolian rangeland vegetation

Academic dissertation
Submitted to the Faculty of Sustainability of Leuphana University
for the award of the degree
'Doctor of Natural Sciences'
-Dr. rer. nat.-
Submitted by

Julian Ahlborn
Born on 24.01.1986 in Wetzlar

Doctoral advisor and reviewer #1: Prof. Dr. Henrik von Wehrden, Lüneburg

Doctoral advisor and reviewer #2: Prof. Dr. Karsten Wesche, Görlitz

Reviewer #3: Prof. Dr. Anja Linstädter, Potsdam

Date of disputation: 08.07.2022

Contents

Copyright notice

Author's current address:
Leibniz-Zentrum für Agrarlandschaftsforschung (ZALF) e. V.
WG Sustainable Grassland Systems

Gutshof 7
14641 Paulinenaue

Germany

Email: julian.ahlborn@posteo.de

Preface

„Vielleicht sind Grenzgänge wirklich ein Jungbrunnen. Wenigstens für das Gedächtnis sind sie es, denn nichts setzt sich in unserer Erinnerung so tief ab wie bestandene Abenteuer. Ob wir diese ereignisreichen Wochen und Monate suchen, weil das Leben damit länger erscheint?“

„…Auf dass du immer ein Nomade bleibst!“

Gobi. Die Wüste in mir. Messner, R. (2005), Fischer Verlag.

I finished my studies on Biogeography in August 2013 in Trier, Germany, with a thesis on the growth of *Populus euphratica* OLIVIER in the riparian Tugai-forest ecosystem in the Xinjiang province in China. This thesis got me interested in dryland ecosystems, and so I was quite excited when I found an open PhD-position in a project on Mongolia's steppe ecosystem in early 2014. I applied for the position in Prof. Henrik von Wehrden's lab and was selected for the job as a research associate at Leuphana University in Lüneburg, starting in May 2014. The first field work period started in June and lasted until August 2014. A second, similar period followed in 2015.

This dissertation is the result of the project "Responses of plant performance and functional diversity across a climate and land-use gradient in Mongolia", which was funded by the German Research Foundation DFG between 2014 and 2018 (grant number 239358027). The project was conceived and designed by Professor Dr. Henrik von Wehrden, Professor Dr. Christine Römermann and Professor Dr. Karsten Wesche. Due to Henrik's and Karsten's long experience of research in Mongolia, the project found a strong local partner in Prof. Dr. Oyuntsetseg Batlai, who helped organizing field work in Mongolia. Both project and dissertation were collaborations by the Leuphana University of Lüneburg, the Friedrich-Schiller University of Jena, the Senckenberg Museum of Natural History in Görlitz and the National University of Mongolia.

Chapter 1 is the core of this dissertation. It includes an introduction, the aims, the datasets which were collected during the field work, a description of the study area, as well as the summary and the synthesis of the empirical work. Chapters 2 – 4 are copies of the three articles that build the backbone of this cumulative dissertation.

I collected data, conducted all analyses myself and drafted the manuscripts for chapters 2 - 4. Birgit Lang provided some data on important species for chapter 3 and helped collecting biomass for chapter 4. Munkhzul Oyunbileg was an associated PhD student, being substantially involved in collecting data for all three manuscripts. She was also a very important consultant for the determination of Mongolian plant species. Batlai Oyuntsetseg organized field work and assistants and provided substantial help with determination of species. Neil Collier provided substantial help with the statistical analysis and coding of chapter 3, and checked the language of the three papers. As stated above, Henrik von Wehrden, Christine Römermann and Karsten Wesche designed the study, supervised field- and lab work, contributed to the framing of the papers and made substantial contributions to all three manuscripts.

A version of chapter 2 has been published as Julian Ahlborn., Henrik von Wehrden, Birgit Lang, Munkhzul Oyunbileg, Batlai Oyuntsetseg, Christine Römermann & Karsten Wesche: Climate – grazing interactions in Mongolian rangelands: Effects of grazing change along a large-scale environmental gradient. *Journal of Arid Environments*, 173 (2020) 104043. Chapter 3 had been submitted to the Journal of Applied Vegetation Science, and was invited for resubmission after revision and rejection. The manuscript will be prepared soon for a resubmission. Chapter 4 has been published as Julian Ahlborn, Karsten Wesche, Birgit Lang, Munkhzul Oyunbileg, Batlai Oyuntsetseg, Christine Römermann, Neil French Collier and Henrik von Wehrden: Interactions between species richness, herbivory and precipitation affect standing biomass in Mongolian rangelands. *Applied Vegetation Science*, 24 / 2 (2021).

The target audience of my dissertation are researchers who are interested in interactions between grazing and climate in dry grassland systems, ecologists who work on plant community composition in dry rangeland systems, and ultimately all people who strive for sustainable grassland systems.

Acknowledgements

The work on this thesis has deeply changed my views, and the following people have strongly contributed to this change in manifold ways.

First of all, I need to thank my two supervisors Henrik von Wehrden and Karsten Wesche. For sending me to one of the greatest places in the world, for their hospitality, their never ending patience and for helping me to develop a comprehensive understanding of probabilities. I am deeply grateful for Henrik’s lessons in optimism and pragmatism, and for Karsten’s lessons in scientific precision. I thank Christine Römermann for introducing me to the world of traits. She was a discreet and indulging advisor. I also want to thank Anja Linstädter for her interest in my work and her review of this dissertation. Her last GFÖ-session really helped me getting this work finished.

Veronica and Neil French Collier made me love doing science and helped me out in every situation of life: teaching me how to code, improving my language, offering beer, sharing BBQ on the lab’s balcony, even sharing their apartment for a couple of months. I would not have finished this thesis without them.

I thank Dawaa, Ganbud and Munkhzul for their indispensable help during the field trips, and more importantly, for teaching me a piece of Mongolian culture. Oyuna and Oyuka helped organising my work in Mongolia and meeting them in UB was always a wonderful experience. I thank the students Anna, Djamilah and Johanna for their assistance during their stay, and especially Carla for her interest, motivation and her infectious cheerfulness. Thanks to Birgit for her cooperation in the field and sharing data with me.

I can’t thank enough the wonderful Fabienne for everything (the list of things is too long). Henrik did well keeping her at the faculty. At this point I shall not forget to mention the staff at Leuphana and the Senckenberg Museum in Görlitz. The people I met there were always extremely helpful (special regards to Hildegard!). I’d also like to thank Heike for her help with multiple issues and her hospitality at their home. I am so happy I had Marlene, Christin and Johan as roommates, even if it was only a short time. Also thanks to Oliver and Judith for all the good conversations and the space on their couch. For the last part of the journey, I need to thank Professor Frank Eulenstein for giving me some space and time to finally finish my thesis, and Joana Bergmann and Tilo Henning for their comments on my synthesis paper.

I am deeply grateful for my family. They always encouraged me to keep swimming.

Finally, my deepest gratitude to my wife Marlen. For her love, her patience and her selfless support. She makes *the* difference in my life.

Summary

Rangelands are the most widespread land-use systems in drylands, where they often represent the only sustainable form of land-use due to the limited water availability. The intensity of the land-use of such rangeland ecosystems in drylands depends to a large extent on the climatic variability in time and space, as on the one hand it influences the growth of biomass and therefore the grazing intensity, but on the other hand it can also destroy entire herds through extreme climatic events. Rangeland systems are seriously threatened by climate change, because climate change will alternate the availability of water in time and space. This is dangerous in that we have not yet fully understood how grazing affects vegetation under different climatic conditions. Inadequate rangeland management can quickly lead to serious degradation of the grazing grounds. This dissertation therefore deals with the question which role climatic variability plays for the effects of grazing on vegetation in dry rangelands. The relatively intact steppes in central Mongolia were chosen as a model system. They are characterised by low precipitation and high climatic variability in the south (100 mm annual precipitation), and comparatively high precipitation and low climatic variability in the north (250 mm). The effects of grazing on vegetation on 15 grazing transects were investigated along the climatic gradient. The central elements were the plant species and their abundances on 10 m x 10 m areas, for which functional characteristics such as height, affiliation of functional groups or leaf nutrients were recorded. The main hypothesis of this dissertation is that grazing has a greater impact on vegetation communities with increasing rainfall. To test this hypothesis, three studies were carried out. In a first study, we found that the vegetation communities in the dry area differ strongly along the climatic gradient, while the plant communities in the wetter area differ more strongly along the grazing gradient. The results of the second study suggested that this difference can be explained by a functional environmental filter that becomes weaker from south to north as the niche spectrum increases. The third study has shown that this is likely a function of the higher availability of resources, which at the same time leads to higher grazing pressure, therewith stressing the vegetation especially in years with droughts. In summary, I conclude that the climate gradient also represents an environmental filter that filters species for certain characteristics, thus having a significant influence on the vegetation. Climatic variability influences the effect of grazing on vegetation, which is particularly problematic where the grazing intensity is high and the species are less adapted to strong climatic fluctuations. Future scenarios predict increasing productivity and therefore

increasing livestock density. This may lead to an increase in floristic and functional diversity across the climate gradient, but also to increasing grazing effects and therefore threads for overgrazing. Increasing climatic variability is likely to intensify this thread, especially in the moister regions, whereas the dry rangelands are likely to be more resilient due to the adaptation of the plants to non-equilibrium dynamics. The fate of Mongolia's rangeland systems therefore clearly lies in the hand of the rangeland managers. The sustainable use of Mongolia's vast steppe ecosystems might depend on a flexible livestock management system which balances the grazing intensity with the available resources, while still considering climatic variability as a key for the management decisions. A potential link-up for future studies might arise from the shortcomings of the studies presented. This dissertation suggests that long-term observations are necessary to better understand the effects of climatic variability. In addition, grazing gradients must be selected more carefully in the future in order to be able to ensure better comparability, and functional analyses should have a stronger relationship to forage quality. With these points in mind, a comparative study of several rangeland ecosystems on a global level must be the ultimate goal. This could be an important step for the sustainable use of drylands in the context of global climate and land use change.

Zusammenfassung

Weidesysteme sind die am weitest verbreiteten Landnutzungssysteme in Trockengebieten, da sie aufgrund der limitierten Wasserverfügbarkeit oft die einzige nachhaltige Form der Landnutzung darstellen. Die Intensität der Nutzung solche sogenannter Rangeland-Ökosysteme hängt in Trockengebieten erheblich von der klimatischen Variabilität in Zeit und Raum ab, da sie einerseits den Aufwuchs von Biomasse und daher die Beweidungsintensität beeinflusst, andererseits aber auch durch extreme Klimaevents ganze Herden vernichten kann. Rangelandsysteme sind erheblich durch den Klimawandel bedroht, weil er die Verfügbarkeit von Wasser in Zeit und Raum durcheinander bringt. Das ist insofern gefährlich, als dass wir noch nicht ganz verstanden haben wie sich Beweidung unter unterschiedlichen Klimabedingungen auf die Vegetation auswirkt. Unangepasstes Weidemanagement kann aber schnell zu ernsthafter Degradation des Weidelands führen. Diese Dissertation beschäftigt sich daher mit der Frage, welche Rolle klimatische Variabilität für die Effekte von Beweidung auf die Vegetation in trockenen Rangelands spielt. Als Modellsystem wurden die noch relativ intakten Steppen im Zentrum der Mongolei gewählt, die durch geringe Niederschläge und hohe klimatische Variabilität im Süden (100 mm Jahresniederschlag) und vergleichsweise hohe Niederschläge und geringe klimatische Variabilität im Norden (250 mm) des Landes gekennzeichnet sind. Entlang des Klimagradienten wurden die Effekte von Beweidung auf die Vegetation auf 15 Beweidungstransekten untersucht. Zentrales Element waren die Arten und ihre Abundanzen auf 10 m x 10 m großen Flächen, zu denen außerdem funktionelle Merkmale wie Höhe, Zugehörigkeit zu funktionellen Gruppen und Blattnährstoffstoffe erfasst wurden. Die Haupthypothese dieser Dissertation besagt, dass sich die Beweidung mit zunehmenden Niederschlägen stärker auf die Vegetationsgesellschaften auswirkt. Um diese Hypothese zu überprüfen, wurden drei Studien durchgeführt. In einer ersten Studie wurde festgestellt, dass sich die Vegetationsgesellschaften im trockenen Bereich stärker entlang des Klimagradienten unterscheiden, während sich die Gesellschaften im feuchteren Bereich stärker entlang der Beweidungsgradienten unterscheiden. Die Ergebnisse der zweiten Studie ließen darauf schließen, dass sich dieser Unterschied mit einem funktionalen Umweltfilter erklären lässt, der von Süden nach Norden durch ein sich vergrößerndes Nischenspektrum schwächer wird. Die dritte Studie hat gezeigt, dass dies durch eine höhere Ressourcenverfügbarkeit ermöglicht wird, die aber dadurch gleichzeitig zu einem höheren Beweidungsdruck führt, was insbesondere in Jahren mit

hoher Trockenheit zu Problemen für die Vegetation führen kann. Zusammenfassend lässt sich daher sagen, dass der Klimagradient zugleich einen Umweltfilter darstellt, der Arten nach ihrer bestimmten Charakteristika filtert und somit erheblichen Einfluss auf vorkommende Vegetation hat. Klimatische Variabilität beeinflusst zudem den Effekt der Beweidung auf die Vegetation, was insbesondere dort problematisch ist, wo die Beweidungsdichte hoch und die Arten weniger angepasst an starke klimatische Schwankungen sind. Zukunftsszenarien sagen eine steigende Produktivität und damit eine steigende Viehdichte voraus. Dies kann zu einer Zunahme der floristischen und funktionalen Vielfalt über den Klimagradienten hinweg führen, aber auch zu zunehmenden Beweidungseffekten und damit zu Überweidung. Zunehmende klimatische Variabilität wird diese Gefahr wahrscheinlich verstärken, insbesondere in den feuchteren Regionen, während die trockenen Weideländer aufgrund der Anpassung der Pflanzen an die klimatischen Bedingungen wahrscheinlich widerstandsfähiger sind. Das Schicksal der Weidelandsysteme der Mongolei liegt somit eindeutig in der Hand der Weidelandmanager. Die nachhaltige Nutzung der mongolischen Steppenökosysteme könnte von einem flexiblen Viehwirtschaftssystem abhängen, das die Beweidungsintensität mit den verfügbaren Ressourcen in Einklang bringt und gleichzeitig die Klimavariabilität als Schlüssel für die Managemententscheidungen berücksichtigt. Anschlusspunkte für zukünftige Studien mögen sich aus den Schwächen der vorgelegten Studie ergeben. So hat diese Dissertation auch gezeigt, dass Langzeitbeobachtungen nötig sind um die Effekte von klimatischer Variabilität besser verstehen zu können. Außerdem müssen Beweidungsgradienten in Zukunft noch sorgfältiger ausgewählt werden, um die Vergleichbarkeit besser gewährleisten zu können, und funktionale Analysen sollten einen stärkeren Bezug zu Futterqualität haben. Unter der Berücksichtigung dieser Punkte muss schließlich eine vergleichende Studie mehrerer Rangeland-Ökosysteme auf globaler Ebene das Ziel sein. Dies könnte ein wichtiger Schritt für die nachhaltige Nutzung von Trockengebieten unter den Vorzeichen des globalen Klima- und Landnutzungswandels sein.

Chapter 1. Mongolian rangeland vegetation under future climate conditions.

Эр хүний жаргал эзгүй хээр

"Man's happiness lies in vacant steppes"

Mongolian proverb

Introduction

Global climate and land-use change are altering our planet's surface at an alarming rate (IPCC, 2019; Song et al., 2018). One of the most important drivers of climate and land-use change are global livestock systems (Herrero et al., 2013). Livestock biomass is already higher than human biomass (Bar-On, Phillips, & Milo, 2018), and this trend is likely to strengthen in the future (Valin et al., 2014). The area required to feed the global livestock population is approximately half the global agricultural area. Of these 2.5 billion ha, 2 billion ha is grassland. Most of this grassland area cannot be converted into cropland, which means that 57% (1.3 billion ha) of the area used for forage production are not suitable for crop production. Consistently, 86 % of the global annual forage for livestock are made of materials currently not eaten by humans (Mottet et al., 2017), showing that livestock production is an important component for global food security in the future. While intensive livestock production systems are a problematic driver of climate and land-use change, the extensive livestock systems are often essential for nourishing poor people in dry and remote areas (Havlík et al., 2014; Rojas-Downing, Nejadhashemi, Harrigan, & Woznicki, 2017).

Most of the unconvertible grassland areas are located in drylands. Drylands are defined by their scarcity of water (FAO, 2008) and cover approximately 40 % of the terrestrial surface (White & Nackoney, 2003). The extent of drylands is expected to increase up to 7 % under future climate scenarios (Koutroulis, 2019), resulting in a dramatic increase of the global population living in drylands (Jianping Huang, Yu, Guan, Wang, & Guo, 2015). In dryland systems livestock production is more common than crop production because of insufficient water availability. Although drylands are expected to expand under future scenarios, the total gross primary production per unit of dryland area is expected to decrease. This is partly a result of the expected ongoing overexploitation of dryland systems, which leads to serious degradation of the ecosystems (Yao et al., 2020). Thus, changes in the climatic conditions will have consequences for the future management of dryland systems.

About 65 %, or 40 million km², of drylands is grazed by livestock in differing intensities and under differing climatic conditions (Uriel et al., 2005). Drylands that are used for the grazing of livestock are commonly referred to as rangelands, which is a term that can be both a description of ecosystems as well as a form of land-use (Lund, 2007). Briske (2017) describes rangeland systems as ecological systems with native or naturalised vegetation such as grasslands, shrub steppe, shrublands, savannas, and deserts that are managed as social–ecological systems to provide multiple ecosystem services for human well-being. As such, threats from climate change originate mainly from predicted transformations of the natural vegetation that might impact the roles of herbaceous biomass and functionality as central elements of the food production. The management of dry rangeland systems is extremely dependent on the availability of water in time and space (Briske, 2017b). Water availability determines the extent of biomass production (Le Houerou, Bingham, & Skerbek, 1988), determines the plants which can exist under the given conditions (Keddy, 1992), and is an important, yet often underestimated, factor for livestock health and production (Lardy et al., 1988). The availability of water is bound to two factors in drylands: the aridity of the area, which is often defined by the relationship between precipitation and evapotranspiration (Whitford, 2002), and the climatic variability, often defined as the coefficient of rainfall variability (von Wehrden, Hanspach, Kaczensky, Fischer, & Wesche, 2012). Measures of aridity enable us to predict the overall productivity of a given dryland system and are a good estimator for the general conditions for plants, livestock and humans. Adding information on climatic variability, however, can improve our understanding of the dynamics of the ecosystem (Easdale & Bruzzone, 2015).

Rangelands are especially dynamic ecosystems that are shaped by both biotic and abiotic factors through time and space (von Wehrden et al., 2012). Several concepts of rangeland dynamics have been postulated since the beginning of the 20th century in order to support their management (Briske, 2017a). Some of these concepts assume that rangelands have a definable carrying capacity for livestock. Under this assumption, biotic factors are the main drivers of rangeland dynamics. The widely accepted state-and transition models, for instance, focus on the responses of plant communities to management decisions (Bestelmeyer et al., 2017). Other concepts acknowledge the highly variable abiotic nature of dry rangeland systems. The concept of non-equilibrium rangeland dynamics assumes that both the limited moisture availability and the frequently occurring natural disasters control livestock effects on rangeland vegetation, which means that abiotic effects are superior over biotic effects in dry rangelands (Ellis & Swift, 1988; Engler & von Wehrden, 2018; Vetter, 2004). Research of the last 30 years has shown that none of these concepts have an ubiquitous validity, because the dryland systems, the plants and climate differ strongly and therefore interact differently, leading to different opinions and views of the functioning of rangeland systems on a global scale (see for instance the discussions of (Illius &

O'Connor, 1999) in (Sullivan & Homewood, 2003) or of (Berger, Buuveibaatar, & Mishra, 2015) in (von Wehrden, Wesche, Chuluunkhuyag, & Fust, 2015)). A major problem in most discussions about rangeland systems seem to be a still not satisfactory understanding of the ecosystem functioning, and especially of the interplay between climate, grazing intensity and the vegetation.

The composition of the vegetation is the central element of rangeland management and of vital importance for a successful livestock production (van Soest, 2018). The amount and composition of vegetative biomass determines the forage mass and its qualitative value in space and time. From an ecosystem service perspective, of interest are therefore functions that control the number and identity of species the biomass is consisting of, their abundances and their functional properties. The number of species decreases with increasing aridity in grasslands (Adler & Levine, 2007), which could be the result of reoccurring extreme events in drylands (Tilman & El Haddi, 1992). Species abundances, however, might be linked to aridity through the need for facilitation under more extreme environmental conditions (Berdugo et al., 2019; Keddy, 1992). As acknowledged by the biotic-centered concepts of rangelands dynamics, grazing management is a second huge factor for plant community composition of rangeland vegetation. For instance, herbivores remove biomass by grazing or browsing, yet also stimulate plant growth through the fertilising effect of dung and urine excretion even under arid conditions (Bagchi and Ritchie 2010). Trampling negatively affects plant tissue and soil physical properties, and therefore compromises plant-soil interactions (Greenwood and McKenzie 2001) and also alters the spectrum of plants which are able to persist under such conditions (Landsberg et al. 2003). On the other hand, plants adapted to trampling may still produce substantial amounts of biomass due to the high availability of nutrients (James et al. 1999), impacting the composition of the rangeland vegetation and therewith the microclimate (Whitford, 2002).
Theoretically, the magnitude of these grazing effects on the vegetation depend on the intensity of grazing, which in turn depends on the productivity of a rangeland (Cingolani, Noy-Meir, & Díaz, 2005).

Understanding the interactions between climate and grazing on rangeland vegetation is still a major challenge in rangeland ecology. Studies which tried to gain a better understanding of this complex are still rare, and often either investigated only one climatic area (e.g. (Ren et al., 2018; Sasaki et al., 2009; Sasaki, Okayasu, Takeuchi, Jamsran, & Jadambaa, 2005)), or very few sites (Fernández-Giménez & Allen-Diaz, 1999) or only a few aspects of vegetation responses (Bazha, Gunin, Danzhalova, Drobyshev, & Prishcepa, 2012). Comprehensive studies which investigate interactions between grazing and climate on plants, their community composition, their biomass, their biodiversity, soil and functional properties are much needed to tackle the challenges of the rangeland management conditions in the future (Li, Li, Zhao, Zheng, & Bai, 2018).

Aims

The overall goal of the DFG-funded research project (see *preface*) was to form a basis for the evaluation of the fate of dry rangelands under climate and land-use change by quantifying the relative effects of climate and grazing on rangeland ecosystem functioning. The central question which orbited around my thesis was therefore what the characteristics of land-use and climate along a large-scale gradient in Mongolian rangeland vegetation are; and especially if and how grazing patterns interact with the set up climate gradient. Regarding the large body of literature in this field, the most important but also probably most controversial hypothesis states that **grazing effects depend on climatic variability** (Sullivan & Rohde, 2002; Vetter, 2005). I choose to focus on this hypothesis and approached its falsification via the broad analysis of plant community-related vegetation patterns.

From the central hypothesis came three aims, each one addressing the effect of grazing-climate interactions on a different ecosystem property: species diversity, taxonomic and functional plant community composition, and biomass production. Specifically, I addressed the following research questions:

1. How does grazing affect the species diversity and the taxonomic composition of rangeland vegetation along the climate gradient?
2. How does grazing affect the functional properties of the plant communities along the climate gradient?
3. How does grazing affect biomass production and its composition along the climate gradient?

Synthesising the observations, results and interpretation of the three analyses should contribute to several knowledge gaps in our understanding of the responses of the vegetation to climate-grazing interactions in dry rangeland systems. Taking up the initial overall goal of this research, answering these questions should furthermore allow for a view into the future under different climate and land-use options and therefore enable recommendations for a further sustainable rangeland management in the future.

Datasets

We collected five datasets to answer the three research questions. The core of the sampling design were 10 m by 10 m randomly selected vegetation relevés, where all species and their abundances (in % cover) were recorded according to the standard literature on the Mongolian flora (Urgamal, Oyuntsetseg, Nyambayar, & Dulamsuren, 2014). This dataset was used to estimate grazing effects on species diversity measures such as species richness, evenness and Simpsons D; as well as the estimation of grazing effects on plant community composition using multivariate vegetation classification methods. The second dataset aimed at the verification of the grazing gradients and included dung counts of livestock. Each defecation within the 10 m by 10 m vegetation relevés was recorded as one dung count and transformed into Mongolian livestock units. This approach has been proven to adequately mirror livestock density (Kowal et al. 2021). The third dataset included biomass samples. This dataset was collected to compare the productivity and to estimate the effects of grazing at each site. The biomass was clipped at ground level within each relevé on randomly chosen 50 cm x 50 cm sub-plots, grouped into pre-defined plant functional groups, first air dried and later oven dried at 65°C for 24h for further weighting. The fourth dataset included soil samples. This dataset aimed to understand the interactions between grazing and nutrient availability for plant growth. Four soil samples of the first 10 cm of the top soil were taken and mixed on each vegetation relevé to estimate plant-available nutrients. The fifth and largest dataset included several measured plant traits as well as traits that were compiled from the literature (see Supplements chapter 1 for an overview) and followed standard protocols for plant trait collection (Pérez-Harguindeguy et al., 2013). This dataset was collected to understand the functional responses of the plant communities to grazing under different climatic conditions, as well as to synthesise these responses with environmental and compositional patterns in the Mongolian steppe ecosystems. The whole vegetation and soil sampling was performed twice to get an estimate of inter-annual differences, once in 2014 and once in 2015. The first sampling period started in the second week of June 2014, while the second sampling period started in the first week of June 2015. More detailed information on data collection can be found in chapters 2-4.

Study area & design

Designing a study that enables the consistent investigation of interactions between grazing, climate and vegetation properties ideally features a study area with two characteristics: a steep yet uniform climate gradient with gradually changing zonal vegetation composition as well as a comparable grazing system. Mongolia is an ideal model system for such a study. Together with China, Mongolia hosts the largest natural grassland in the world (Pfeiffer, Dulamsuren, Jäschke, & Wesche, 2018). A total of 80% or 1.2 million km² of Mongolia's surface are covered with grasslands and arid rangelands (Suttie, Reynolds, & Batello, 2005). The majority of these grasslands are considered to be still intact (Batsaikhan et al., 2014; Pfeiffer, Dulamsuren, & Wesche, 2019) but the strongly increasing livestock numbers since the 90's (Lkhagvadorj, Hauck, Dulamsuren, & Tsogtbaatar, 2013) have fueled a discussion about increasing land-use degradation (Addison, Friedel, Brown, Davies, & Waldron, 2012; Bazha et al., 2012; von Wehrden et al., 2015), which highlights Mongolia as a model region for the sustainable coexistence between future livestock management and grassland ecosystems under climate change.

The climate is continental with extreme diurnal and annual temperature amplitudes and quick season changes between the long, cold winters and hot summers (Dashkhuu, Kim, Chun, & Lee, 2015; Dulamsuren & Hauck, 2008; Pfeiffer et al., 2019). The country's annual mean temperature is around 0°C. The surrounding mountain ranges cause a strong moisture gradient from the north to the south as well, which is in turn responsible for the characteristic north-south sequence of latitudinal vegetation (Lavrenko & Karamysheva, 1993) and soil belts (Tamura, Asano, & Jamsran, 2013). Half of the average precipitation occurs between June and August. This leads to a rather short growth period, but also to sufficient rainfall for plant growth even in regions with less than 150 mm per year (Pfeiffer et al., 2018). High aridity is accompanied with high rainfall variability in space and time, which limits the continuous use of pastures, ultimately being responsible for Mongolia's characteristic transhumant pastoral livelihood. In its extreme form, the climatic variability is responsible for a phenomenon called *dzud*. Dzuds are extreme winters with heavy snowfall combined with serious droughts during the vegetative growth period that can lead to drastic diebacks of livestock numbers (Middleton & Sternberg 2013).

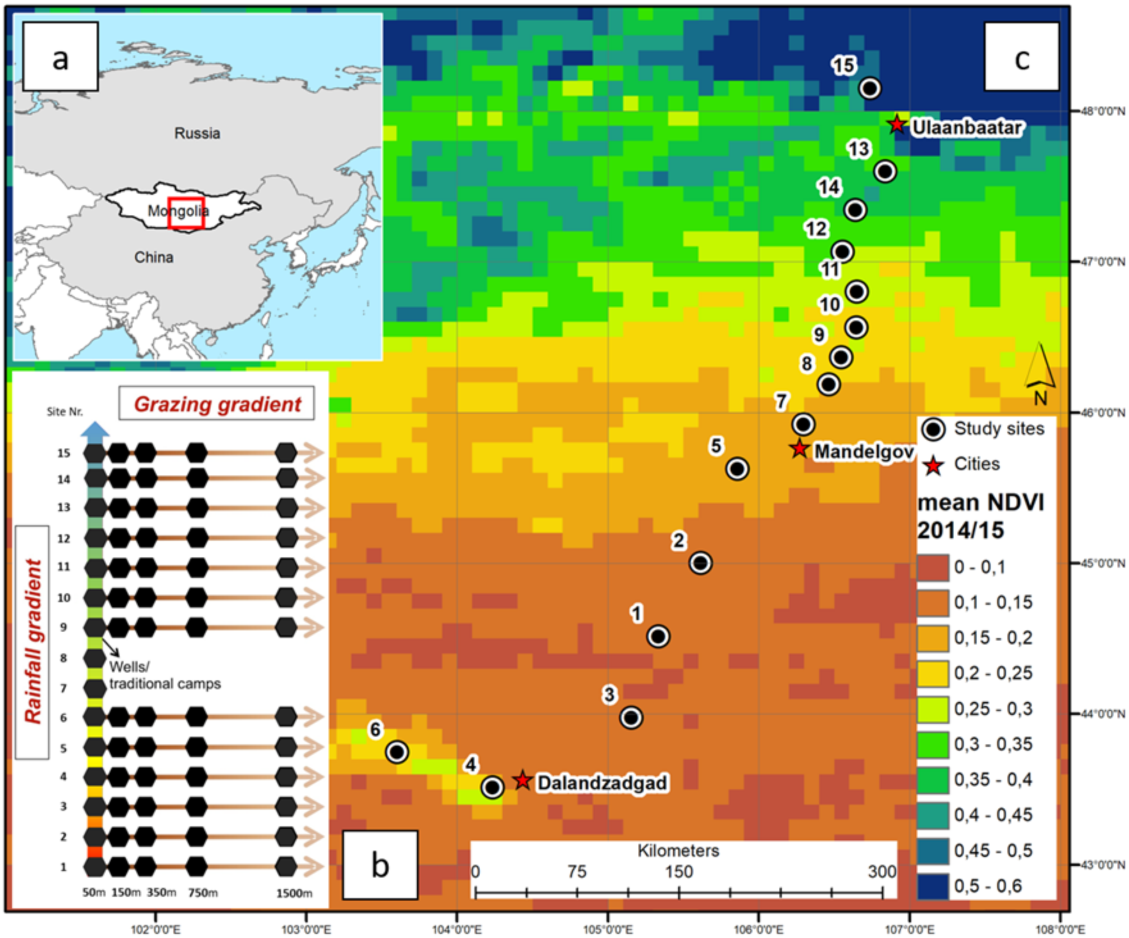


Figure 1.1: Map of the study area. a) shows the location of the study area within Central Asia, b) shows the study design and c) shows the locations of the study sites within the study area. Colors resemble the mean NDVI during the time of the field campaigns in 2014 and 2015 (NDVI data is based on MODIS). Figure taken from chapter 4.

The study behind this thesis (see *preface*) made use of the distinct climate gradient and the uniform livestock management system in Mongolia. 15 study sites were selected along a 600 km long north-south gradient (Fig. 1.1) , where mean annual precipitation ranges from 100 mm and mean annual temperatures from 4°C in the dry southern part, to 250 mm and 1°C in the wetter northern part of the gradient (Fick & Hijmans, 2017).

This gradient reflects three major vegetation belts of the palaearctic steppe biome: the forest steppe, the typical steppe and the desert steppe with their latitudinal associated soils chernozems, (dark) kastanozems and brown semidesert soils (Tamura et al., 2013). This north-south gradient can be considered a climate gradient: precipitation, temperature and precipitation variability are highly correlated (Fig. 1.2), and both the vegetation and the soils show a clear, consecutive north – south sequence. Therefore, this gradient will be called a “climate gradient” throughout this dissertation, even if only mean annual precipitation was used as the primary proxy across the analyses.

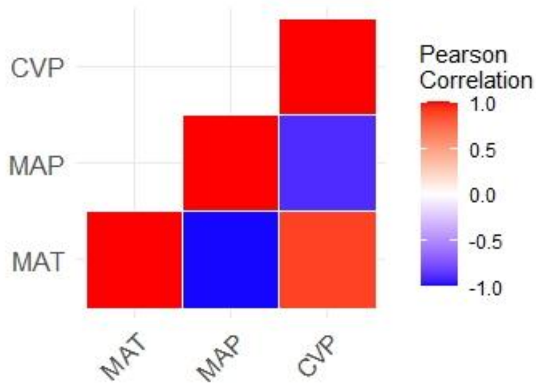
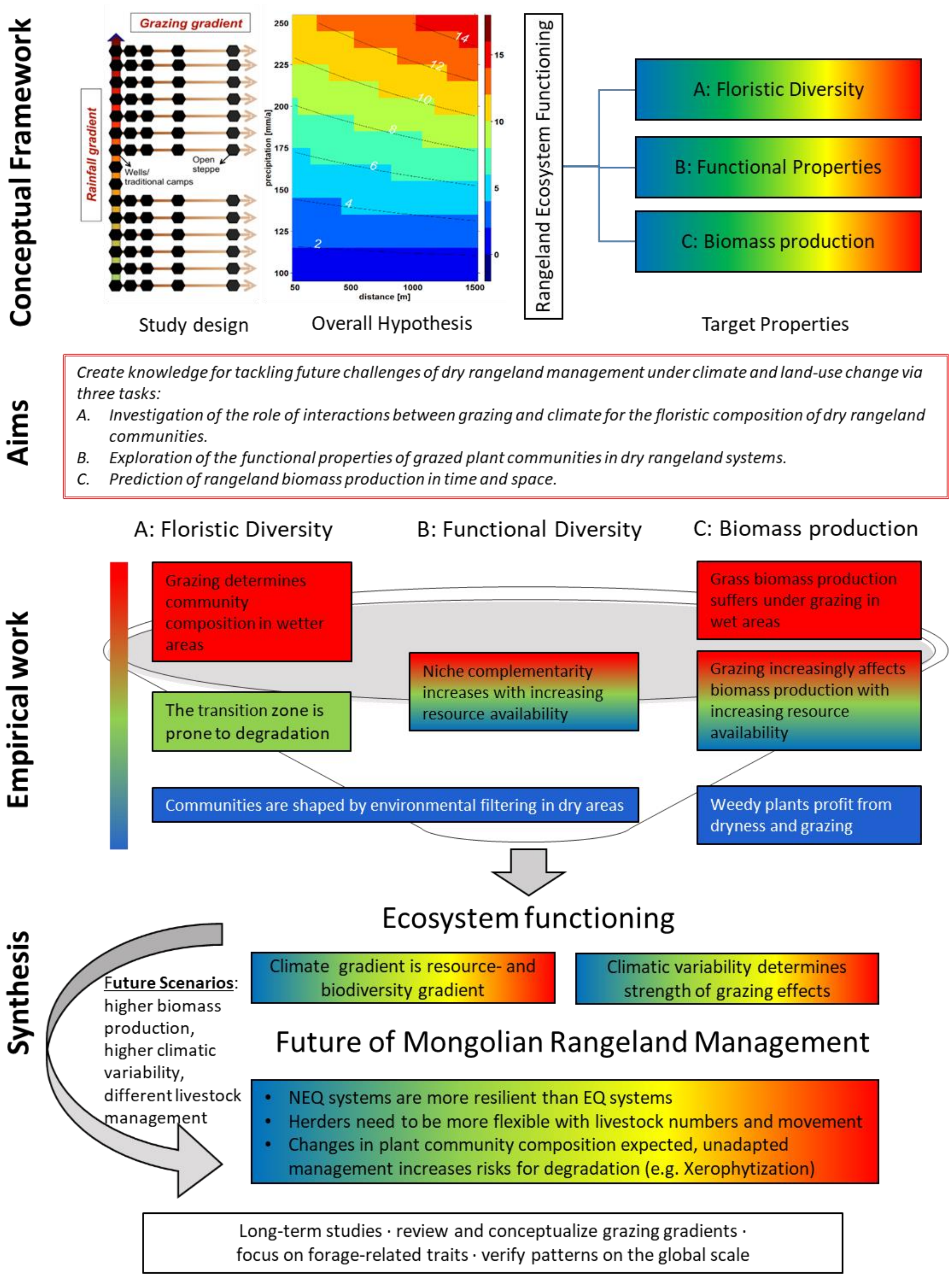


Figure 1.2: Correlation matrix of the coefficient of rainfall variability (CVP), mean annual precipitation (MAP) and mean annual temperature (MAT) for the 15 study sites. CVP was derived from Wehrden et al. 2012, MAP and MAT were derived from Hijmans et al. 2016.

In order to compare the effects of grazing on the different vegetation communities along the climate gradient, transects of 1500 m were chosen at each study site. Starting from a local grazing hotspot such as a well, a camp or a winter place, plots with 5 replicates were selected in a straight line within a distance of 50 m, 150 m, 350 m, 750 m and 1500 m from the hotspots, adding up to a total of 375 plots (15 sites x 5 distances x 5 repetitions). This approach is mathematically robust (Manthey & Peper, 2010) and the specific distances had been shown before to capture grazing intensities in Mongolian steppe ecosystems (Stumpp, Wesche, Retzer, & Miehe, 2005).

Graphical abstract



Summary of the empirical work

Chapter 2 addresses the role of grazing in determining the composition of plant communities in rangelands ranging from dry to relatively moist conditions. The study used the dataset that comprised 375 vegetation relevés of plant species and their abundances. This dataset was collected in 2014.

We used a detrended correspondence analysis (DCA, a multivariate ordination method) to quantify floristic similarities and distances within our research design. The DCA revealed that plant communities in the dry south differed more between the sites, while communities within the wet north were floristically more similar among each other. This result suggests that environmental filtering dominates plant community composition in dry areas, while increasing competition for resources could explain the higher similarity of plant communities in more moist areas. Moreover, grazing effects were restricted to so-called "sacrifice zones" in dry areas.

Subsequently, we calculated three biodiversity indicators – species richness, Simpson's D, evenness – and used mixed effect modelling in a candidate modelling approach to test if and how interactions of grazing and climate affect species diversity. The data showed positive effects of mean annual precipitation on species richness, but also an increasingly negative effect of grazing intensity on the plots with intermediate grazing intensity. This can be interpreted as a result of previously reported degradation in Mongolia’s comparably productive north. Simpson's D responses to grazing were unimodal, suggesting that the plant communities at the extreme ends of the grazing gradients were often dominated by some species compared to the communities under intermediate grazing. Evenness did neither respond to grazing, nor to climate. In summary, the results of these indices were rather inconsistent.

Finally, we were looking for plant species which could indicate specific grazing intensities within their preferred climate. Indicator species analysis suggested that one third of all recorded species are useful indicator species for either climate, for grazing intensity, or both. This confirms the high degree of specialisation of species along the climate gradient. Species associated with intensive grazing could be almost exclusively referred to the spectrum of ruderal species. This is most likely linked to the specific conditions of the sacrifice zones, where grazing effects are mostly decoupled from climate effects. Under more moist conditions, some characteristic steppe species occur preferably under intermediate grazing, which was not the case under dry conditions. This supports NEQ-theory which predicts no or minor grazing effects under dry conditions. The indicator species analysis also yielded evidence for xerophytisation in the transition zone between the supposed NEQ and EQ systems, indicating overgrazing in this region.

We derived three central conclusions from this study: (1) Environmental filtering determines community composition under dry conditions, (2) Grazing determines community compositions in moister rangelands and (3) There is evidence that degradation occurs in the transition zones between supposed EQ and NEQ systems. We suggest that the management of livestock densities should pay particular attention to the transition zones in the future in order to minimize degradation.

Based on the observations made in chapter 2, **chapter 3** focuses on the functional mechanisms of plant community composition. The main goal of this study was to test the previously stated hypothesis that plant community composition in supposed NEQ systems are driven by environmental filtering, whereas plant community composition in supposed EQ systems is determined by rules of competition, i.e. niche complementarity.

We separated the climate gradient at the putative border between EQ and NEQ systems into two parts, which reflect the biomes of desert and grassland. Beginning with an initial dataset of 12 traits from the 117 most abundant species, we selected a trait set with the most responsive traits for each region using an iterative RLQ-analysis. The first few extensive analyses revealed that one site was exceptional due to salty soil conditions, whereas not enough plant trait data was available for two other sites, leading to the exclusion of three sites. Three traits in the desert and four traits in the grassland mirrored the functional properties of the plant communities, regarding their response to climate and grazing, in the most parsimonious way.

The two selected trait sets were then further processed within their regions via the following approach: (1) A RLQ/4th corner combination was used to investigate the reaction of single traits towards climate and grazing. The analysis showed that the type of grazing hotspot (camp, well or winter place) had a strong impact on the traits in both regions. This result underlines the distortive role of the sacrifice zones. (2) Based on the two trait sets, we calculated Masons & Villegers functional diversity indices functional richness, functional dispersion and functional divergence, to gain information about the functional structure of the communities. The functional structures differed considerably. Functional richness was higher under dry conditions than under wet conditions and higher under moderate grazing than under intensive or extensive grazing.

We concluded that environmental filtering plays a more important role for the plant community assembly in dry areas. Higher functional divergence under EQ dynamics suggests that niche complementarity increases with increasing resource availability. With respect to the future grazing management, we suggest that differences of the functional properties of the plant communities between dry and wet rangelands needs to be taken into account.

After focusing on climate-dependent effects of grazing on the mechanisms of plant community assembly in chapters 2 and 3, **chapter 4** was dedicated to the probably most important ecosystem service of grasslands: the provisioning of biomass for forage in time and space. To quantify the climate-specific grazing effects on biomass production, this study utilised the biomass we sampled during the vegetation periods in 2014 and 2015. Again, three aspects were analysed. The first analysis dealt with the question if effects of grazing on total biomass are dependent on climate. We first noticed that the inter- and intra-annual variability of biomass was higher in moister rangelands. After correcting for this pattern, we could show that grazing effects on total biomass indeed increased with increasing resource availability.

In the second step, we tested several hypotheses regarding the role of diversity for biomass production in grasslands. We were able to confirm the positive effect of species diversity for biomass production, but this effect seemed to be dependent on the distribution of rainfall within a growth period. Moreover, we found that grazing had negative consequences for the diversity-productivity relationship.

In a last step, we studied how specific functional groups react to grazing under different climate conditions. Here, we could show that the main biomass builders grasses and herbs responded oppositely to climate and grazing. Biomass of grasses decreased with grazing intensity, and this effect increased with increasing resource availability. Herbal biomass, however, profited from higher grazing intensity and this effect decreased with increasing rainfall.

With respect to the future management of these rangelands, we suggest a more flexible handling of livestock density in the moister areas, as well as the conversation of biodiversity, to maintain enough and/or emergency forage during harsh times.

Synthesis

Climate and land-use change are threatening the capacity of drylands to recover from disturbances around the globe. This capacity, better known as resilience, is threatened by multiple factors, such as altered rainfall regimes, overgrazing or biodiversity loss (Shukla et al., 2019). Being able to predict the consequences of rangeland management under predicted future climate conditions and land-use change is essential for sustaining food security of potentially billions of people in future drylands. Critical gaps in our basic understanding of interactions between grazing and climate on rangeland ecosystems have already contributed to widespread degradation among dry grassland systems, and counteracting the development towards a worsening of rangeland condition is therefore an urgent task.

This dissertation aims to shed light on the climate-mediated impacts of grazing on important ecosystem properties of dry grasslands by studying a relatively intact rangeland ecosystem in Mongolia. Facilitating a statistically comprehensive and data driven approach on plant community composition, the included chapters contribute important knowledge to our understanding of vegetation patterns in dry rangeland systems. The main goal of this synthesis is to discuss possible developments of the studied ecosystem properties plant species diversity, community composition and biomass production to grazing and climatic variability under future climate and land-use scenarios. In the following, I will first discuss the current responses of the three ecosystem properties to grazing and climate using my empirical work. Then I will use the existing literature to draw a picture of the future climate conditions in Mongolia and predict consequences of climate change for the three ecosystem properties. Lastly, I'll provide a list of further research topics, which I selected to further elaborate on questions arising from this thesis.

System properties

The main hypothesis of this dissertation was that the effects of grazing on dry rangeland vegetation depend on climatic variability. Two ideas build the backbone of this hypothesis: First, high climatic variability is responsible for the scarcity of resources (such as moisture and plant available nutrients) in time and space in dry grassland systems (Fang, Piao, Tang, Peng, & Ji, 2001; Yang, Fang, Ma, & Wang, 2008). Second, higher climatic variability also means extremer conditions for the vegetation and livestock. Accordingly, plant communities require physical adaptions to the general lack of resources and to extreme events. Such events can be floods

(Murray-Tortarolo & Jaramillo, 2020), droughts, or the in Mongolia dreaded *dzuds*, which can all lead to drastic diebacks of livestock (Middleton & Sternberg 2013). These two ideas are relevant for sustainable grassland management, because effective rangeland management decisions depend heavily on the relationship between climatic variability and the productivity of rangelands (Le Houerou et al., 1988). Consequently, differing climatic variability should result in differing land-use intensities and effects, and these differences should be detectable in the ecosystem properties along a climate and land-use gradient.

Species diversity

Species diversity is defined as a function of species richness and the abundance of species, the evenness, which is part of many popular species diversity indicators such as Shannon's H or Simpson's D (Baillie & Upham, 2012). Species diversity is an extremely popular measure for ecosystem functioning in grasslands, because it allows for a simple quantification of the efficiency of the resource use (and therefore the productivity) and the level of disturbance in an ecosystem (Bradley J Cardinale, Palmer, & Collins, 2002; Tilman & Downing, 1996; Zavaleta, Pasari, Hulvey, & Tilman, 2010). For dryland systems, one can hypothesise that high species diversity is associated with (relatively) high resource availability, high facilitation between species, and high productivity (Durán et al., 2018). In contrast, low species diversity is associated with high environmental stress (Le Bagousse-Pinguet et al., 2017). Disturbance, e.g. grazing, can alter these relationships under both productive and unproductive conditions (Cingolani et al., 2005). In Eurasian steppe ecosystems, species diversity has previously found to increase linearly with mean annual precipitation (Bai et al., 2007). The responses of species diversity to grazing are dependent on the precipitation regime in time (Ren, Schönbach, Wan, Gierus, & Taube, 2012) and space (Wang & Wesche, 2016).

Our data on species diversity in the Mongolian steppe ecosystem generally confirmed these hypotheses. Both species richness and Shannon's H were lowest under dry conditions and increased linearly with mean annual precipitation in both years 2014 and 2015 (Fig 1.3). High grazing intensity was clearly associated with low species diversity, which was especially evident at the sacrifice zones around grazing hotspots (chapter 2). Regarding the interactions between grazing and climatic variability, we expected increasing effects of grazing with increasing resource availability on species diversity (Cingolani et al., 2005).

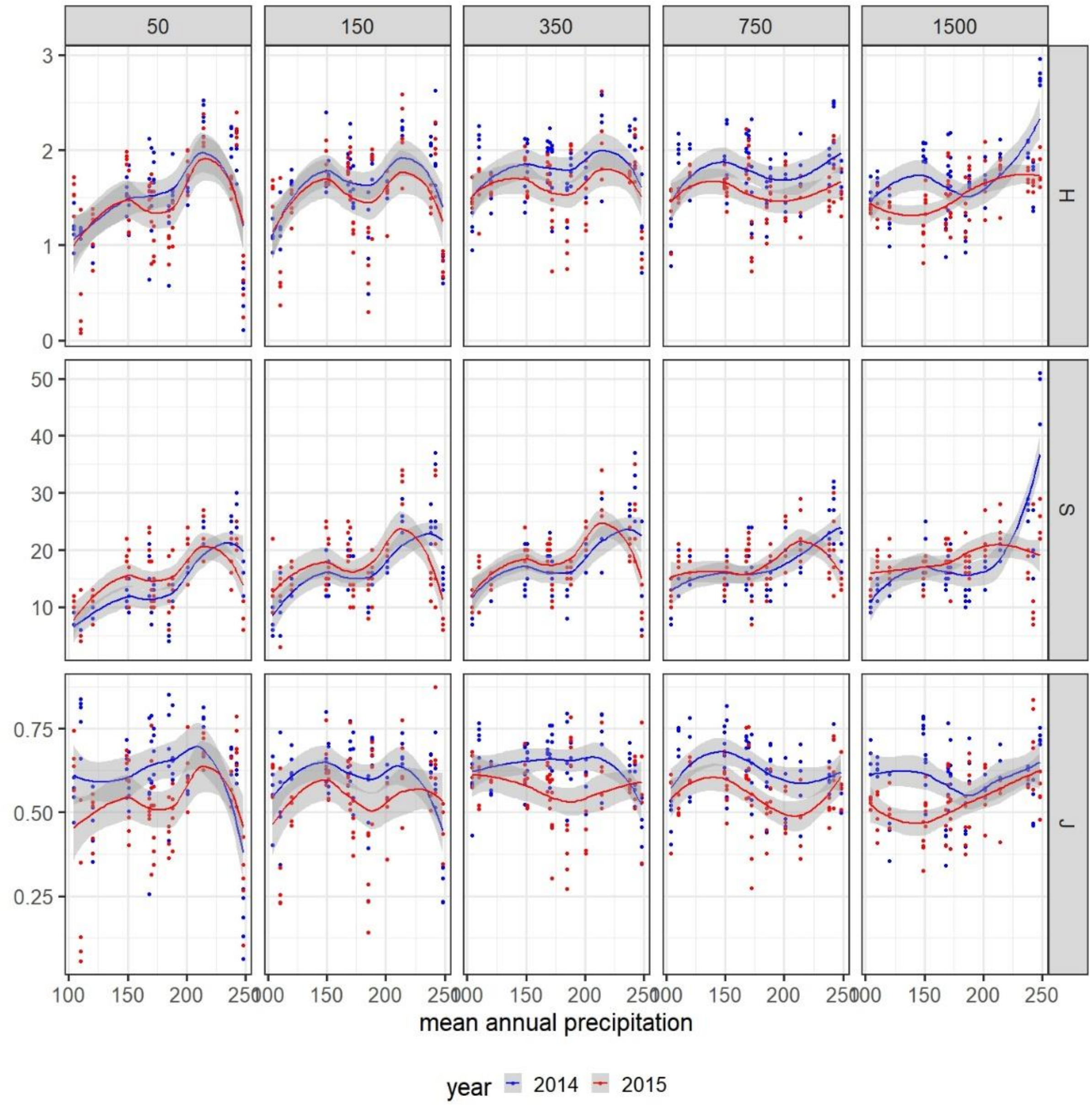


Figure 1.3: Loess models of species richness (H), Shannon diversity (S) and Pilou's evenness (J) for the years 2014 (blue) and 2015 (red). The horizontal facets resemble the distances to the grazing hotspots, the x-axis captures the mean annual precipitation.

The effects we found were small, but still detectable: with decreasing climatic variability, species richness was increasingly affected at the medium distances of the grazing gradients (chapter 2). Interactions were also present for Simpsons' D, but the grazing effect dominated the best fitting model. Two things could be reasons for the low effect sizes in our models. First, the inconsistency in the choice of the grazing hotspots along the climate gradient may have covered clearer effects. Sacrifice zones are azonal sites and less strictly bound to climatic conditions than typical rangeland vegetation (Landsberg, James, Morton, Müller, & Stol, 2003; Wang et al., 2017). The mixture of types of grazing hotspots along the climate gradient may have diminished the effects, which would be rather a systematic error than an ecological effect (see also the discussion under “shortcomings and further research”). Second, simple loess models showed that there was a levelling in the increase in species diversity in the middle of the climate gradient (Fig 1.3). This pattern may have led to less clear results of the linear mixed effects models, and stresses the hypothesis of a simple, linear relationship between climatic variability and grazing intensity along the investigated gradients.

Plant community composition and functional properties

Plant community composition plays a key role in controlling net primary production and ecosystem stability of dry grassland ecosystems (Cleland et al., 2013). Plant community composition in grasslands is determined by the abiotic environmental factors such as temperature and precipitation (Cleland et al., 2013), and specifically in case of rangelands, by biotic factors such as grazing (Díaz et al., 2007). Traditionally, plant community ecology has focused on taxonomical approaches in order to study impacts of abiotic and biotic constraints on population dynamics (Shipley, Vile, & Garnier, 2006). New conceptual frameworks and advances in computer science and associated analyses during the last two decades have promoted a more functional view of plant communities. In this dissertation, I investigated both taxonomic (chapter 2) and the functional community composition (chapters 2&3). Numerous studies of vegetation along environmental gradients have shown that especially the investigation of the different facets of functional plant community composition can unravel important abiotic and biotic constrains in ecosystems (Baastrup-Spohr, Sand-Jensen, Nicolajsen, & Bruun, 2015; Bernard-Verdier et al., 2012; Carmona, Mason, Azcárate, Peco, & Bartha, 2015; Cornwell & Ackerly, 2009; Klanderud, Vandvik, & Goldberg, 2015).

Our study of the taxonomical plant community composition showed that the floristic similarity of plant communities was lower between sites in the dry south, while floristic similarity of the communities differed less between sites in the wetter north (chapter 2). In turn, the floristic similarity along the grazing gradients was higher in the dry areas, than it was in the wetter north. This pattern suggests that plant communities in the dry areas have a high specialisation, probably due to the strong climatic constrains, and that grazing causes very little differences in the composition of the communities. Notable grazing effects on the floristic composition in the dry areas were only present in the sacrifice zones. Apart from these spatially limited areas, plant communities did not differ remarkably in their floristic composition along the grazing gradients. Plant communities in the north may have a higher floristic similarity between sites, because the lower environmental constrains allow for a more differentiated exploration of the available resources, and therefore a higher diversity of available niche space. The higher grazing intensity in the more wetter and productive areas in the north is then probably responsible for a larger floristic gradient within these sites. The analysis of the functional composition was consistent with the results on the taxonomic composition. The functional diversity of the dry sites was significantly lower than in their northern counterparts. The idea of a higher specialisation of the communities in the dry areas was backed by a smaller set of traits that rendered these less diverse communities (chapter 3), whereas the functional composition of the communities in the wetter north was characterised by a higher complexity of traits. Regarding the effects of grazing on the functional composition, the analysis revealed that the biggest differences were found between sacrifice zones and their surroundings. The specific conditions at the sacrifice zones were illustrated by a positive association between soil and leaf nutrients, as well as by a domination of species with sclerificated plant tissue and bambusoid growth (see Pérez-Harguindeguy et al. (2013) for more details). This is in line with other studies that found that community composition in sacrifice zones is rather dominated by effects of high nutrient intake and trampling than by climatic constrains (Grime, 1977; C. D. James, Landsberg, & Morton, 1999; Wang et al., 2017).

Biomass

Biomass production is probably the most important ecosystem service in dry grassland systems (White & Nackoney, 2003). Biomass production translates into the provisioning of forage for livestock, and therefore controls stocking densities and herd sizes. In regions where the livestock management systems are highly mobile, such as in many parts of Central Asia, biomass production also controls the movement of the herds. In turn, biomass production in rangelands is mainly affected by three variables: 1) the climatic variability in drylands, because the higher the climatic variability, the lower the productivity of the rangelands (von Wehrden & Wesche, 2007); 2) grazing intensity, because grazers affect the vegetation and therefore standing biomass through trampling, foraging etc. (Milchunas, Sala, & Lauenroth, 1988); and 3) biodiversity, because higher biodiversity may also result in higher biomass production and higher stability (Hector et al., 2010). Yet, a current review of the patterns and drivers of the biodiversity–stability relationships under climate extremes found that more diverse ecosystems do not systematically buffer the impacts of climate extremes on ecosystem functioning better than less diverse ecosystems do (Boeck et al., 2018).

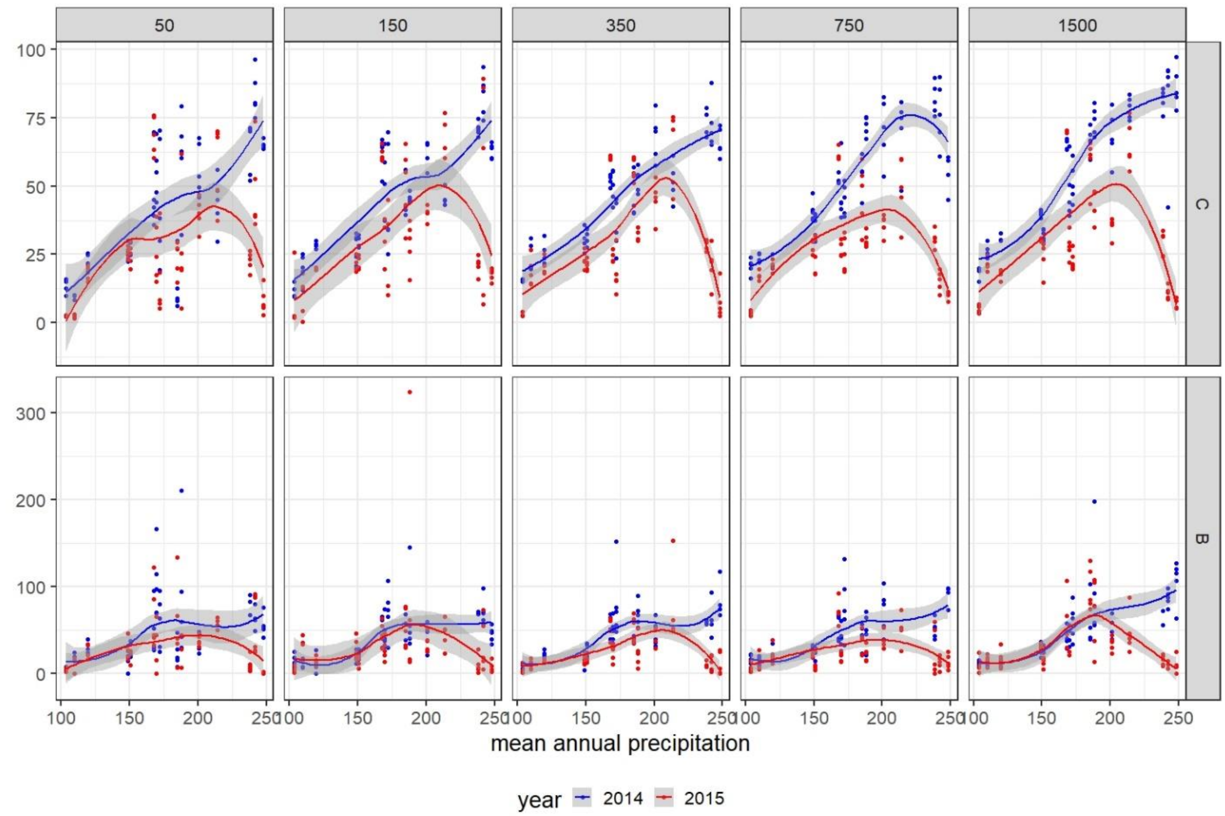


Figure 1.4: Loess models for plant cover in % (C) and biomass (B) for the years 2014 (blue) and 2015 (red). The horizontal facets resemble the distances to the grazing hotspots, on the x-axis the mean annual precipitation. The graphic illustrates the relationship between mean annual precipitation and productivity, as well as the increasing effect of inter- and intra-annual climate effects for the productivity.

The data collected for this dissertation confirm that the predicted negative relationship between climatic variability and productivity in rangelands holds for Mongolia's grassland systems as well. Plant biomass and cover increased with increasing mean annual precipitation (Fig 1.4). As stated above, precipitation variability and mean annual precipitation were negatively correlated (the higher the variability, the lower the mean annual precipitation, see Supplement B of chapter 2). The results therefore support the idea that resource availability is a function of the temporal and spatial moisture availability in Mongolian rangelands (von Wehrden & Wesche 2007; Wesche & Treiber 2012).

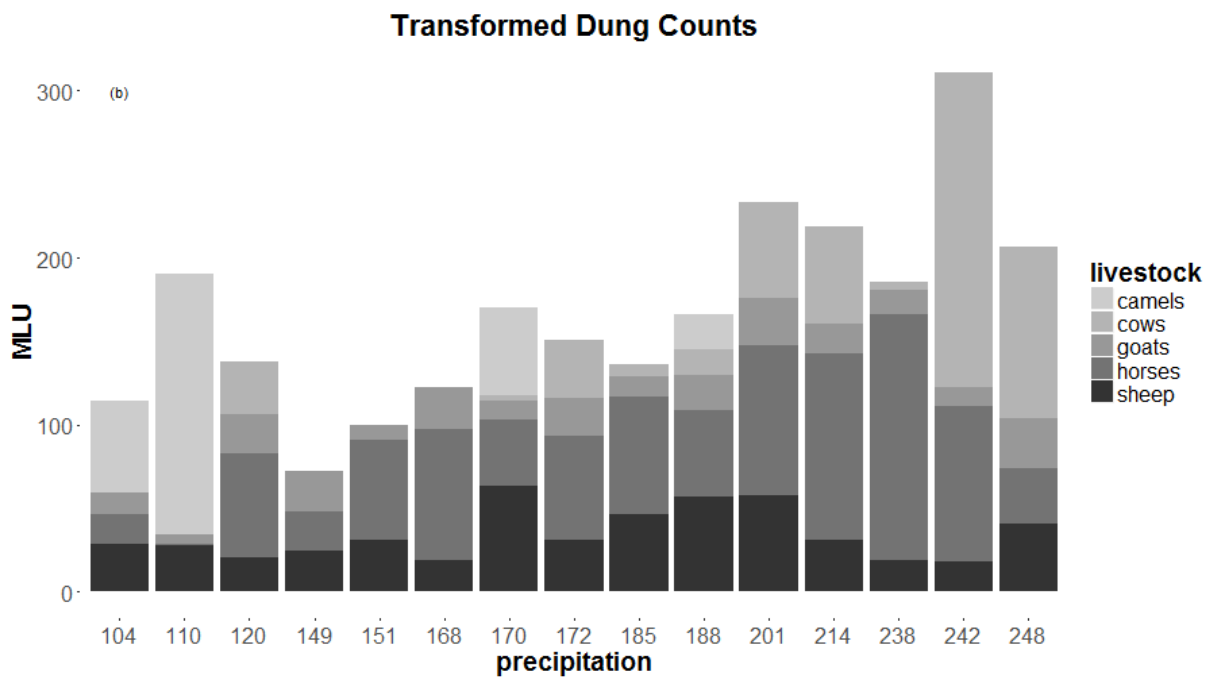


Figure 1.5: Sums of the transformed dung count data for each study site. MLU are Mongolian Livestock Units (after Suttie and Reynolds 2003). The greyscale indicates the livestock types.

Interestingly, our data also illustrated another facet of the relationship between productivity and climatic variability: both inter- and intra-annual differences had a greater impact on the productivity in the productive areas, than in the dry and climatically variable areas. We also found that grazing increasingly affected biomass production with increasing precipitation (chapter 4). This is likely a result of the stocking density, which correlates with the increasing biomass production and therefore the increasing forage availability along the climate gradient (Fig 1.5). The interaction between precipitation and grazing, however, also suggests that grazing itself has a smaller impact on the vegetation in dry and climatically variable areas, then it has compared to the areas with higher productivity. Although the precipitation regime differed strongly between 2014 and 2015, and both intra- and inter-annual differences caused remarkable differences in the standing biomass, the analysis in chapter 4 shows that the interactive effect between precipitation and grazing on standing biomass *per se* was not affected by the climatic variability. Instead, effects of inter-and intra-annual differences on the relationship between biomass and grazing were rather found to be dependent on biodiversity. Chapter 4 shows that biodiversity had a positive effect on biomass production in 2014, a year with sufficient moisture availability, and that this effect was dependent on the grazing intensity. In 2015, where all sites suffered from a drought early in the year, no effects of biodiversity on biomass production were found. Moreover, chapter 4 suggests that the functional composition plays a major role for the interaction between grazing intensity and climate on biomass production. In the dry south, effects of grazing intensity on selected functional groups were lower than the effects in the wetter north, and the results suggest that these effects also differed between the years. Especially herbaceous biomass was higher during times of delayed rainfall, whereas grass biomass production suffered under the temporal moisture limitation. This is in line with data from sites with comparable climatic variability in the United States (Gherardi & Sala, 2015).

Interpretations of ecosystem functioning

The investigation of the ecosystem properties plant species diversity, plant community composition and plant biomass production along a climate and grazing gradient in Mongolia has expanded our understanding about the functioning of Mongolian rangeland ecosystems in two important points: 1) the gradient of climatic variability translates into a gradient of resources with strong environmental constraints, where the lack of moisture and the frequent droughts may act as a filter for species with specific trait combinations. Increasing resource availability in form of moisture and nutrients and decreasing environmental stress leads to increasing numbers and dimensions of ecological niches. 2) Climatic variability in both its temporal and spatial dimensions determines the strength of the effects of grazing on the vegetation.

Resource gradient and environmental filtering

The high climatic variability in both time and space in southern Mongolia leads to a constant limitation of water for plant growth. This lack of moisture can be considered a steady state, which is only interrupted by short and sparse precipitation events that enable a short time of nutrient uptake and therewith plant growth (Reynolds, Kemp, Ogle, & Fernández, 2004; Wiens, 1984). Together with the droughts, which are only a prolonged and more serious limitation of water, these conditions pose a strong environmental filter for specific functional properties of plants. This concept of environmental filtering (Kraft et al., 2015) can explain increasing species numbers along environmental gradients (Laliberté, Zemunik, & Turner, 2014). Although criticised lately for the inflationary use in ecological studies (Cadotte & Tucker, 2017), the concept has high potential for the explanation of plant community composition in drylands (Le Bagousse-Pinguet et al., 2017). According to the concept, only few specialised plant species with specific adaptions to the local conditions can persist and reproduce under the strong environmental constrains (Keddy, 1992). This hypothetical "sieve" explains the low species diversity at the dry end of the gradient (chapter 2), as it filters for species with abilities to withstand long periods without precipitation, such as dwarf shrubs or tussock grasses (chapter 3). These species may have disadvantages towards other plant species under less harsh conditions, such as their often slow growth rates (Whitford, 2002). The increase in species diversity along the climate gradient can be therefore explained by an increase in the number and dimensions of ecological niches (Connell & Orias, 1964). The increase in functional diversity along the climate gradient supports this idea (chapter 3). Plant communities at the northern, wetter part of the gradient are more diverse both in terms of floristic and functional composition, because their environment provides them with a higher variety of resources in comparison to the dry areas in the south. Facilitation among the different species may further boost a higher complexity of the communities (Brooker et al., 2008). The biomass data also supported the idea of a gradient of strong environmental constrains: increasing mean annual precipitation and decreasing climatic variability lead to a higher biomass production, which is most likely a result of lower environmental stress and higher resource availability (chapter 4). Higher availability of water and therefore nutrients (Whitford, 2002) allows for an increase in biomass production within all dry grasslands species (Wesche & Ronnenberg 2010), which allows for an exploitation of a greater variety of resources (or niches), as well as stronger biotic interactions between species through facilitation (Maestre, Callaway, Valladares, & Lortie, 2009; Zhang et al., 2018). This is supported by the studied relationship between species richness and biomass and confirms ecological theories that higher diversity (and therewith potentially more complex facilitation effects among plant species) increases biomass production (chapter 4, (Bradley J Cardinale et al., 2002; Bradley J. Cardinale et al., 2007)).

Climatic variability & grazing

Biomass production is known to be tightly coupled with climatic variability in dry rangelands, which also means that livestock management decisions are strongly dependent on climatic variability (Le Houerou et al., 1988). Popular models of rangeland dynamics assume that increasing productivity and stability of rangelands allows for higher stocking densities, which in turn leads to increasing grazing effects (Cingolani et al., 2005). In Mongolia, the pastoral and transhumant lifestyles (Blench, 2001) enable a flexible utilisation of locally available forage resources (Fernández-Giménez, 2006; Teickner et al., 2020). Livestock densities have been reported to be higher in the centre and the north of the country (Pfeiffer et al., 2019; Rao et al., 2015). Our dung count data showed that the livestock numbers (or stocking density) and the composition of the herds varied with the climatic variability, with (in average) high climatic variability resulting in low stocking densities and a higher proportion of drought-adapted animals such as camels in the local herds (Fig 1.5). Lower climatic variability is associated with higher forage production, which results in higher livestock density. An important question is now whether the effects of grazing on the vegetation *increase* along the resource gradient. No differences in the effects of grazing would mean that forage production and stocking density are balanced (Illius & O'Connor, 1999). Our analyses of biomass and species diversity (chapters 2 & 4) revealed an increase of the effect of grazing intensity on biomass and species diversity. This suggests that the rangeland vegetation is not only determined by climatic factors and livestock activity, but also by an *interaction* between climatic variability and grazing intensity.

A common hypothesis is that the southern, dry and variable part of the climate gradient with desert grasslands being the dominating vegetation type represents a non-equilibrium rangeland system, whereas the northern, moist part with meadow steppe being the main vegetation type represents an equilibrium system (Fernández-Giménez & Allen-Diaz, 1999; von Wehrden et el., 2012; Wesche & Retzer, 2005; chapter 3). Classifying Mongolian rangelands into NEQ and EQ systems could simplify directing management decisions and conservation efforts under future climate conditions for rangeland managers and policy makers. The analyses of this dissertation suggest that there are fundamental differences in the role of climatic variability for the effects of grazing on the plant communities between dry (supposed NEQ) and moist steppe ecosystems (supposed EQ). The inter-annual differences in the precipitation regime between 2014 and 2015 have shown that the impacts of droughts hit productive rangelands harder than the dry, unproductive rangelands. These dry rangelands may be adapted to droughts, and at the same time, the NEQ dynamics prevent overgrazing, rendering these systems as highly resilient rangeland systems towards overgrazing (Addison et al., 2012; Fernández-Giménez & Allen-Diaz, 1999; Wesche & Retzer, 2005). Productive systems, on the other hand, have shown to be much more dependent on the biotic factors, such as stocking density (controls grazing effects) and biodiversity (controls biomass).

To ensure a sustainable rangeland management, it would be therefore important to locate the border or transition between NEQ and EQ systems. In theory, the supposed border between NEQ and EQ systems is marked by a coefficient of rainfall variance of 33% (Ellis & Swift, 1988; von Wehrden et al., 2012). However, both Ellis and Swift (1988) and Wiens (1984) argue for the system being a continuum, rather than a dichotomy. This view was later supported by the findings of (Fernández-Giménez & Allen-Diaz, 1999), which showed mechanics of both NEQ and EQ systems in the desert steppe, the meadow steppe and the mountain steppe. The border could be therefore rather a zone, which shifts from year to year, and chapter 2 supported this idea: There is evidence that high grazing intensity can cause a xerophytisation of the vegetation in dry grassland systems, which is also associated with a smaller species pool (Lisetskii, Chernyavskikh, & Degtyar, 2011; Zemmrich, Hilbig, & Oyuunchimeg, 2010). We found hints for xerophytisation within the transition zone between the areas with supposed equilibrium and non-equilibrium dynamics. This area also marks the boundary between the desert steppe and the steppe in Mongolia, and also the northern boundary of the Gobi desert. Sternberg and his colleagues have found that the margins of the Gobi desert differ from year to year, depending on the annual rainfall regime (Sternberg, Rueff, & Middleton, 2015). A mismatch between the livestock numbers and the yearly fluctuating forage availability may have caused overgrazing of the vegetation in this area, leading to a change in the functional composition of the plant communities. Similar results have been found in rangelands in Senegal (Miehe, Kluge, von Wehrden, & Retzer, 2010). This area in the transition zone between NEQ and EQ systems might be therefore an area, where the impacts of dzuds and droughts regularly mix with times of increased higher moisture and forage availability. One the one hand, this supports the idea of a transition zone between NEQ and EQ systems, and on the other hand, the transition zone suggests that the climate-induced imbalance of the systems might be a huge problem in the future.

Mongolia's rangeland ecosystems under future climate scenarios

Climate scenarios

The potential consequences of climate change for drylands have luckily gained increasing attention during the last decade (IPCC, 2019). In Central Asia, discussion about rangeland degradation are often reduced to herd sizes, livestock types or land-use change (Addison et al., 2012; Eckert, Hüsler, Liniger, & Hodel, 2015). Such a focus on management decisions ignores the importance of climate, and more importantly, the potential of the cumulative effects of the climate for degradation driven by uninformed management decisions. Recent research has shown that in Mongolia and adjacted areas, most effects of rangeland degradation within the last 30 years can be traced back to climatic reasons (Filei, Slesarenko, Boroditskaya, & Mishigdorj, 2018; Lehnert, Wesche, Trachte, Reudenbach, & Bendix, 2016). In general, the biggest effects of climate change on dryland ecosystems in Central Asia are expected from increasing temperatures, altered start and duration of growth periods, as well as altered precipitation regimes (Huang et al., 2017). Enhanced moisture availability can be also expected from increased mean annual precipitation in Central Asia (Huang et al., 2017). However, the increase in precipitation availability in Mongolia is likely to occur during the cold season, which would mostly benefit areas with soils with a high storage capacity (Sato, Kimura, & Kitoh, 2007), and more importantly lead more often to heavy snowfall during winter (Middleton & Sternberg 2013).
The most critical change for rangeland systems are expected from the increasing climatic variability in the future (Pendergrass, Knutti, Lehner, Deser, & Sanderson, 2017). High climatic variability will increase the "patchiness" of the resource availability in time and space (Wiens, 1984). It will increase the frequency of extreme events such as droughts and heavy snowfall, and it is likely to increase inter- and intra-annual differences in forage availability (Middleton, Rueff, Sternberg, Batbuyan, & Thomas, 2015). Increasing climatic variability is therefore probably the most important driver for livestock management in the future, thus mediating the effects of grazing on the vegetation in Mongolian rangelands.

Predicted consequences for plant communities in Mongolia

In summary, the literature suggests that the climate becomes warmer, moister and more variable in Mongolia. Warmer temperatures are predicted to lead to longer vegetation periods, which may in turn lead to shorter winters and an earlier start of the growth period for a variety of plant species. This may relax the environmental filter and increase the potential habitat area for many plant species, leading to an increase of plant species and functional diversity across the whole climate gradient (Fig. 1.6a). This effect may be intensified by increasing precipitation, but that is dependent on the question whether the increased precipitation will be available during the growth period, or predominantly occurs as snowfall during the winter as suggested by Sato et al. (2007). The same applies to an increase in biomass. In a recent modelling study which used the biomass data from this dissertation, Kowal & Ahlborn et al. (Kowal, Ahlborn, Jamsranjav, Avirmed, & Chaplin-Kramer, 2021) could show that the increasing temperatures and precipitation predicted for Mongolia might have positive impacts on biomass production, especially in today's rather unproductive regions. According to this study, biomass for forage production is expected to increase in the less productive regions even under scenarios with a doubling of livestock numbers. The authors suppose that this effect is mainly driven by an extended vegetation period, possibly interacting with a better moisture supply during spring and autumn. Although recent in-situ observations suggest that the changes in temperatures do not contribute to a prolonged growth period (Wang et al., 2019), while an increase in biomass production is still likely under the assumption that elevated atmospheric CO^2 concentrations contribute to an increase in biomass (Wang et al., 2021).

Chapter 3 has shown that an increase in biomass production is likely to be followed by an increase in stocking densities across Mongolia (Fig 1.6b). Mongolian herders adapt the size and composition of their herds, as well as their movement strategies to the available resources (see box below and Teickner et al. 2020). Increasing biomass production will therefore lead to increasing grazing intensity, and to higher grassing pressure for the vegetation. Based on the results of this dissertation, we can expect that the magnitude of the grazing effects will increase along the climate gradient (Fig 1.6c). Though effects of grazing will increase in the dry areas as well due to increased productivity, Kowal et al. (2021) models have shown that the additional resources in the dry areas are likely to meet the demands of the increasing livestock numbers, while the rangelands in the moister areas are likely to be overused. This is a function of the increasing effect size of grazing with increasing resource availability in Mongolia.

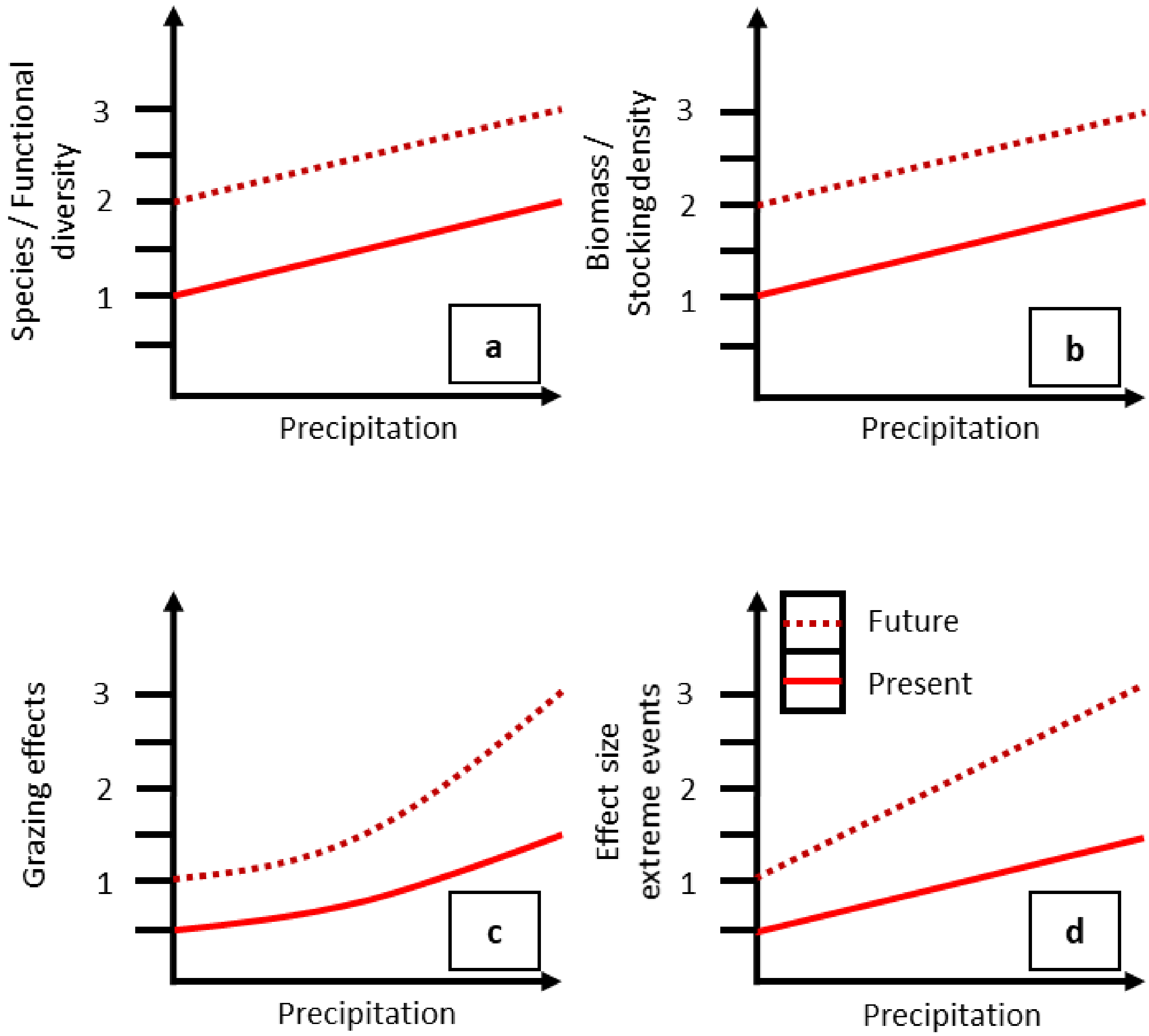


Figure 1.6: Predicted changes of plant diversity (a), biomass and stocking density (b), effects of grazing intensity (c) and of the effect size of extreme events (d) under future climate scenarios. Precipitation indicates the resource gradient, numbers are hypothetical. The solid line represents current functions, the dotted line the predicted functions in the future.

However, a leverage point for the health of Mongolian rangelands might be the increasing climatic variability. Current research has shown that ecosystems with higher diversity do not necessarily buffer extreme events better that less diverse ecosystems (De Boeck et al., 2018). Chapter 4 confirmed this hypothesis for Mongolia. In the dry steppes of the south, plant communities are adapted to extreme conditions. Assuming that these areas represent a NEQ system, extreme events are part of the rangeland dynamics and plants are adapted to them. Even with increasing productivity, increasing frequency of extreme events is likely to keep grazing effects relatively low, compared to the moister areas. Neither the management, nor the plants in the moister areas might have such a level of adaption to extreme events, as dynamics are there rather driven by biotic factors. Therefore, extreme events are likely to have an increasing effect size with increasing resource availability in the future (Fig 1.6d).

Future rangeland management need to incorporate the changing dynamics of Mongolia's rangelands. Although the moister rangelands in the north might produce more biomass in the future, higher climatic variability is challenging the balance between growing livestock numbers and the availability of forage. Similarly, the increasing biomass production in the south does not override the NEQ dynamics with frequent droughts and dzuds. Livestock managers in the future need to be more flexible in both terms of herd sizes and movement strategies. Of particular interest is probably the above mentioned transition zone between the supposed EQ and NEQ systems. Higher productivity in combination with higher climatic variability means that the border between the two systems might shift more often and over a larger spatial area (Fig 1.7). Under unchanged rangeland management, it is possible that the vegetation responds with the expansion of xerophytisation. The conservation of the biodiversity is therefore an indispensable task. Conserving biodiversity prevents xerophytisation and can ensure the provision of forage quality and quantity through the insurance effect (Yachi & Loreau, 1999).

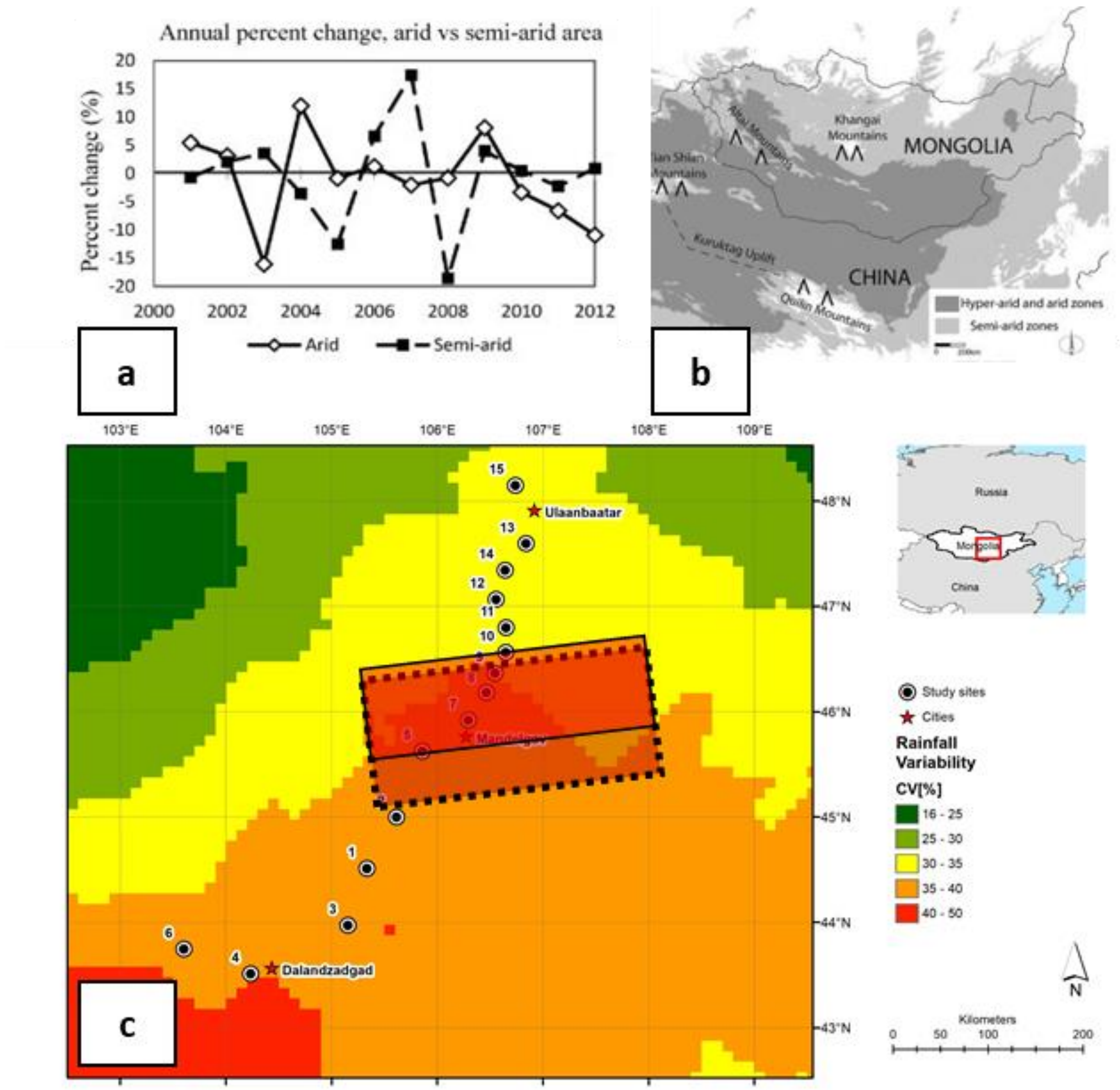


Figure 1.7: Illustration of the supposed transition zone between EQ and NEQ systems. a) shows the annual change of the extent of semi-arid and arid areas in Mongolia. b) shows the average distribution of semi-arid and arid areas. c) illustrates the predicted extent of the transition based on the coefficient of rainfall variance (CV, taken from von Wehrden et al., 2012) and the map in b). The solid line in c) illustrates the current extent of the transition zone, the dotted line a possible future extent. a) and b) are taken from Sternberg et al. 2015.

BOX

Moving with Continuity and Change – Understanding pastoral livelihoods in Mongolia from a sustainability perspective

Preface: Interviews were held with all herder families at the fifteen study sites. Initially, they aimed at basic information such as herd sizes or type of livestock. I adapted the questions myself in a rather non-professional approach in order to gain an understanding how Mongolian pastoralists think about their future. Carla Rutsch made the best out of this fragmentary dataset. The following text was taken from Carla Rutsch's Bachelor thesis, submitted 22.01.2018, Leuphana University Lüneburg. Compiled and slightly modified with the permission of the author.

While ancient grazing strategies generally have been assessed as sound practices grounding the persistence of both, the pastoral society and economy, and the natural environment, urbanisation tendencies and apparent evidence of rangeland degradation have currently given reason to question the present system's sustainability. Doubts arise: What characterises current pastoral livelihoods in Mongolia? Which patterns of continuity and change do they reveal? And how may herders' livelihoods with their continuities and changes be interpreted from a sustainability perspective? These three questions have formed the core of this research.

In order to explore the dispute on the relationship between pastoral livelihoods and sustainability and for gaining a deeper understanding of underlying socio-ecological relationships, during 2014 and 2015 informal standardised interviews were conducted with herding households on the 15 study sites along the climate gradient in Mongolia. Basing on a mixture of closed and open questions, the interviews aimed at getting insights into current pastoral livelihoods and local people's concerns, particularly with regard to sustainability. Complementing, the concepts of continuity and change revealed as central patterns present throughout the data. Inductive analytical methods were combined with interdisciplinary literature reviews: carried and structured by the descriptive concept of livelihoods, the analytical concepts of continuity and change, and the normative concept of sustainability.

Embraced by moving forces, transhumant pastoralism arose with its own patterns of movement. Responding and adapting to natural and social environments, pastoral households in Mongolia have been relating to constantly variable ecological exigencies on the one hand and shifting economic and political circumstances on the other; both apparently only conditionally influenceable by rural families.

Along with continuously diverse herds, and predominantly balanced amounts of livestock, migration showed to remain a key herding strategy among the interviewed families. Simultaneously, new livelihood plans did or might complement the pastoral subsistence and financial economy with additional sources of income, while the high-rated value of formal education suggested shifting future and herding perspectives for younger generations.

Herd management still seemed to be carried by communal, reciprocal norms and organisation, tightly grounding on natural conditions, and following its forces and dynamics. As these grazing strategies allow compensating for particularly climatically shaped resource heterogeneity, they have been assessed as central for both, pastoral livelihood stability and environmental integrity. However, partly large herds within more vulnerable equilibrium rangeland systems and predominantly short distances of seasonal migration, as observed at the study sites, might have been functional for households' short-term security but in the long run have to be evaluated as potentially problematic from both, an environmental and a social sustainability perspective. Equally ambivalent, livelihood diversification and formal education seemed to loosen herders' dependent relationship to their herds, what elsewhere has been linked to weakening societal agreements on the one hand, and to reduced household risks and widened coping capabilities on the other. Their significance for sustainability thus remains conflictive.

In summary, spatially and temporally, and reactively and proactively, pastoral livelihood systems appeared to be permeated by change – in turn entailing further (sometimes reversible) changes within the whole socio-ecological system. Still, and withstanding the seeming contradiction in terms, precisely these spatial and temporal livelihood changes can be read as carrying on with the central continuity of traditional pastoral strategies of the past millennia: Flexibly synchronising grazing movement and social mobility with their natural and social environment has shown to give viable pastoral livelihoods their remarkable resilience. That resilience, those delicate interplays of continuities and changes, cannot always be equated with sustainability – neither generally nor among the conducted case study. Yet, it has to be considered that local behavioral patterns don't stand alone but do always mirror deeper societal, political, and economic structures.

Challenges and future research

Every study comes with its own shortcomings, partly owing to the design, and partly owing to unforeseen circumstances during field and lab work or during the general process of the study. However, these challenges inaugurate possibilities for further research. In the following, I will shortly discuss each of these challenges and outline possible starting points for further studies.

The need for long-term studies

The complexity of a dataset is mainly limited by the effort invested in the time spent in the field and in the personnel doing the actual data collection (Marta, Lacasella, Romano, & Ficetola, 2019). Designing a study which allows for the investigation of interactions between grazing and climate in dry rangeland systems places high demands both on the necessary dataset and the study area. We tried to sample a dataset which would enable us to compare complex vegetation patterns along a long climate gradient and between two growth periods. Due to the high variability of the studied ecosystem, a main problem was the phenological condition of the vegetation during the actual sampling of the study sites. This problem became evident in chapter 4, where I tried to compare the biomass along the climate gradient and between the years. We were not able to sample the vegetation at the peak of their growth due to the necessary sampling intensity and the resulting length of the sampling campaign (Fig 1.8, Appendix S3 chapter 4). While modeling approaches can help to disentangle sampling biases in biomass production, for instance as shown by my analysis using satellite-based NDVI data, other important ecosystem properties such as species and functional diversity are more problematic, since they cannot be captured by satellite imaginary yet.

Long term studies can help to disentangle variation in ecological datasets (Magurran et al., 2010). A good example for Central Asia is the MAGIM project, which successfully studied the effects of grazing and their variability on several ecosystem properties over a period of 6 years (Hoffmann et al., 2016). Another successful approach was published by Bai and colleagues (Bai et al., 2004), who unraveled important ecosystem functions by studying a 24-year lasting dataset. However, these studies were restricted to a single location and doing this extensive work multiple times would result in exploding costs for data collection. Another promising and less expensive option is the resampling of sites (Khishigbayar et al., 2015). Besides the actual sampling, this approach requires the storage of data in data bases, as most journals today ask for this anyways. I therefore suggest to work on a comparable meta-dataset which includes basic information such as time of sampling, climate data, location and soil properties as well as data on vegetation such as species identity and abundance, and subsequently resample selected sites to get a better large-scale picture of the variability. First efforts in this direction have already been published (Bruelheide et al., 2019). This approach might enable us to quantify the role of inter- and intra-annual variability for interacting climate and land-use effects on plant-community related vegetation patterns.

Figure 1.8: Comparison of the same spot in 2014 (left) and 2015 (right). The right photo was taken only one week earlier in the year 2015 than in 2014.

Grazing gradients

Studying the effects of grazing on vegetation properties demands a robust proxy of grazing intensity. In rangeland ecosystems, the method of choice is sampling along transects (Manthey & Peper, 2010). In Central Asia, grazing intensity is overwhelmingly often studied along transects, which are rooted in so called grazing hotspots such as camps, wells or winter places (Wang & Wesche, 2016). The distances used in this thesis have shown to be adequate for capturing varying grazing intensity before (Stumpp et al., 2005), but one of the most common question either on conferences or from reviewers were, whether these distances do really reflect grazing intensity. While the method itself is quite established at least in Central Asia, we ran into two challenges regarding the study of grazing intensity. 1. We installed fences in early 2014 to have a proxy for vegetation growth in absence of grazing. However, almost all of these fences were destroyed by freely roaming livestock within the first 4 weeks. Therefore we didn't have a clear baseline for biomass and forage production under the absence of grazing. 2. While on the search for possible study sites in adequate distances to each other along the climate gradient, it was impossible to find entirely comparable grazing hotspots. As chapter 2 and 3 show, the selection of the type of grazing hotspot had a strong effect on the plant communities within the first 350 m. So called "sacrifice zones", for instance, are characterised by long-term trampling and nutrient intake rather than climatic constraints (Andrew & Lange, 1986; Moreno García et al., 2014; Wesuls, Oldeland, Dray, & Prinzing, 2012). To disentangle such azonal effects from zonal effects, a better investigation of plant community composition depending on the grazing hotspot is necessary. This thesis suggests that more or less frequent roaming of livestock in Mongolia does not inflict serious damage to rangelands (at least in dry areas), but land-use and climate change might alternate duration and frequency of herders visits, probably leading to local overgrazing. As Rutsch's work (2018, BOX) has shown, time and number of visits already strongly differ between herder families and more or less independently from the climatic condition of the site. A recent study using GPS trajectory data (Teickner et al., 2020) rendered Rutsch's findings as a representative sample in Mongolia. The authors identified three movement strategies, which were dependent on environmental and socioeconomic conditions, such as the productivity of the grasslands or the herd size. Therefore, future studies on the effects of grazing intensity on the vegetation should incorporate the duration and number of herder visits to gain a better understanding of grazing hotspots in Central Asia and to ensure a better comparability of the study sites.

Trait analyses

The extensive collection of plant functional trait data was a key characteristic of this project. The goal of this sampling was to create a dataset which could show how grazing intensity affects plant functional traits across the climate gradient. The sampling concentrated on traits that reflect a variety of different growth parameters and ecosystem processes, and that are suitable for detecting plant responses to climate and grazing (Bello, Lepš, & Sebastià, 2006; Díaz et al., 2007; Pakeman, 2004).

There were two problems with this dataset. First, intra-annual differences in intraspecific trait variability were remarkably high (Fig. 1.8). Lang et al. (2020) found that the responses of intra-specific trait variability to grazing and mean annual precipitation differed highly among the most abundant species of the study area. This is in line with the unclear results in chapter 3, where we used community weighted means to detect climate-grazing interactions in the observed plant communities. Community-weighted means can only yield clear results, when the whole community shows a clear response towards a variable.

As suggested by Ren et al. (2012), intra-specific rainfall variability may be a much more important factor for trait variability than inter-annual rainfall variability. But for the majority of the data collected for this dissertation, it was impossible to separate time effects (changes due to different sampling times within the growing season) from environmental effects. Lang et al's (2020) extensive work also suggests that it's likely that a bigger dataset wouldn't have yielded better results. Instead, sufficient sampling over time may reveal more effects of climate-grazing interactions in plant-community composition.

The second problem was the pre-selection of traits. Forage quality is an extremely important variable in agricultural studies (van Soest, 2018), but is often neglected by ecologist. While the selected traits included in this dissertation did cover a large variety of growth parameters and ecosystem processes without a doubt, it probably undervalued traits which address the forage value for animals. Including more detailed data such as acid detergent fiber (ADF) might be quite labor intensive, but has shown to be very helpful in the estimation of the forage value in time and space (Campos-Arceiz, Takatsuki, & Lhagvasuren, 2004; Jamsranjav et al., 2018; Lee, 2018; Olson, Murray, & Fuller, 2010). Future studies should definitely include more qualitative data on forage value. This could shed more light on livestock's forage preferences in time and space, and more importantly, help herders in their management decisions under climate change. A recent example for such an approach is the MoreStep-project (www.morestep.com).

Transferability

This dissertation points at the future threats for Mongolian rangelands, but the consequences of changing climate for rangelands are of ubiquitous, global significance. Predictions of global climate change from numerous studies show that all rangelands will be seriously affected (Huang et al., 2017; IPCC, 2019; Koutroulis, 2019). A major problem for the adaption of rangeland management systems to future conditions is the complexity of the expected changes. Some rangelands are expected to receive increasing amounts of precipitation, such as in Africa or in Central Asia (Huang et al., 2017), but this increase might not result in higher precipitation availability. Increasing temperatures will be often accompanied by increasing evapotranspiration. For Mongolia, Sato et al. (Sato et al., 2007) expected less precipitation variability for the vegetation period, ultimately leading to a decrease in available biomass. As a result, it's expected that the effects of land-use will be an even more serious driver of degradation than the effects of changing climate *per se* (Filei et al., 2018). The same accounts for large parts of Africa, where a general increase of precipitation is contradicted by decreasing precipitation during the vegetation period (Naidoo, Davis, & Van Garderen, 2013). For large parts of the North American rangelands, less changes in total precipitation are expected. Instead, rangeland scientist acknowledge the interactive effects of increasing precipitation variability and the manifold interactions between livestock production systems, soil carbon content, fire regimes, livestock metabolism and plant community composition (Polley et al., 2013).

Such complexity is also a reason why there are so many views and discussions about the effects of grazing in rangeland systems (Lund, 2007). Basically all concepts of rangeland dynamics are approaches to define similarities among the rangeland systems (Cingolani et al., 2005; Ellis & Swift, 1988; Milchunas et al., 1988), but they didn't help to find a consensus (Vetter, 2004). A reason might be that the concepts have not been tested within one dataset on a global basis. We know that there are unifying rules of the effects of grazing on the global rangelands, such as the coefficient of rainfall variability (von Wehrden et al., 2012). We also know, that such coarse climatic similarities can be used to predict grazing effects regardless of the livestock management systems (Engler & von Wehrden, 2018). Fernando Maestre and colleagues have impressively demonstrated that a dryland dataset with global extent can significantly increase our understanding of the underlying ecosystem functions (Gross et al., 2017; Le Bagousse-Pinguet et al., 2019; Le Bagousse-Pinguet et al., 2017; Maestre et al., 2012). A similar dataset which addresses the impacts of grazing along gradients of precipitation variability could equally help to understand the underlying ecosystem functions in rangelands. Based on the results of this dissertation, the locations of the study sites should be selected by their coefficient of rainfall variability. For instance, von Wehrden et al. (2012) give a good overview of potential study areas. The climate gradient of each study site should cover areas of mid-term dryland expansions and contractions (Sternberg et al., 2015), in order to collect better information on the transition zones between dry, variable and moist, more stable areas. Grazing gradients should be standardised (length, distances, or measures of soil compaction) or backed by detailed data on livestock densities via questionnaires, data of the local administrations or gps-tracking devices. Studying plant community diversity, biomass production and the forage value of the plants in such a framework could help to make major advances in our understanding of the future of rangeland management systems.

Conclusions

The fate of Mongolia’s rangeland systems clearly lies in the hand of the rangeland managers. The sustainable use of Mongolia’s vast steppe ecosystems might be dependent on a flexible livestock management system which balances the grazing intensity with the available resources, while considering climatic variability as a key for the management decisions. Increasing productivity in the future is likely to increase livestock numbers, but this dissertation suggests that the increase in forage availability correlates with increasing risk of degradation of the steppe ecosystems. While the vegetation of the dry, unproductive rangelands with high climatic variability seem to be resilient and capable to withstand higher grazing intensity through the non-equilibrium dynamics, moister rangelands are threatened by the predicted increase in livestock numbers. Rangeland vegetation that is characterised by a strong link between the availability of forage and the stocking density run the risk of overgrazing, and therefore the loss of species which contribute to the provisioning of forage in time and space. The analysis of the transition zone between equilibrium and non-equilibrium can serve as a warning for the future. Where grazing intensity and the availability of forage are unbalanced, vegetation might shift towards a less diverse and less valuable rangeland.

Chapter 2. Climate – grazing interactions in Mongolian rangelands: Effects of grazing change along a large-scale environmental gradient.

Julian Ahlborn[a,b,c,*], Henrik von Wehrden[b], Birgit Lang[d], Christine Römermann[d,e], Munkhzul Oyunbileg[g], Batlai Oyuntsetseg[h], Karsten Wesche[c,e,f]

[a] Leibniz-Centre for Agricultural Landscape Research, Sustainable Grassland Systems, Gutshof 7, D-14641, Paulinenaue, Germany

[b] Leuphana University Lueneburg, Institute of Ecology, Faculty of Sustainability, Scharnhorststr. 1, D-21335, Lueneburg, Germany

[c] Senckenberg Museum of Natural History, Goerlitz, PO Box 300 154, D-02806, Goerlitz, Germany

[d] Friedrich Schiller University, Institute of Ecology and Evolution, Philosophenweg 16, D-07743, Jena, Germany

[e] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Germany

[f] International Institute Zittau, Technische Universität Dresden, Markt 23, 02763, D-Zittau, Germany

[g] Mongolian Academy of Science, Institute of General and Experimental Biology, 3600, Ulaanbaatar, Mongolia

[h] National University of Mongolia, Botany Department, School of Biology and Biotechnology, 14200, Ulaanbaatar, Mongolia

Published in

Journal of Arid Environments, 173 (2020), 104043

https://doi.org/10.1016/j.jaridenv.2019.104043

Abstract

There are still major gaps in our understanding of rangeland degradation. Assessing the interactions between climate and grazing effects could help to explain what unifies and separates rangelands, and may therefore promote a more sustainable management of livestock. We studied 15 local land-use transects along a 600 km long climatic gradient in Central Asia to test the hypothesis that grazing effects differ between relatively moist equilibrium (EQ) and dry non-equilibrium (NEQ) rangeland systems. We analysed plant community composition, species diversity and indicator species for different grazing intensities. We found pronounced differences in community composition along our climate gradient, revealed climate-related grazing effects on richness, responses of Simpson's diversity, and also found different grazing indicator species along the larger transect. We conclude that in NEQ rangelands, grazing effects are limited to sacrifice zones and environmental filtering dominates vegetation composition. With increasing precipitation, resource availability gains in importance leading to more complex communities dominated by grazing-tolerant species under EQ dynamics. Hints for xerophytization in the transition zone between EQ and NEQ highlight the vulnerability of rangelands that temporally shift from one state to the other. This calls for extra care in the management of livestock numbers in these transition areas.

Chapter 3. Plant Functional Diversity in Equilibrium and Non-Equilibrium Systems: A case study from Mongolian rangelands.

Julian Ahlborn[1,2]*, Birgit Lang[3], Henrik von Wehrden[1], Karsten Wesche[2,4,5], Munkhzul Oyunbileg[6], Oyuntsetseg Batlai[7], Neil Collier and Christine Römermann[3,4]

[1] Leuphana University Lueneburg, Faculty of Sustainability, Scharnhorststr. 1, D-21335 Lueneburg, Germany;

[2] Senckenberg Museum of Natural History, Goerlitz, PO Box 300 154, D-02806 Goerlitz, Germany;

[3] Friedrich Schiller University, Institute of Ecology and Evolution, Philosophenweg 16, D-07743 Jena, Germany;

[4] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Germany;

[5] International Institute Zittau, Technische Universität Dresden, Markt 23, 02763 D-Zittau, Germany;

[6] Mongolian Academy of Science, Institute of General and Experimental Biology, 3600, Ulaanbaatar, Mongolia

[7] National University of Mongolia, School of Arts and Science, Department of Biology, 14200 Ulaanbaatar, Mongolia.

Submitted to

Journal of Applied Vegetation Science in 2018,

rejected with an invitation for resubmission after revision

Abstract

Questions: Do grazing effects on functional diversity differ between non-equilibrium (NEQ) and equilibrium (EQ) rangelands? Is the fluctuating resource availability in NEQ reflected by strong environmental filtering, and does grazing reflect niche complementarity under EQ conditions?

Location: 600 km precipitation gradient in Mongolia, Central Asia

Methods: 300 plots were established on 12 grazing gradients in two desert and steppe biomes of Central Asia. Plant species abundances and environmental data were recorded for every plot, and 12 plant functional traits were collected for 117 most abundant species. Trait sets for each biome were selected via iterative RLQs and trait-environment relationships were tested by a combination of RLQ and 4th corner analysis. Grazing responses of community-weighted means and measures of functional diversity (richness, evenness, dispersion) under EQ and NEQ conditions were tested by generalized linear mixed effect models.

Results: Three traits (growth form, canopy height, leaf potassium content) in the desert and four traits (growth form, canopy height, leaf phosphorous content, life form) in the grassland biome reflected two main axes which corresponded with grazing and precipitation. The conditions around camps and wells filtered very specific trait combinations in both biomes. Functional structure differed between sites under NEQ and within sites under EQ dynamics. Functional richness was higher under EQ conditions and higher under moderate grazing than under intensive or extensive grazing. Functional divergence was higher under EQ dynamics. Livestock had impacts on most traits under both NEQ and EQ conditions.

Conclusions: Trait convergence within sites and trait divergence between sites supports theory that abiotic environmental filtering plays a major role for community assembly under NEQ dynamics. Niche complementarity is higher under EQ conditions, where resource availability is higher and more stable. Grazing affects functional diversity under both NEQ and EQ, but the effect of sacrifice zones might distort grazing effects in our study. This study underlines the importance of adaptions of current rangeland management to local climatic conditions.

Chapter 4. Interactions between species richness, herbivory and precipitation affect standing biomass in Mongolian rangelands.

[1,2,3]*Julian Ahlborn, [3,4,5] Karsten Wesche, [6] Birgit Lang, [7] Munkhzul Oyunbileg, [8] Batlai Oyuntsetseg, [5,6] Christine Römermann, [9]Neil French Collier [2] Henrik von Wehrden

[1] Leibniz Centre for Agricultural Landscape Research, WG Sustainable Grassland Systems, Gutshof 7, D-14641 Paulinenaue, Germany;

[2] Leuphana University Lueneburg, Institute of Ecology, Faculty of Sustainability, Universitaetsallee 1, D-21335 Lueneburg, Germany;

[3] Senckenberg Museum of Natural History, Goerlitz, PO Box 300 154, D-02806 Goerlitz, Germany;

[4] International Institute Zittau, Technische Universität Dresden, Markt 23, D-02763 Zittau, Germany;

[5] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Germany;

[6] Friedrich Schiller University, Institute of Ecology and Evolution, Philosophenweg 16, D-07743 Jena, Germany;

[7] Mongolian Academy of Science, Institute of General and Experimental Biology, Ulaanbaatar 3600, Mongolia

[8] Department of Biology, School of Arts and Sciences, National University of Mongolia, Ulaanbaatar 14201, Mongolia

[9] Institute for Health & Sport (IHeS), Victoria University, Melbourne, Australia

*corresponding author: julian.ahlborn@zalf.de, orcid ID 0000-0002-4406-9654

Published in

Applied Vegetation Science, Vol 24, Issue 2 (2021)

https://doi.org/10.1111/avsc.12581

Abstract

Questions: Livestock management in rangelands depends on the production of plant biomass. Biomass production is driven by the temporal and spatial variability in precipitation, but our understanding of how precipitation variability mediates grazing effects on biomass production is still fragmented. Along a 600 km precipitation gradient we extracted biomass data to ask the questions: 1) What are the effects of grazing intensity on biomass production? 2) Does grazing intensity interact with plant species richness to affect biomass production? 3) How do plant functional groups respond to grazing and precipitation?

Location: Mongolia

Methods: Biomass was sampled along 15 grazing intensity transects within the precipitation gradient over two consecutive years. We modelled spatial variability in aboveground plant biomass using mixed-effects models. NDVI data was combined with field-sampled biomass data to correct for inter-annual precipitation variation. The effects of species richness were modelled with respect to possible interactions with grazing intensity, and the composition of plant functional groups was modelled with respect to possible interactions between grazing intensity and precipitation.

Results: Biomass was negatively correlated with grazing intensity and this effect increased as precipitation increased. Biomass was positively correlated with species richness in both years, but the strength of this effect and the interaction between species richness and grazing intensity differed between 2014 and 2015 in line with highly variable precipitation between both years. The plant functional groups grasses, sedges, legumes, wormwood and forbs had contrasting responses to grazing and precipitation.

Conclusion: Biomass production in drylands is more vulnerable to changes in precipitation variability and grazing intensities in relatively moist and productive rangelands than in dry and unproductive ones. Future rangeland management needs to address potentially increasing precipitation variability in order to promote desired forage plants, and to preserve the positive effects of biodiversity for biomass production.

Keywords

grasslands, plant functional groups, species richness, drylands, NDVI, livestock, precipitation gradient.

Data accessibility statement

Data openly available via the public data repository PANGAEA,

DOI: https://doi.pangaea.de/10.1594/PANGAEA.932936

Literature

Addison, J., Friedel, M., Brown, C., Davies, J., & Waldron, S. (2012). A critical review of degradation assumptions applied to Mongolia's Gobi Desert. *The Rangeland Journal, 34*(2), 125. doi:10.1071/RJ11013

Adler, P. B., & Levine, J. M. (2007). Contrasting relationships between precipitation and species richness in space and time. *Oikos, 116*(2), 221–232. doi:10.1111/j.0030-1299.2007.15327.x

Adler, P. B., Seabloom, E. W., Borer, E. T., Hillebrand, H., Hautier, Y., Hector, A., . . . Yang, L. H. (2011). Productivity is a poor predictor of plant species richness. *Science (New York, N.Y.), 333*(6050), 1750–1753. doi:10.1126/science.1204498

Ahlborn, J., von Wehrden, H., Lang, B., Oyunbileg, M., Oyuntsetseg, B., Römermann, C., & Wesche, K. (2020). Climate – grazing interactions in Mongolian rangelands: Effects of grazing change along a large-scale environmental gradient. *Journal of Arid Environments*. 173, 104043. doi: 10.1016/j.jaridenv.2019.104043

Andrew, M. H., & Lange, R. T. (1986). Development of a new piosphere in arid chenopod shrubland grazed by sheep. 2. Changes to the vegetation. *Australian Journal of Ecology, 11*(4), 411–424. doi:10.1111/j.1442-9993.1986.tb01410.x

Baastrup-Spohr, L., Sand-Jensen, K., Nicolajsen, S. V., & Bruun, H. H. (2015). From soaking wet to bone dry: predicting plant community composition along a steep hydrological gradient. *Journal of Vegetation Science, 26*(4), 619-630. doi:https://doi.org/10.1111/jvs.12280

Bai, Y., Han, X., Wu, J., Chen, Z., & Li, L. (2004). Ecosystem stability and compensatory effects in the Inner Mongolia grassland. *Nature, 431*(7005), 181. doi:10.1038/nature02850

Bai, Y., Wu, J., Pan, Q., Huang, J., Wang, Q., LI, F., . . . Han, X. (2007). Positive linear relationship between productivity and diversity: evidence from the Eurasian Steppe. *Journal of Applied Ecology, 44*(5), 1023–1034. doi:10.1111/j.1365-2664.2007.01351.x

Baillie, J. E. M., & Upham, K. (2012). Species diversity within and among ecosystems. In R. A. Meyers (Ed.), *Encyclopedia of Sustainability Science and Technology* (pp. 10085-10095). New York, NY: Springer New York.

Bar-On, Y. M., Phillips, R., & Milo, R. (2018). The biomass distribution on Earth. *Proceedings of the National Academy of Sciences, 115*(25), 6506. doi:10.1073/pnas.1711842115

Bartoń, K. (2015). MuMIn: Multi-model inference: R package (Version 1.15.6).

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects models using lme4: R package.

Batjargal, Z. *Desertification in Mongolia: RALA Report No. 200.* Retrieved from Mongolia:

Batsaikhan, N., Buuveibaatar, B., Chimed, B., Enkhtuya, O., Galbrakh, D., Ganbaatar, O., . . . Whitten, T. (2014). Conserving the world's finest grassland amidst ambitious national development. *Conservation Biology, 28*(6), 1736-1739. doi:10.1111/cobi.12297

Bazha, S. N., Gunin, P. D., Danzhalova, E. V., Drobyshev, Y. I., & Prishcepa, A. V. (2012). Pastoral degradation of steppe ecosystems in Central Mongolia. In M. J. A. Werger & M. A. van Staalduinen (Eds.), *Eurasian Steppes. Ecological Problems and Livelihoods in a Changing World* (Vol. 6, pp. 289–319). Dordrecht: Springer Netherlands.

Bello, F., Lepš, J., & Sebastià, M.-T. (2006). Variations in species and functional plant diversity along climatic and grazing gradients. *Ecography, 29*(6), 801–810. doi:10.1111/j.2006.0906-7590.04683.x

Berdugo, M., Maestre, F. T., Kéfi, S., Gross, N., Le Bagousse-Pinguet, Y., & Soliveres, S. (2019). Aridity preferences alter the relative importance of abiotic and biotic drivers on plant species abundance in global drylands. *Journal of Ecology, 107*(1), 190-202. doi:10.1111/1365-2745.13006

Berger, J., Buuveibaatar, B., & Mishra, C. (2015). The cashmere connection, biodiversity, and climate: response to von Wehrden et al. 2014. *Conservation biology : the journal of the Society for Conservation Biology, 29*(1), 290–292. doi:10.1111/cobi.12415

Bernard-Verdier, M., Navas, M. L., Vellend, M., Violle, C., Fayolle, A., & Garnier, E. (2012). Community assembly along a soil depth gradient: Contrasting patterns of plant trait convergence and divergence in a Mediterranean rangeland. *Journal of Ecology, 100*(6), 1422–1433. doi:10.1111/1365-2745.12003

Bernhardt-Römermann, M., Römermann, C., Nuske, R., Parth, A., Klotz, S., Schmidt, W., & Stadler, J. (2008). On the identification of the most suitable traits for plant functional trait analyses. *Oikos, 117*(10), 1533–1541. doi:10.1111/j.0030-1299.2008.16776.x

Bernhardt-Römermann, M., Römermann, C., Sperlich, S., & Schmidt, W. (2011). Explaining grassland biomass - the contribution of climate, species and functional diversity depends on fertilization and mowing frequency. *Journal of Applied Ecology, 48*(5), 1088–1097. doi:10.1111/j.1365-2664.2011.01968.x

Bestelmeyer, B. T., Ash, A., Brown, J. R., Densambuu, B., Fernández-Giménez, M., Johanson, J., . . . Shaver, P. (2017). State and transition models: Theory, applications, and challenges. In D. D. Briske (Ed.), *Rangeland Systems: Processes, Management and Challenges* (pp. 303-345). Cham: Springer International Publishing.

Bestelmeyer, B. T., Okin, G. S., Duniway, M. C., Archer, S. R., Sayre, N. F., Williamson, J. C., & Herrick, J. E. (2015). Desertification, land use, and the transformation of global drylands. *Frontiers in Ecology and the Environment, 13*(1), 28–36. doi:10.1890/140162

Blench, R. (2001). *Pastoralism in the new millenium*. Rome: FAO.

Bolker, B., & Team, R. D. C. (2016). bbmle: Tools for general maximum likelihood estimation (Version 1.0.18). Retrieved from https://CRAN.R-project.org/package=bbmle

Box, E. O. (1996). Plant functional types and climate at the global scale. *Journal of Vegetation Science, 7*(3), 309–320.

Briske, D. D. (2017). Rangeland systems: Foundation for a conceptual framework. In D. D. Briske (Ed.), *Rangeland Systems: Processes, Management and Challenges* (pp. 1-21). Cham: Springer International Publishing.

Briske, D. D. (Ed.) (2017). *Rangeland systems: Processes, management and challenges*. Cham, Switzerland: Springer Open.

Briske, D. D., Fuhlendorf, S. D., & Smeins, F. E. (2005). State-and-transition models, thresholds, and rangeland health: A Synthesis of Ecological Concepts and Perspectives. *Rangeland Ecology & Management, 58*(1), 1–10. doi:10.2111/1551-5028(2005)58<1:SMTARH>2.0.CO;2

Brooker, R. W., Maestre, F. T., Callaway, R. M., Lortie, C. J., Cavieres, L. A. K., Georges, Liancourt, P., . . . Michalet, R. (2008). Facilitation in plant communities: The past, the present, and the future. *Journal of Ecology*(96), 18–34. doi:10.1111/j.1365-2745.2007.01295.x

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., . . . Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal, 9*(2), 378–400.

Bruelheide, H., Dengler, J., Jiménez-Alfaro, B., Purschke, O., Hennekens, S. M., Chytrý, M., . . . Zverev, A. (2019). sPlot – A new tool for global vegetation analyses. *Journal of Vegetation Science, 30*(2), 161-186. doi:10.1111/jvs.12710

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed.). New York: Springer.

Caceres, M., & Legendre, P. (2009). Associations between species and groups of sites: Indices and statistical inference. *Ecology, 90*(12), 3566–3574.

Cáceres, M., Legendre, P., & Moretti, M. (2010). Improving indicator species analysis by combining groups of sites. *Oikos, 119*(10), 1674–1684. doi:10.1111/j.1600-0706.2010.18334.x

Cadotte, M. W., Carscadden, K., & Mirotchnick, N. (2011). Beyond species: Functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology, 48*(5), 1079–1087. doi:10.1111/j.1365-2664.2011.02048.x

Cadotte, M. W., & Tucker, C. M. (2017). Should environmental filtering be abandoned? *Trends in Ecology & Evolution, 32*(6), 429–437. doi:10.1016/j.tree.2017.03.004

Campos-Arceiz, A., Takatsuki, S., & Lhagvasuren, B. (2004). Food overlap between Mongolian gazelles and livestock in Omnogobi, southern Mongolia. *Ecological Research, 19*(4), 455–460. doi:10.1111/j.1440-1703.2004.00658.x

Cardinale, B. J., Palmer, M. A., & Collins, S. L. (2002). Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature, 415*(6870), 426-429.

Cardinale, B. J., Wright, J. P., Cadotte, M. W., Carroll, I. T., Hector, A., Srivastava, D. S., . . . Weis, J. J. (2007). Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences, 104*(46), 18123-18128. doi:10.1073/pnas.0709069104

Carmona, C. P., Mason, N. W. H., Azcárate, F. M., Peco, B., & Bartha, S. (2015). Inter-annual fluctuations in rainfall shift the functional structure of Mediterranean grasslands across gradients of productivity and disturbance. *Journal of Vegetation Science, 26*(3), 538–551. doi:10.1111/jvs.12260

Cheng, J., Chu, P., Chen, D., Bai, Y., & Niu, S. (2016). Functional correlations between specific leaf area and specific root length along a regional environmental gradient in Inner Mongolia grasslands. *Functional Ecology, 30*(6), 985–997. doi:10.1111/1365-2435.12569

Cingolani, A. M., Noy-Meir, I., & Díaz, S. (2005). Grazing effects on rangeland diversity: a synthesis of contemporary models. *Ecological Applications, 15*(2), 757–773.

Cleland, E. E., Collins, S. L., Dickson, T. L., Farrer, E. C., Gross, K. L., Gherardi, L. A., . . . Suding, K. N. (2013). Sensitivity of grassland plant community composition to spatial vs. temporal variation in precipitation. *Ecology, 94*(8), 1687-1696. doi:https://doi.org/10.1890/12-1006.1

Connell, J. H., & Orias, E. (1964). The ecological regulation of species diversity. *The American Naturalist, 98*(903), 399-

414. doi:10.1086/282335

Cornwell, W. K., & Ackerly, D. D. (2009). Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs, 79*(1), 109–126.

Dashkhuu, D., Kim, J. P., Chun, J. A., & Lee, W.-S. (2015). Long-term trends in daily temperature extremes over Mongolia. *Weather and Climate Extremes, 8*, 26-33. doi:https://doi.org/10.1016/j.wace.2014.11.003

De Boeck, H. J., Bloor, J. M. G., Kreyling, J., Ransijn, J. C. G., Nijs, I., Jentsch, A., & Zeiter, M. (2018). Patterns and drivers of biodiversity–stability relationships under climate extremes. *Journal of Ecology, 106*(3), 890–902. doi:10.1111/1365-2745.12897

DeAngelis, D. L., & Waterhouse, J. C. (1987). Equilibrium and nonequilibrium concepts in ecological models. *Ecological Monographs, 57*(1), 1–21. doi:10.2307/1942636

Díaz, S., & Cabido, M. (2001). Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution, 16*(11), 646–655. doi:10.1016/S0169-5347(01)02283-2

Díaz, S., Lavorel, S., McIntyre, S., Falczuk, V., Casanoves, F., Milchunas, D. G., . . . Campell, B. D. (2007). Plant trait responses to grazing - a global synthesis. *Global Change Biology, 13*(2), 313–341. doi:10.1111/j.1365-2486.2006.01288.x

Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N. D., Wikramanayake, E., . . . Saleem, M. (2017). An ecoregion-based approach to protecting half the terrestrial realm. *BioScience, 67*(6), 534–545. doi:10.1093/biosci/bix014

Dingaan, M. N. V., Walker, S., Tsubo, M., & Newby, T. (2016). Influence of grazing on plant diversity-productivity relationship in semi-arid grassland of South Africa. *Applied Ecology and Environmental Research, 14*(4), 1–13. doi:10.15666/aeer/1404_001013

Dolédec, S., Chessel, D., ter Braak, C. J. F., & Champely, S. (1996). Matching species traits to environmental variables: A new three-table ordination method. *Environmental and Ecological Statistics, 3*(2), 143–166. doi:10.1007/BF02427859

Dorji, T., Totland, Ø., & Moe, S. R. (2013). Are droppings, distance from pastoralist camps, and pika burrows good proxies for local grazing pressure? *Rangeland Ecology & Management, 66*(1), 26–33. doi:10.2111/REM-D-12-00014.1

Dray, S., Choler, P., Dolédec, S., Peres-Neto, P. R., Thuiller, W., Pavoine, S., & ter Braak, C. J. F. (2014). Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. *Ecology, 95*(1), 14–21. doi:10.1890/13-0196.1

Dray, S., & Legendre, P. (2008). Testing the species traits–environment relationships: The fourth-corner problem revisited. *Ecology, 89*(12), 3400–3412. doi:10.1890/08-0349.1

Dufrene, M., & Legendre, P. (1997). Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs, 67*(3), 345. doi:10.2307/2963459

Dulamsuren, C., & Hauck, M. (2008). Spatial and seasonal variation of climate on steppe slopes of the northern Mongolian mountain taiga. *Grassland science, 54*(4), 217-230.

Durán, J., Delgado-Baquerizo, M., Dougill, A. J., Guuroh, R. T., Linstädter, A., Thomas, A. D., & Maestre, F. T. (2018). Temperature and aridity regulate spatial variability of soil multifunctionality in drylands across the globe. *Ecology, 99*(5), 1184–1193. doi:10.1002/ecy.2199

Dwyer, J. M., & Laughlin, D. C. (2017). Constraints on trait combinations explain climatic drivers of biodiversity: The importance of trait covariance in community assembly. *Ecology letters, 20*(7), 872–882. doi:10.1111/ele.12781

Easdale, M. H., & Bruzzone, O. (2015). Anchored in 'average thinking' in studies of arid rangeland dynamics – The need for a step forward from traditional measures of variability. *Journal of Arid Environments, 116*, 77–81. doi:10.1016/j.jaridenv.2015.02.006

Eckert, S., Hüsler, F., Liniger, H., & Hodel, E. (2015). Trend analysis of MODIS NDVI time series for detecting land degradation and regeneration in Mongolia. *Journal of Arid Environments, 113*, 16–28. doi:10.1016/j.jaridenv.2014.09.001

efloras. (2008). Flora of China. Retrieved from http://www.efloras.org

Ellis, J. E., Coughenour, M. B., & Swift, D. M. (1991). Climate variability, ecosystem stability, and the implications for range and livestock development.: New Concepts. In R. P. Cincotta, C. W. Gay, & G. K. Perrier (Eds.), *New Conceps In International Rangeland Development*. Logan, UT: The Department of Range Science, College of Natural Ressources, Utah State University.

Ellis, J. E., & Swift, D. M. (1988). Stability of African pastoral ecosystems: Alternate paradigms and implications for development. *Journal of Range Management Archives, 41*(6), 450–459.

Engler, J.-O., & von Wehrden, H. (2018). Global assessment of the non-equilibrium theory of rangelands: Revisited and refined. *Land Use Policy, 70*, 479–484. doi:10.1016/j.landusepol.2017.11.026

Fang, J., Piao, S., Tang, Z., Peng, C., & Ji, W. (2001). Interannual variability in net primary production and precipitation. *Science (New York, N.Y.), 293*(5536), 1723. doi:10.1126/science.293.5536.1723a

FAO. (2008). *Water and cereals in drylands*. London: Earthscan.

Fernández-Giménez, M. E. (2006). Land use and land tenure in Mongolia: A brief history and current issues. In D. J. Bedunah, D. E. McArthur, & M. Fernandez-Gimenez (Eds.), *Rangelands of Central Asia: Proceedings of the Conference on Transformations, Issues, and Future Challenges*. Fort Collins, CO.

Fernández-Giménez, M. E., & Allen-Diaz, B. (1999). Testing a non-equilibrium model of rangeland vegetation dynamics in Mongolia. *Journal of Applied Ecology, 36*(6), 871–885. doi:10.1046/j.1365-2664.1999.00447.x

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International journal of climatology, 37*(12), 4302-4315.

Filei, A., Slesarenko, L., Boroditskaya, A., & Mishigdorj, O. (2018). Analysis of desertification in Mongolia. *Russian Meteorology and Hydrology, 43*(9), 599-606.

Fox, J. W. (2013). The intermediate disturbance hypothesis should be abandoned. *Trends in Ecology & Evolution, 28*(2), 86–92. doi:10.1016/j.tree.2012.08.014

García-Palacios, P., Gross, N., Gaitán, J., & Maestre, F. T. (2018). Climate mediates the biodiversity-ecosystem stability relationship globally. *Proceedings of the National Academy of Sciences of the United States of America, 115*(33), 8400–8405. doi:10.1073/pnas.1800425115

Garnier, E., Navas, M.-L., & Grigulis, K. (2016). *Plant functional diversity: Organism traits, community structure, and ecosystem properties.* (First edition ed.). Oxford, United Kingdom: Oxford University Press.

Ghahramani, A., Howden, S. M., del Prado, A., Thomas, D. T., Moore, A. D., Ji, B., & Ates, S. (2019). Climate change impact, adaptation, and mitigation in temperate grazing systems: A Review. *Sustainability, 11*(24), 7224.

Gherardi, L. A., & Sala, O. E. (2015). Enhanced precipitation variability decreases grass-and increases shrub-productivity. *Proceedings of the National Academy of Sciences, 112*(41), 12735-12740.

Godde, C. M., Boone, R. B., Ash, A. J., Waha, K., Sloat, L. L., Thornton, P. K., & Herrero, M. (2020). Global rangeland production systems and livelihoods at threat under climate change and variability. *Environmental Research Letters, 15*(4), 044021. doi:10.1088/1748-9326/ab7395

Götzenberger, L., Bello, F., Bråthen, K. A., Davison, J., Dubuis, A., Guisan, A., . . . Zobel, M. (2011). Ecological assembly rules in plant communities—approaches, patterns and prospects. *Biological Reviews, 87*(1), 111–127. doi:10.1111/j.1469-185X.2011.00187.x

Grime, J. P. (1974). Vegetation classification by reference to strategies. *Nature, 250*(5461), 26–31. doi:10.1038/250026a0

Grime, J. P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist, 111*(982), 1169–1194. doi:10.1086/283244

Grime, J. P. (1998). Benefits of plant diversity to ecosystems: Immediate, filter and founder effects. *Journal of Ecology, 86*(6), 902–910. doi:10.1046/j.1365-2745.1998.00306.x

Gross, K., Cardinale, B. J., Fox, J. W., Gonzalez, A., Loreau, M., Polley, H. W., . . . van Ruijven, J. (2014). Species richness and the temporal stability of biomass production: a new analysis of recent biodiversity experiments. *The American Naturalist, 183*(1), 1–12. doi:10.1086/673915

Gross, N., Le Bagousse-Pinguet, Y., Liancourt, P., Berdugo, M., Gotelli, N. J., & Maestre, F. T. (2017). Functional trait diversity maximizes ecosystem multifunctionality. *Nature ecology & evolution, 1*(5), 1-9.

Grubov, V. I. (2001). *Key to the vascular plants of Mongolia*. Enfield, NH: Science Publishers.

Guo, T., Lohmann, D., Ratzmann, G., & Tietjen, B. (2016). Response of semi-arid savanna vegetation composition towards grazing along a precipitation gradient—The effect of including plant heterogeneity into an ecohydrological savanna model. *Ecological Modelling, 325*, 47-56. doi:https://doi.org/10.1016/j.ecolmodel.2016.01.004

Harris, R. B. (2010). Rangeland degradation on the Qinghai-Tibetan plateau: A review of the evidence of its magnitude and causes. *Journal of Arid Environments, 74*(1), 1–12. doi:10.1016/j.jaridenv.2009.06.014

Hautier, Y., Seabloom, E. W., Borer, E. T., Adler, P. B., Harpole, W. S., Hillebrand, H., . . . Hector, A. (2014). Eutrophication weakens stabilizing effects of diversity in natural grasslands. *Nature, 508*(7497), 521–525. doi:10.1038/nature13014

Havlík, P., Valin, H., Herrero, M., Obersteiner, M., Schmid, E., Rufino, M. C., . . . Notenbaert, A. (2014). Climate change mitigation through livestock system transitions. *Proceedings of the National Academy of Sciences, 111*(10), 3709. doi:10.1073/pnas.1308044111

Hector, A., Hautier, Y., Saner, P., Wacker, L., Bagchi, R., Joshi, J., . . . Loreau, M. (2010). General stabilizing effects of plant diversity on grassland productivity through population asynchrony and overyielding. *Ecology, 91*(8), 2213–2220. doi:10.1890/09-1162.1

Hejcman, M., Češková, M., Schellberg, J., & Pätzold, S. (2010). The Rengen Grassland Experiment: Effect of soil chemical properties on biomass production, plant species composition and species richness. *Folia Geobotanica, 45*(2), 125–142. doi:10.1007/s12224-010-9062-9

Herrero, M., Havlík, P., Valin, H., Notenbaert, A., Rufino, M. C., Thornton, P. K., . . . Obersteiner, M. (2013). Biomass use, production, feed efficiencies, and greenhouse gas emissions from global livestock systems. *Proceedings of the National Academy of Sciences, 110*(52), 20888-20893.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International journal of climatology, 25*(15), 1965–1978. doi:10.1002/joc.1276

Hilbig, W. (1995). *The vegetation of Mongolia*. Amsterdam: SPB Academic Pub.

Hill, M. O., & Gauch, H. G. (1980). Detrended correspondence analysis: An improved ordination technique. *Vegetatio, 42*(1), 47–58. doi:10.1007/BF00048870

Hoffmann, C., Giese, M., Dickhoefer, U., Wan, H., Bai, Y., Steffens, M., . . . Han, X. (2016). Effects of grazing and climate variability on grassland ecosystem functions in Inner Mongolia: synthesis of a 6-year grazing experiment. *Journal of Arid Environments, 135*, 50-63.

Huang, D., Wang, K., & Wu, W. L. (2007). Dynamics of soil physical and chemical properties and vegetation succession characteristics during grassland desertification under sheep grazing in an agro-pastoral transition zone in Northern China. *Journal of Arid Environments, 70*(1), 120–136. doi:10.1016/j.jaridenv.2006.12.009

Huang, J., Li, Y., Fu, C., Chen, F., Fu, Q., Dai, A., . . . Wang, G. (2017). Dryland climate change: Recent progress and challenges. *Reviews of Geophysics, 55*(3), 719–778. doi:10.1002/2016RG000550

Huang, J., Yu, H., Guan, X., Wang, G., & Guo, R. (2015). Accelerated dryland expansion under climate change. *Nature Climate Change, 6*, 166 EP -. doi:10.1038/nclimate2837

Illius, A. W., & O'Connor, T. G. (1999). On the relevance of nonequilibrium concepts to arid and semiarid grazing systems. *Ecological Applications, 9*(3), 798. doi:10.2307/2641330

Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., . . . Eisenhauer, N. (2015). Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature, 526*(7574), 574–577. doi:10.1038/nature15374

James, C. D., Landsberg, J., & Morton, S. R. (1999). Provision of watering points in the Australian arid zone: a review of effects on biota. *Journal of Arid Environments, 41*(1), 87–121. doi:10.1006/jare.1998.0467

James, J. J., Tiller, R. L., & Richards, J. H. (2005). Multiple resources limit plant growth and function in a saline-alkaline desert community. *Journal of Ecology, 93*(1), 113-126. doi:10.1111/j.0022-0477.2004.00948.x

Jamsranjav, C., Reid, R. S., Fernández-Giménez, M. E., Tsevlee, A., Yadamsuren, B., & Heiner, M. (2018). Applying a dryland degradation framework for rangelands: The case of Mongolia. *Ecological Applications, 28*(3), 622–642. doi:10.1002/eap.1684

Jäschke, Y., Heberling, G., & Wesche, K. (2019). Environmental controls override grazing effects on plant functional traits in Tibetan rangelands. *Functional Ecology*(00), 1–14. doi:10.1111/1365-2435.13492

Jigjidsuren, S., & Johnson, D. A. (2003). *Forage plants of Mongolia: Mongol orny malyn tėžėėlijn urgamal*. Ulaanbaatar.

Johnson, D. A., Sheehy, D. P., Miller, D., & Damiran, D. (2006). Mongolian rangelands in transition. *Sechleresse, 17*, 133–141.

Jongman, R. H. G., ter Braak, C. J. F., & van Tongeren, O. F. R. (2007). *Data analysis in community and landscape ecology* (New ed. with corr., 10. pr., transferred to digital pr ed.). Cambridge [u.a.]: Cambridge Univ. Press.

Keddy, P. A. (1992). Assembly and response rules: Two goals for predictive community ecology. *Journal of Vegetation Science, 3*(2), 157–164. doi:10.2307/3235676

Khishigbayar, J., Fernández-Giménez, M. E., Angerer, J. P., Reid, R. S., Chantsallkham, J., Baasandorj, Y., & Zumberelmaa, D. (2015). Mongolian rangelands at a tipping point? Biomass and cover are stable but composition shifts and richness declines after 20 years of grazing and increasing temperatures. *Journal of Arid Environments, 115*, 100–112. doi:10.1016/j.jaridenv.2015.01.007

Klanderud, K., Vandvik, V., & Goldberg, D. (2015). The importance of biotic vs. abiotic drivers of local plant community composition along regional bioclimatic gradients. *PloS one, 10*(6), e0130205. doi:10.1371/journal.pone.0130205

Koutroulis, A. G. (2019). Dryland changes under different levels of global warming. *Science of The Total Environment, 655*, 482–511.

Kowal, V. A., Ahlborn, J., Jamsranjav, C., Avirmed, O., & Chaplin-Kramer, R. (2021). Modeling integrated impacts of climate change and grazing on Mongolia's rangelands. *Land, 10*. doi:https://doi.org/10.3390/xxxxx

Kraft, N. J. B., Adler, P. B., Godoy, O., James, E. C., Fuller, S., & Levine, J. M. (2015). Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology, 29*(5), 592–599. doi:10.1111/1365-2435.12345

Laliberte, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology, 91*(1), 299–305.

Laliberté, E., Legendre, P., & Shipley, B. (2014). FD: Measuring functional diversity from multiple traits, and other tools for functional ecology: R package (Version 1.0-12).

Laliberté, E., Zemunik, G., & Turner, B. L. (2014). Environmental filtering explains variation in plant diversity along resource gradients. *Science, 345*(6204), 1602. doi:10.1126/science.1256330

Lambin, E. F., & Meyfroidt, P. (2011). Global land use change, economic globalization, and the looming land scarcity. *Proceedings of the National Academy of Sciences, 108*(9), 3465–3472. doi:10.1073/pnas.1100480108

Landsberg, J., James, C. D., Morton, S. R., Müller, W. J., & Stol, J. (2003). Abundance and composition of plant species along grazing gradients in Australian rangelands. *Journal of Applied Ecology, 40*(6), 1008–1024. doi:10.1111/j.1365-2664.2003.00862.x

Lang, B., Ahlborn, J., Oyunbileg, M., Geiger, A., von Wehrden, H., Wesche, K., . . . Römermann, C. (2020). Grazing effects on intraspecific trait variability vary with changing precipitation patterns in Mongolian rangelands. *Ecology and evolution, 10*(2), 678–691. doi:10.1002/ece3.5895

Lang, B., Geiger, A., Oyunbileg, M., Ahlborn, J., von Wehrden, H., Wesche, K., . . . Römermann, C. (2018). Intraspecific trait variation patterns along a precipitation gradient in Mongolian rangelands. *Flora*. *254*, 135-146.

Lardy, G., Stoltenow, C. L., Johnson, R., Boyles, S., Fisher, G., Wohlgemuth, K., & Lundstrom, D. (1988). Livestock and water.

Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Functional Ecology, 16*(5), 545–556. doi:10.1046/j.1365-2435.2002.00664.x

Lavorel, S., McIntyre, S., Landsberg, J., & Forbes, T. D. A. (1997). Plant functional classifications: from general groups to specific groups based on response to disturbance. *Trends in Ecology & Evolution, 12*(12), 474–478. doi:10.1016/S0169-5347(97)01219-6

Lavrenko, E., & Karamysheva, Z. (1993). Steppes of the former Soviet Union and Mongolia. *Ecosystems of the world, 8*, 3-59.

Le Bagousse-Pinguet, Y., Gross, N., Maestre, F. T., Maire, V., Bello, F., Fonseca, C. R., . . . Liancourt, P. (2017). Testing the environmental filtering concept in global drylands. *Journal of Ecology, 105*(4), 1058–1069. doi:10.1111/1365-2745.12735

Le Bagousse-Pinguet, Y., Soliveres, S., Gross, N., Torices, R., Berdugo, M., & Maestre, F. T. (2019). Phylogenetic, functional, and taxonomic richness have both positive and negative effects on ecosystem multifunctionality. *Proceedings of the National Academy of Sciences, 116*(17), 8419-8424.

Le Houerou, H. N., Bingham, R. L., & Skerbek, W. (1988). Relationship between the variability of primary production and the variability of annual precipitation in world arid lands. *Journal of Arid Environments, 15*(1), 1–18.

Lee, M. A. (2018). A global comparison of the nutritive values of forage plants grown in contrasting environments. *Journal of Plant Research, 131*(4), 641–654. doi:10.1007/s10265-018-1024-y

Lehnert, L. W., Wesche, K., Trachte, K., Reudenbach, C., & Bendix, J. (2016). Climate variability rather than overstocking causes recent large scale cover changes of Tibetan pastures. *Scientific Reports, 6*, 24367. doi:10.1038/srep24367

Leyer, I., & Wesche, K. (2007). *Multivariate Statistik in der Ökologie: Eine Einführung* ([Online-Ausg. des] korrigierten [gedr.] Nachdr ed.). Berlin; Heidelberg: Springer.

Li, W., Li, X., Zhao, Y., Zheng, S., & Bai, Y. (2018). Ecosystem structure, functioning and stability under climate change and grazing in grasslands: current status and future prospects. *Current Opinion in Environmental Sustainability, 33*, 124-135. doi:https://doi.org/10.1016/j.cosust.2018.05.008

Linstädter, A., Schellberg, J., Brüser, K., García, C. A. M., Oomen, R. J., Du Preez, C. C., . . . Ewert, F. (2014). Are there consistent grazing indicators in drylands? Testing plant functional types of various complexity in South Africa's grassland and savanna Biomes. *PloS one, 9*(8), e104672. doi:10.1371/journal.pone.0104672

Lisetskii, F. N., Chernyavskikh, V. I., & Degtyar, O. V. (2011). Pastures in the zone of temperate climate: trends for development, dynamics, ecological fundamentals of rational use. In N. T. Prochazka (Ed.), *Pastures: dynamics, economics and management* (pp. 51-84). New York.

Liu, J., Ma, X., Duan, Z., Jiang, J., Reichstein, M., & Jung, M. (2020). Impact of temporal precipitation variability on ecosystem productivity. *WIREs Water, 7*(6), e1481. doi:https://doi.org/10.1002/wat2.1481

Lkhagvadorj, D., Hauck, M., Dulamsuren, C., & Tsogtbaatar, J. (2013). Twenty years after decollectivization: Mobile livestock husbandry and its ecological impact in the Mongolian Forest-Steppe. *Human Ecology, 41*(5), 725-735. doi:10.1007/s10745-013-9599-3

Lund, H. G. (2007). Accounting for the world's rangelands. *Rangelands, 29*(1), 3–10. doi:10.2111/1551-

501X(2007)29[3:AFTWR]2.0.CO;2
Macarthur, R., & Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist, 101*(921), 377–385. doi:10.1086/282505
Maestre, F. T., Callaway, R. M., Valladares, F., & Lortie, C. J. (2009). Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology, 97*(2), 199–205. doi:10.1111/j.1365-2745.2008.01476.x
Maestre, F. T., Quero, J. L., Gotelli, N. J., Escudero, A., Ochoa, V., Delgado-Baquerizo, M., . . . Zaady, E. (2012). Plant species richness and ecosystem multifunctionality in global drylands. *Science (New York, N.Y.), 335*(6065), 214–218. doi:10.1126/science.1215442
Magurran, A. E., Baillie, S. R., Buckland, S. T., Dick, J. M., Elston, D. A., Scott, E. M., . . . Watt, A. D. (2010). Long-term datasets in biodiversity research and monitoring: assessing change in ecological communities through time. *Trends in Ecology & Evolution, 25*(10), 574-582. doi:https://doi.org/10.1016/j.tree.2010.06.016
Májeková, M., Paal, T., Plowman, N. S., Bryndová, M., Kasari, L., Norberg, A., . . . Bello, F. (2016). Evaluating functional diversity: Missing trait data and the importance of species abundance structure and data transformation. *PloS one, 11*(2), e0149270. doi:10.1371/journal.pone.0149270
Manthey, M., & Peper, J. (2010). Estimation of grazing intensity along grazing gradients – the bias of nonlinearity. *Journal of Arid Environments, 74*(10), 1351–1354. doi:10.1016/j.jaridenv.2010.05.007
Marques, F. F. C., Buckland, S. T., Goffin, D., Dixon, C. E., Borchers, D. L., Mayle, B. A., & Peace, A. J. (2001). Estimating deer abundance from line transect surveys of dung: Sika deer in southern Scotland. *Journal of Applied Ecology, 38*(2), 349–363. doi:10.1046/j.1365-2664.2001.00584.x
Marta, S., Lacasella, F., Romano, A., & Ficetola, G. F. (2019). Cost-effective spatial sampling designs for field surveys of species distribution. *Biodiversity and Conservation*, 1-18.
Mason, N. W. H., Irz, P., Lanoiselée, C., Mouillot, D., & Argillier, C. (2008). Evidence that niche specialization explains species–energy relationships in lake fish communities. *Journal of Animal Ecology, 77*(2), 285–296. doi:10.1111/j.1365-2656.2007.01350.x
Mayfield, M. M., & Levine, J. M. (2010). Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology letters, 13*(9), 1085–1093. doi:10.1111/j.1461-0248.2010.01509.x
Mazerolle, M. J. (2016). AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c): R package (Version 2.0-4). Retrieved from http://CRAN.R-project.org/package=AICcmodavg
Middleton, N., Rueff, H., Sternberg, T., Batbuyan, B., & Thomas, D. (2015). Explaining spatial variations in climate hazard impacts in western Mongolia. *Landscape Ecology, 30*(1), 91–107. doi:10.1007/s10980-014-0091-2
Middleton, N. J., & Sternberg, T. (2013). Climate hazards in drylands: A review. *Earth-Science Reviews, 126*, 48–57. doi:10.1016/j.earscirev.2013.07.008
Miehe, S., Kluge, J., von Wehrden, H., & Retzer, V. (2010). Long-term degradation of Sahelian rangeland detected by 27 years of field study in Senegal. *Journal of Applied Ecology, 47*(3), 692–700. doi:10.1111/j.1365-2664.2010.01815.x
Milchunas, D. G., & Lauenroth, W. K. (1993). Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs, 63*(4), 327–366.
Milchunas, D. G., Lauenroth, W. K., Chapman, P. L., & Kazempour, M. K. (1989). Effects of grazing, topography, and precipitation on the structure of a semiarid grassland. *Vegetatio, 80*(1), 11–23. doi:10.1007/BF00049137
Milchunas, D. G., Sala, O. E., & Lauenroth, W. K. (1988). A generalized model of the effects of grazing by large herbivores on grassland community structure. *The American Naturalist, 132*(1), 87–106. doi:10.1086/284839
Mohammat, A., Wang, X., Xu, X., Peng, L., Yang, Y., Zhang, X., . . . Piao, S. (2013). Drought and spring cooling induced recent decrease in vegetation growth in Inner Asia. *Agricultural and Forest Meteorology, 178-179*, 21–30. doi:10.1016/j.agrformet.2012.09.014
Moreno García, C. A., Schellberg, J., Ewert, F., Brüser, K., Canales-Prati, P., Linstädter, A., . . . Fraser, L. (2014). Response of community-aggregated plant functional traits along grazing gradients: insights from African semi-arid grasslands. *Applied Vegetation Science, 17*(3), 470–481. doi:10.1111/avsc.12092
Mottet, A., de Haan, C., Falcucci, A., Tempio, G., Opio, C., & Gerber, P. (2017). Livestock: On our plates or eating at our table? A new analysis of the feed/food debate. *Global Food Security, 14*, 1-8. doi:https://doi.org/10.1016/j.gfs.2017.01.001
Mouillot, D., Graham, N. A. J., Villéger, S., Mason, N. W. H., & Bellwood, D. R. (2013). A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution, 28*(3), 167–177. doi:10.1016/j.tree.2012.10.004
Mouillot, D., Villéger, S., Scherer-Lorenzen, M., & Mason, N. W. H. (2011). Functional structure of biological

communities predicts ecosystem multifunctionality. *PloS one, 6*(3), e17476. doi:10.1371/journal.pone.0017476

Müller, B., Frank, K., & Wissel, C. (2007). Relevance of rest periods in non-equilibrium rangeland systems – A modelling analysis. *Agricultural Systems, 92*(1), 295–317. doi:10.1016/j.agsy.2006.03.010

Murray-Tortarolo, G. N., & Jaramillo, V. J. (2020). Precipitation extremes in recent decades impact cattle populations at the global and national scales. *Science of The Total Environment*, 139557.

Naidoo, S., Davis, C., & Van Garderen, E. A. (2013). Forests, rangelands and climate change in southern Africa. *Forests and climate change working paper, 12*.

Newbold, T., Hudson, L. N., Arnell, A. P., Contu, S., Palma, A., Ferrier, S., . . . Purvis, A. (2016). Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment. *Science, 353*(6296), 288–291. doi:10.1126/science.aaf2201

Noy-Meir, I. (1973). Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics, 4*(1), 25–51. doi:10.1146/annurev.es.04.110173.000325

Oba, G., Weladji, R. B., Lusigi, W. J., & Stenseth, N. C. (2003). Scale-dependent effects of grazing on rangeland degradation in northern Kenya: A test of equilibrium and non-equilibrium hypotheses. *Land Degradation & Development, 14*(1), 83–94. doi:10.1002/ldr.524

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., . . . Wagner, H. (2017). vegan: Community ecology package (Version 2.4-2).

Olsen, S. R., Cole, C. V., & Watanabe, F. S. (1954). *Estimation of available phosphorus in soils by extraction with sodium bicarbonate*. Washington D.C.: US Government Printing Office.

Olson, K. A., Murray, M. G., & Fuller, T. K. (2010). Vegetation composition and nutritional quality of forage for gazelles in Eastern Mongolia. *Rangeland Ecology & Management, 63*(5), 593–598. doi:10.2111/REM-D-09-00122.1

Pakeman, R. J. (2004). Consistency of plant species and trait responses to grazing along a productivity gradient: a multi-site analysis. *Journal of Ecology, 92*(5), 893–905. doi:10.1111/j.0022-0477.2004.00928.x

Pendergrass, A. G., Knutti, R., Lehner, F., Deser, C., & Sanderson, B. M. (2017). Precipitation variability increases in a warmer climate. *Scientific Reports, 7*(1), 17966. doi:10.1038/s41598-017-17966-y

Peres-Neto, P. R., Dray, S., & ter Braak, C. J. F. (2017). Linking trait variation to the environment: Critical issues with community-weighted mean correlation resolved by the fourth-corner approach. *Ecography, 40*(7), 806–816. doi:10.1111/ecog.02302

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., . . . Cornelissen, J. H. C. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany, 61*(3), 167. doi:10.1071/BT12225

Pfeiffer, M., Dulamsuren, C., Jäschke, Y., & Wesche, K. (2018). Grasslands of China and Mongolia: Spatial extent, land use and conservation. In V. R. Squires, J. Dengler, L. Hua, & H. Feng (Eds.), *Grasslands of the world: diversity, management and conservation*: CRC Press.

Pfeiffer, M., Dulamsuren, C., & Wesche, K. (2019). Grasslands and shrublands of Mongolia. In *Reference Module in Earth Systems and Environmental Sciences*: Elsevier.

Polley, H. W., Briske, D. D., Morgan, J. A., Wolter, K., Bailey, D. W., & Brown, J. R. (2013). Climate change and North American rangelands: trends, projections, and implications. *Rangeland Ecology & Management, 66*(5), 493-511.

Rao, M. P., Davi, N. K., D'Arrigo, R. D., Skees, J., Nachin, B., Leland, C., . . . Byambasuren, O. (2015). Dzuds, droughts, and livestock mortality in Mongolia. *Environmental Research Letters, 10*(7), 074012. doi:10.1088/1748-9326/10/7/074012

Ren, H., Eviner, V. T., Gui, W., Wilson, G. W. T., Cobb, A. B., Yang, G., . . . Bai, Y. (2018). Livestock grazing regulates ecosystem multifunctionality in semi-arid grassland. *Functional Ecology, 32*(12), 2790–2800. doi:10.1111/1365-2435.13215

Ren, H., Schönbach, P., Wan, H., Gierus, M., & Taube, F. (2012). Effects of grazing intensity and environmental factors on species composition and diversity in typical steppe of Inner Mongolia, China. *PloS one, 7*(12), e52180. doi:10.1371/journal.pone.0052180

Ren, H., Taube, F., Stein, C., Zhang, Y., Bai, Y., & Hu, S. (2018). Grazing weakens temporal stabilizing effects of diversity in the Eurasian steppe. *Ecology and evolution, 8*(1), 231–241. doi:10.1002/ece3.3669

Reynolds, J. F., Kemp, P. R., Ogle, K., & Fernández, R. J. (2004). Modifying the 'pulse–reserve'paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. *Oecologia, 141*(2), 194-210.

Rojas-Downing, M. M., Nejadhashemi, A. P., Harrigan, T., & Woznicki, S. A. (2017). Climate change and livestock: Impacts, adaptation, and mitigation. *Climate Risk Management, 16*, 145-163. doi:https://doi.org/10.1016/j.crm.2017.02.001

Rosbakh, S., Römermann, C., & Poschlod, P. (2015). Specific leaf area correlates with temperature: New evidence of trait variation at the population, species and community levels. *Alpine Botany, 125*(2), 79–86. doi:10.1007/s00035-015-0150-6

Roxburgh, S. H., Shea, K., & Wilson, J. B. (2004). The intermediate disturbance hypothesis: Patch dynamics and mechanisms of species coexistence. *Ecology, 85*(2), 359–371. doi:10.1890/03-0266

Ruppert, J. C., Holm, A., Miehe, S., Muldavin, E., Snyman, H. A., Wesche, K., . . . Ward, D. (2012). Meta-analysis of ANPP and rain-use efficiency confirms indicative value for degradation and supports non-linear response along precipitation gradients in drylands. *Journal of Vegetation Science, 23*(6), 1035–1050. doi:10.1111/j.1654-1103.2012.01420.x

Sala, O. E., & Paruelo, J. M. (1997). Ecosystem services in grasslands. In G. C. Daily (Ed.), *Nature's services*. Washington, DC: Island Press: Washington, DC.

Sarkar, D. (2008). *Lattice: Multivariate Data Visualization with R*. New York: Springer.

Sasaki, T., Okayasu, T., Ohkuro, T., Shirato, Y., Jamsran, U., & Takeuchi, K. (2009). Rainfall variability may modify the effects of long-term exclosure on vegetation in Mandalgobi, Mongolia. *Journal of Arid Environments, 73*(10), 949–954. doi:10.1016/j.jaridenv.2009.04.008

Sasaki, T., Okayasu, T., Takeuchi, K., Jamsran, U., & Jadambaa, S. (2005). Patterns of floristic composition under different grazing intensities in Bulgan, South Gobi, Mongolia. *Grassland science, 51*(3), 235–242. doi:10.1111/j.1744-697X.2005.00029.x

Sasaki, T., Okubo, S., Okayasu, T., Jamsran, U., Ohkuro, T., & Takeuchi, K. (2009). Two-phase functional redundancy in plant communities along a grazing gradient in Mongolian rangelands. *Ecology, 90*(9), 2598–2608.

Sasaki, T., Okubo, S., Okayasu, T., Jamsran, U., Ohkuro, T., & Takeuchi, K. (2011). Indicator species and functional groups as predictors of proximity to ecological thresholds in Mongolian rangelands. *Plant Ecology, 212*(2), 327–342. doi:10.1007/s11258-010-9825-7

Sato, T., Kimura, F., & Kitoh, A. (2007). Projection of global warming onto regional precipitation over Mongolia using a regional climate model. *Journal of Hydrology, 333*(1), 144–154. doi:10.1016/j.jhydrol.2006.07.023

Schellenberger Costa, D., Gerschlauer, F., Pabst, H., Kühnel, A., Huwe, B., Kiese, R., . . . Kühn, I. (2017). Community-weighted means and functional dispersion of plant functional traits along environmental gradients on Mount Kilimanjaro. *Journal of Vegetation Science, 28*(4), 684–695. doi:10.1111/jvs.12542

Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods, 9(7)*, 671-675.

Shanafelt, D. W., Dieckmann, U., Jonas, M., Franklin, O., Loreau, M., & Perrings, C. (2015). Biodiversity, productivity, and the spatial insurance hypothesis revisited. *Journal of Theoretical Biology, 380*, 426–435. doi:10.1016/j.jtbi.2015.06.017

Shipley, B. (2007). Comparative plant ecology as a tool for integrating across scales. *Annals of Botany, 99*(5), 965–966. doi:10.1093/aob/mcm039

Shukla, P. R., Skea, J., Calvo Buendia, E., Masson-Delmotte, V., Pörtner, H. O., Roberts, D. C., ... & Malley, J. (2019). IPCC, 2019: Climate Change and Land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems.

Siebenkäs, A., Schumacher, J., & Roscher, C. (2016). Resource availability alters biodiversity effects in experimental grass-forb mixtures. *PloS one, 11*(6), e0158110. doi:10.1371/journal.pone.0158110

Sneath, D. (1998). State policy and pasture degradation in Inner Asia. *Science, 281*(5380), 1147–1148. doi:10.1126/science.281.5380.1147

Song, X.-P., Hansen, M. C., Stehman, S. V., Potapov, P. V., Tyukavina, A., Vermote, E. F., & Townshend, J. R. (2018). Global land change from 1982 to 2016. *Nature, 560*(7720), 639-643. doi:10.1038/s41586-018-0411-9

Sonkoly, J., Kelemen, A., Valkó, O., Deák, B., Kiss, R., Tóth, K., . . . Török, P. (2019). Both mass ratio effects and community diversity drive biomass production in a grassland experiment. *Scientific Reports, 9*(1), 1–10. doi:10.1038/s41598-018-37190-6

Sternberg, T., Rueff, H., & Middleton, N. (2015). Contraction of the Gobi Desert, 2000–2012. *Remote Sensing, 7*, 1346–1358. doi:10.3390/rs70201346

Sternberg, T., Thomas, D., & Middleton, N. (2011). Drought dynamics on the Mongolian steppe, 1970-2006. *International journal of climatology, 31*(12), 1823–1830. doi:10.1002/joc.2195

Sternberg, T., Tsolmon, R., Middleton, N., & Thomas, D. (2011). Tracking desertification on the Mongolian steppe through NDVI and field-survey data. *International Journal of Digital Earth, 4*(1), 50–64. doi:10.1080/17538940903506006

Stumpp, M., Wesche, K., Retzer, V., & Miehe, G. (2005). Impact of grazing livestock and distance from water source on soil fertility in Southern Mongolia. *Mountain Research and Development, 25*(3), 244–251. doi:10.1659/0276-4741(2005)025[0244:IOGLAD]2.0.CO;2

Sullivan, S., & Homewood, K. (2003, 2003). *On non-equilibrium and nomadism: Knowledge, diversity and global modernity in drylands (and beyond...)*. Earthscan: London.

Sullivan, S., & Rohde, R. (2002). On non-equilibrium in arid and semi-arid grazing systems. *Journal of Biogeography, 29*(12), 1595–1618. doi:10.1046/j.1365-2699.2002.00799.x

Suttie, J. M., & Reynolds, S. G. (Eds.). (2003). *Transhumant grazing systems in temperate Asia*. Rome: FAO.

Suttie, J. M., Reynolds, S. G., & Batello, C. (2005). *Grasslands of the world*. Rome: Food and Agricultural Organization of the United Nations.

Takatsuki, S., Sato, M., & Morinaga, Y. (2018). Effects of grazing on grassland communities of the forest-steppe of northern Mongolia: A comparison of grazed versus ungrazed places. *Grassland science, 64*(3), 167–174. doi:10.1111/grs.12195

Tamura, K., Asano, M., & Jamsran, U. (2013). Soil diversity in Mongolia. In N. Yamamura, N. Fujita, & A. Maekawa (Eds.), *The Mongolian Ecosystem Network: Environmental Issues Under Climate and Social Changes* (pp. 99-103). Tokyo: Springer Japan.

Team, R. C. (2018). R: A language and environment for statistical computing (Version 3.5.1). Vienna, Austria: R Foundation of Statistical Computing. Retrieved from https://www.r-project.org/

Teickner, H., Knoth, C., Bartoschek, T., Kraehnert, K., Vigh, M., Purevtseren, M., . . . Pebesma, E. (2020). Patterns in Mongolian nomadic household movement derived from GPS trajectories. *Applied Geography, 122*, 102270. doi:https://doi.org/10.1016/j.apgeog.2020.102270

Testa, S., Mondino, E. C. B., & Pedroli, C. (2014). Correcting MODIS 16-day composite NDVI time-series with actual acquisition dates. *European Journal of Remote Sensing, 47*(1), 285–305. doi:10.5721/EuJRS20144718

Thioulouse, J., Dray, S., Dufour, A.-B., Siberchicot, A., Jombart, T., & Pavoine, S. *Multivariate Analysis of Ecological Data with ade4*. Retrieved from

Tilman, D. (2001). Functional diversity. In S. A. Levin (Ed.), *Encyclopedia of biodiversity.* (Vol. 2001, pp. 109/120): Academic Press.

Tilman, D., & Downing, J. A. (1996). Biodiversity and stability in grasslands. In F. B. Samson & F. L. Knopf (Eds.), *Ecosystem Management* (pp. 3–7). New York, NY: Springer New York.

Tilman, D., & El Haddi, A. (1992). Drought and biodiversity in grasslands. *Oecologia, 89*(2), 257-264.

Urgamal, M., Oyuntsetseg, B., Nyambayar, D., & Dulamsuren, C. (2014). *Conspectus of the vascular plants of Mongolia*. Ulaanbaatar.

Uriel, S., Adeel, Z., Niemeijer, D., Puigdefabregas, J., White, R., & Lal, R. (2005). Dryland Systems. In M. E. Assessment (Ed.), *Ecosystems and human well-being. Washington, DC: Island Press, 2005.* (pp. 623–662). Washington (DC): Island Press.

Valencia, E., Maestre, F. T., Le Bagousse-Pinguet, Y., Quero, J. L., Tamme, R., Börger, L., . . . Gross, N. (2015). Functional diversity enhances the resistance of ecosystem multifunctionality to aridity in Mediterranean drylands. *New Phytologist, 206*(2), 660-671. doi:https://doi.org/10.1111/nph.13268

Valin, H., Sands, R. D., Van der Mensbrugghe, D., Nelson, G. C., Ahammad, H., Blanc, E., . . . Havlik, P. (2014). The future of food demand: understanding differences in global economic models. *Agricultural Economics, 45*(1), 51-67.

van Soest, P. J. (2018). *Nutritional ecology of the ruminant*: Cornell university press.

Vetter, S. (2004). Rangelands at equilibrium and non-equilibrium. A review of the debate. In S. Vetter (Ed.), *Rangelands at equilibrium and non-equilibrium* (pp. 5–15). Bellville: Programme for Land and Agririan Studies.

Vetter, S. (2005). Rangelands at equilibrium and non-equilibrium: recent developments in the debate. *Journal of Arid Environments, 62*(2), 321–341. doi:10.1016/j.jaridenv.2004.11.015

Villéger, S., Mason, N. W. H., & Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology, 89*(8), 2290–2301. doi:10.1890/07-1206.1

von Wehrden, H., Hanspach, J., Kaczensky, P., Fischer, J., & Wesche, K. (2012). Global assessment of the non-equilibrium concept in rangelands. *Ecological Applications, 22*(2), 292–399.

von Wehrden, H., & Wesche, K. (2007). Relationships between climate, productivity and vegetation in southern Mongolian drylands. *Basic Applied Dryland Research, 1*(2), 100–120.

von Wehrden, H., Wesche, K., Chuluunkhuyag, O., & Fust, P. (2015). Correlation of trends in cashmere production and declines of large wild mammals: response to Berger et al. 2013. *Conservation Biology, 29*(1), 286–289. doi:10.1111/cobi.12414

Wang, G., Huang, Y., Wei, Y., Zhang, W., Li, T., & Zhang, Q. (2019). Climate warming does not always extend the plant growing season in Inner Mongolian grasslands: Evidence from a 30-year in situ observations at eight experimental sites. *Journal of Geophysical Research: Biogeosciences, 124*(7), 2364-2378. doi:https://doi.org/10.1029/2019JG005137

Wang, G., Luo, Z., Huang, Y., Sun, W., Wei, Y., Xiao, L., . . . Zhang, W. (2021). Simulating the spatiotemporal variations in aboveground biomass in Inner Mongolian grasslands under environmental changes. *Atmos. Chem. Phys., 21*(4), 3059-3071. doi:10.5194/acp-21-3059-2021

Wang, X., Chen, F., Hasi, E., & Li, J. (2008). Desertification in China: An assessment. *Earth-Science Reviews, 88*(3-4), 188–206. doi:10.1016/j.earscirev.2008.02.001

Wang, Y., Heberling, G., Görzen, E., Miehe, G., Seeber, E., & Wesche, K. (2017). Combined effects of livestock grazing and abiotic environment on vegetation and soils of grasslands across Tibet. *Applied Vegetation Science, 20*(3), 327–339. doi:10.1111/avsc.12312

Wang, Y., & Wesche, K. (2016). Vegetation and soil responses to livestock grazing in Central Asian grasslands: A review of Chinese literature. *Biodiversity and Conservation*. doi:10.1007/s10531-015-1034-1

Wesche, K., Ambarlı, D., Kamp, J., Török, P., Treiber, J., & Dengler, J. (2016). The Palaearctic steppe biome: A new synthesis. *Biodiversity and Conservation, 25*(12), 2197–2231. doi:10.1007/s10531-016-1214-7

Wesche, K., & Retzer, V. (2005). Is degradation a major problem in semi-desert environments of the Gobi region in southern Mongolia? *Erforsch. biol. Ress. Mongolei (Halle/Saale), 9*, 133–146.

Wesche, K., & Ronnenberg, K. (2010). Effects of NPK fertilisation in arid southern Mongolian desert steppes. *Plant Ecology, 207*(1), 93–105. doi:10.1007/s11258-009-9656-6

Wesche, K., Ronnenberg, K., Retzer, V., & Miehe, G. (2010). Effects of large herbivore exclusion on southern Mongolian desert steppes. *Acta Oecologica, 36*(2), 234–241. doi:10.1016/j.actao.2010.01.003

Wesche, K., & Treiber, J. (2012). Abiotic and biotic determinants of steppe productivity and performance – A view from Central Asia. In M. J. A. Werger & M. A. van Staalduinen (Eds.), *Eurasian Steppes. Ecological Problems and Livelihoods in a Changing World* (Vol. 6, pp. 3–43). Dordrecht: Springer Netherlands.

Wesche, K., & von Wehrden, H. (2011). Surveying Southern Mongolia: application of multivariate classification methods in drylands with low diversity and long floristic gradients. *Applied Vegetation Science, 14*(4), 561–570. doi:10.1111/j.1654-109X.2011.01148.x

Westoby, M., Walker, B., & Noy-Meir, I. (1989). Opportunistic management for rangelands not at equilibrium. *Journal of Range Management, 42*(4), 266. doi:10.2307/3899492

Wesuls, D., Oldeland, J., Dray, S., & Prinzing, A. (2012). Disentangling plant trait responses to livestock grazing from spatio-temporal variation: the partial RLQ approach. *Journal of Vegetation Science, 23*(1), 98–113. doi:10.1111/j.1654-1103.2011.01342.x

White, R. P., & Nackoney, J. (2003). Drylands, people, and ecosystem goods and services: A web-based geospatial analysis. Retrieved from http://pdf.wri.org/drylands.pdf.

Whitford, W. G. (2002*). Ecology of desert systems*. San Diego: Academic Press.

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*: Springer-Verlag New York.

Wiens, J. A. (1984). On understanding a non-equilibrium world: myth and reality in community patterns and processes. In D. R. Strong, D. Simberloff, L. G. Abele, & A. B. Thistle (Eds.), *Ecological communities: conceptual issues and the evidence.* (pp. 439–457). Princeton, New Jersey, USA: Princeton University Press.

Wu, J., Shen, Z., Shi, P., Zhou, Y., & Zhang, X. (2014). Effects of grazing exclusion on plant functional group diversity of alpine grasslands along a precipitation gradient on the Northern Tibetan Plateau. *Arctic, Antarctic, and Alpine Research, 46*(2), 419–429. doi:10.1657/1938-4246-46.2.419

Yahdjian, L., Sala, O. E., & Havstad, K. M. (2015). Rangeland ecosystem services: shifting focus from supply to reconciling supply and demand. *Frontiers in Ecology and the Environment, 13*(1), 44–51. doi:10.1890/140156

Yachi, S., Loreau, M. (1999). Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proceedings of the National Academy of Sciences of the United States of America,* 96(4), 1463-1468. Doi: 10.1073/pnas.96.4.1463.

Yang, Y., Fang, J., Ma, W., & Wang, W. (2008). Relationship between variability in aboveground net primary production and precipitation in global grasslands. *Geophysical Research Letters, 35*(23). doi:10.1029/2008GL035408

Yao, J., Liu, H., Huang, J., Gao, Z., Wang, G., Li, D., . . . Chen, X. (2020). Accelerated dryland expansion regulates future variability in dryland gross primary production. *Nature Communications, 11*(1), 1665. doi:10.1038/s41467-020-15515-2

Zavaleta, E. S., Pasari, J. R., Hulvey, K. B., & Tilman, G. D. (2010). Sustaining multiple ecosystem functions in grassland communities requires higher biodiversity. *Proceedings of the National Academy of Sciences, 107*(4), 1443–1446. doi:10.1073/pnas.0906829107

Zemmrich, A., Hilbig, W., & Oyuunchimeg, D. (2010). Plant communities along an elevation gradient under special consideration of grazing in Western Mongolia. *Phytocoenologia, 40*(2), 91–115. doi:10.1127/0340-269X/2010/0040-0443

Zhang, H. Y., Lü, X. T., Knapp, A. K., Hartmann, H., Bai, E., Wang, X. B., . . . Han, X. G. (2018). Facilitation by leguminous shrubs increases along a precipitation gradient. *Functional Ecology, 32*(1), 203–213. doi:10.1111/1365-2435.12941

Zhang, Y., Loreau, M., He, N., Wang, J., Pan, Q., Bai, Y., & Han, X. (2018). Climate variability decreases species richness and community stability in a temperate grassland. *Oecologia, 188*(1), 183–192. doi:10.1007/s00442-018-4208-1

Supplementary Material

Chapter 1

Table: Plant functional traits that were measured in the project (data from the "species approach" was used for chapter 3; the "community approach" was the dataset collected for this dissertation) and their role as integrated measures for different growth parameters and ecosystem processes according to the literature (Pakeman, 2004, de Bello et al., 2006, Diaz et al., 2007, Sasaki et al., 2009b, Wittmer et al., 2010, Xu & Zhou, 2008; compare also Fraser et al., 2009, Schweingruber & Poschlod, 2005). The third and fourth column "species approach" gives information on the number of replicates per site on which measurements were carried out (6-8- replicate individuals on as many sites as possible; Sp- Species-level (no intraspecific variation); NA – not applicable/ not measured).

Species performance		Species approach	Community approach
Species cover	abundance for species fitness / performance	NA	X
Canopy height	species fitness / competitive vigor; proxy for rooting depth	6-8	6
Plant width	species fitness / competitive vigor, determine spp. abundance on the individual level	6-8	6
Aboveground biomass	biomass production, species fitness	6-8	6
Photosynthetic rate	species fitness/ performance; responds sensitively to abiotic & biotic stress	6-8	NA
Number of inflorescences	plant fecundity	6-8	NA
Fundamental traits/ ecophysiology			
Specific leaf area	mass-based maximum photosynthetic rate, growth rate, competitive strength	6-8	6
Photosynthetic pathway	Water use efficiency, response to global warming	SP	SP
Nitrogen fixation / legumes	capability for protein production, enhancement of soil nutrient contents	SP	SP
Leaf tissue Nitrogen content	proxy for crude protein content as a key aspect of forage value & resource acquisition (C- content measured parallel),	6-8	6
Leaf tissue P and K content	resource acquisition; competitive ability; nutritional quality	6-8	6
Foliar δ13 C	water use efficiency; species fitness/ performance;	6-8	NA
Stomata density & size	water use efficiency (especially in water-limited systems); stomatal conductance; net CO2 assimilation rate	6-8	NA
Seed mass, seed shape	establishment, seed bank persistence, dispersal	6-8	NA
Morphology / Life History			
Growth form	summary parameter of plant functional type	SP	SP

Presence of specialised subterranean structures	tolerance against variability in grazing and climate	SP	SP
Leaf distribution along the stem	accessibility, competitive strength	SP	SP
Resprouting capacity	grazing tolerance	SP	NA
Species demography			
Plant age	dynamics of species demography, population structure	6-8	NA
Longevity	dynamics of spp. demography/response to short term events	SP	SP
Forage value			
Presence of thorns	Investment in defenses, accessibility of biomass	SP	SP
Preference by livestock	Direct estimate of forage values according to Mongolian herders	SP	SP
Biogeography			
Distribution limits	Proximity of sampling sites to boundaries of distribution	SP	NA
Nativity status	Indigenous or not	SP	SP

Author contributions

Chapter 2

JA collected data, conducted the analysis, and wrote most of the manuscript. JA, KW, CR and HVW drafted the paper idea. MO contributed in data collection. OB organized field work. CR, KW and HVW designed the study, raised funding and significantly improved the quality of the manuscript. All authors gave approval to the final version of the manuscript

Chapter 3

JA collected data, did the analysis, developed the manuscript and wrote most of the text. BL collected and provided a substantial part of trait data for the analysis. MO and OB organised field work, collected and prepared data, and provided substantial help with determination of species. NFC provided important contributions to the statistic, made valuable comments to the manuscript and checked our language. HVW, KW and CR designed the study, supervised field- and lab work and made leading contributions to the manuscript.

Chapter 4

JA collected data, conducted the analysis, and wrote most of the manuscript. JA, KW, CR and HVW drafted the paper idea. BL and MO contributed in data collection. OB organized field work. NC assisted with the analysis and coding and made major contributions to the writing style and language. CR, KW and HVW designed the study, raised funding and significantly improved the quality of the manuscript. All authors gave approval to the final version of the manuscript.

Declaration

I hereby certify that the submitted dissertation entitled '**Climate-grazing interactions in Mongolian rangeland vegetation**' has been written by me without using unauthorized aids. I did not use any aids and writings other than those indicated. All passages taken from other writings either verbatim or in substance have been marked by me accordingly. I hereby confirm that in carrying out my dissertation project I have not employed the services of a professional broker of dissertation projects, nor will I do so in the future. This dissertation, in its present or any other version, has not yet been submitted to any other university for review. I have not taken or registered to take another doctoral examination.

Paulinenaue, 15.11.2021,

____

Julian Ahlborn