Herbivore Communities and Plant Diversity as Key Drivers of Savanna Ecosystem Resilience in a Changing Climate - A Model Assessment

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Declaration of Authorship

I affirm that I have completed all aspects of the research presented in this thesis without any external assistance. I also declare that I have not submitted the dissertation in this or any other form to any other institution as a dissertation. Any information obtained from published or unpublished sources has been properly acknowledged within the text. The primary content of Chapters II through IV were collaboratively written with co-authors and can stand alone as independent articles. The previously published Chapters II and III have been refined based on feedback provided by reviewers and editors. Chapter IV has been submitted to a scientific journal and is currently undergoing the review process.

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(Katja Irob)

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Merci.

"In nature, nothing exists alone."

\- Rachel Carson

Contents

Summary

English Summary

Savannas play a crucial role in providing essential ecosystem services, including carbon sequestration, biodiversity conservation, and water regulation. However, these ecosystems face threats from changing climatic conditions and unsustainable rangeland practices. Intensive livestock grazing has led to widespread degradation of savanna systems, characterised by shrub encroachment and loss of ecosystem functions. Shifting rangeland use from cattle grazing to native herbivores is proposed to reverse these negative trends, but the consequences for ecosystem properties and processes are not yet clear. Climate change and extreme events such as droughts exacerbate the challenges faced by savannas, potentially affecting the provision of essential ecosystem services on which local people's livelihoods depend. Ensuring savanna resilience to environmental stressors, especially increased aridity, is essential for sustaining these vital services. This resilience largely depends on the interaction between herbivores, vegetation composition, and climate. Unfortunately, our understanding of this interaction is limited, and current research has not addressed how savannas will respond to uncertain future climate conditions under different rangeland management practices.

In this thesis, I used the ecohydrological simulation model EcoHyD to investigate the effects of different rangeland practices on vegetation and water resources of a semi-arid savanna under current and future climate. This research makes two important contributions, first by examining the impacts of different future climate projections at a regional scale, which has not been the case in previous studies, and second by modelling rangeland types beyond grazing.

In Chapter II of the study, I examined the impacts of grazing and browsing herbivores on plant diversity and ecosystem functioning. The results showed that intensive grazing negatively affects grass cover and water availability, whereas browsing herbivores increased vegetation cover, plant functional diversity, and water use. However, these outcomes may depend on herbivore community composition and climate contexts, especially when extreme events like prolonged droughts occur. In Chapter III, I addressed these context-dependencies by investigating how different rangeland management options (i.e., grazer-dominated, mixed-feeders or browser-dominated herbivore communities) impact savanna ecosystems during droughts of varying durations. I found that diverse herbivore communities with a higher proportion of browsers combined with high plant functional diversity improve plant community resistance to drought and recovery after drought events, thus leading to enhanced ecosystem functioning and resilience. However, to fully understand ecosystem responses to climate change, temperature increases, precipitation changes and droughts need to be considered together. In Chapter IV, I therefore analysed the potential use of wild herbivore communities in regional climate adaptation plans to ensure the long-term resilience of savanna rangelands to the impacts of all aspects of uncertain climate change. My results have shown that while climate change alone does not necessarily lead to ecosystem degradation, in combination with poor management practices such as intensive grazing it can quickly lead to critical thresholds being exceeded. On the other hand, I have found that reducing the density of grazers and including mixed herbivores and browsers can promote ecosystem stability and resilience. Crossing tipping points can thus be delayed, or even avoided.

In conclusion, my research suggests that utilising diverse herbivores and functionally diverse plant communities in rangeland management strategies can improve ecosystem resilience, minimise the risk of irreversible degradation, and better manage uncertainties associated with climate change.

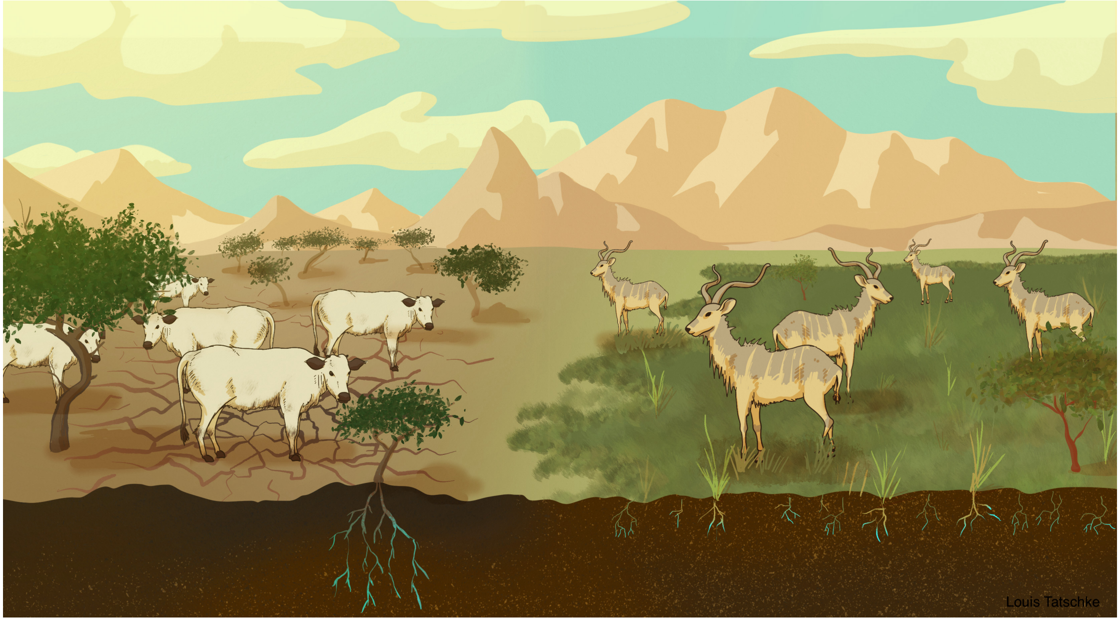
Deutsche Zusammenfassung

Savannen erbringen wesentliche Ökosystemleistungen für das menschliche Wohlergehen. Dies schließt die Kohlenstoffbindung, die Erhaltung der biologischen Vielfalt und die Wasserregulierung ein. Diese Ökosysteme sind jedoch durch sich ändernde klimatische Bedingungen und nicht nachhaltige Landnutzungspraktiken bedroht. Intensive Rinderbeweidung hat zu einer weit verbreiteten Degradierung der Savannensysteme geführt, die durch die aggressive Ausbreitung holziger Pflanzen und den Verlust von Ökosystemfunktionen gekennzeichnet ist. Die Umstellung der Landnutzung von Rinderbeweidung auf einheimische Herbivoren soll diese negativen Trends umkehren. Die tatsächlichen Folgen für die Eigenschaften und Prozesse der Ökosysteme sind jedoch noch unklar. Der Klimawandel und Extremereignisse wie Dürren verschärfen die Herausforderungen, denen Savannen ausgesetzt sind. Möglicherweise haben sie auch Auswirkungen auf die Bereitstellung essentieller Ökosystemleistungen, auf denen der Lebensunterhalt lokaler Bevölkerungsgruppen beruht. Die Erhaltung der Resilienz von Savannen gegenüber Umweltstressoren wie zunehmender Trockenheit ist entscheidend für die Aufrechterhaltung der von ihnen erbrachten Ökosystemleistungen. Diese Resilienz hängt von der Wechselwirkung zwischen Herbivoren, Vegetation und Klima ab. Leider ist unser Wissen über diese Wechselwirkung begrenzt, und die derzeitige Forschung hat sich nicht damit befasst, wie Savannen auf ungewisse zukünftige Klimabedingungen unter verschiedenen Bewirtschaftungsmethoden reagieren werden.

In dieser Arbeit habe ich das ökohydrologische Simulationsmodell EcoHyD verwendet, um die Auswirkungen verschiedener Arten der Weidelandbewirtschaftung auf Vegetation und Wasserressourcen einer halbtrockenen Savanne unter aktuellen und zukünftigen Klimabedingungen zu untersuchen. Diese Studie leistet zwei wichtige Beiträge: Zum einen untersucht sie die Auswirkungen verschiedener künftiger Klimaprojektionen auf regionaler Ebene, was in früheren Studien bisher vernachlässigt wurde. Zum Anderen modelliert sie Bewirtschaftungsformen des Weidelandes, die über die der Rinderbeweidung hinausgehen. In Kapitel II der Studie habe ich die Auswirkungen der Beweidung durch Gräser und Laub fressende Tiere ("Grazer") und durch Sträucher und holziger Vegetation fressender Tiere ("Browser") auf die Pflanzenvielfalt und das Funktionieren des Ökosystems untersucht. Die Ergebnisse zeigen, dass sich intensive Beweidung durch Grazer negativ auf Grasbedeckung und Wasserverfügbarkeit auswirkt, während Browser die Vegetationsbedeckung, die funktionale Vielfalt der Pflanzen und die Wassernutzung erhöhen. Diese Ergebnisse können jedoch je nach Zusammensetzung der Herbivorengemeinschaft und klimatischen Bedingungen, insbesondere unter Extremereignissen wie lang anhaltenden Dürren variieren. In Kapitel III ging ich auf diese Kontextabhängigkeit ein.

Dabei untersuchte ich, wie sich verschiedene Formen der Savannen-Weidelandbewirtschaftung (d.h. von Grazern dominierte, gemischte oder von Browsern dominierte Herbivorengemeinschaften,) auf Savannenökosysteme während unterschiedlich langer Dürreperioden auswirken. Ich konnte zeigen, dass vielfältige Herbivorengemeinschaften mit einem höheren Anteil an Browsern in Kombination mit einer größeren funktionalen Vielfalt der Pflanzen die Resilienz der Pflanzengemeinschaften gegenüber Trockenheit und die Erholung nach Dürreereignissen verbessern. Dies wiederum verbesserte die Funktionalität und Widerstandsfähigkeit des gesamten Ökosystems. Für ein umfassendes Verständnis der Reaktionen von Ökosystemen auf den Klimawandel ist jedoch die gleichzeitige Berücksichtigung von steigenden Temperaturen, Niederschlagsveränderungen und Dürren erforderlich. Deshalb habe ich in Kapitel IV die potenzielle Anwendung von Wildtiergemeinschaften in regionalen Anpassungsplänen analysiert, um die langfristige Resilienz von Savannen gegenüber den Auswirkungen aller Aspekte des Klimawandels zu gewährleisten. Meine Ergebnisse haben gezeigt, dass der Klimawandel allein zwar nicht zwangsläufig zu einer Degradierung der Ökosysteme führt. In Kombination mit schlechten Bewirtschaftungsmethoden, wie intensiver Beweidung, können jedoch schnell kritische Kipppunkte überschritten werden. Andererseits habe ich festgestellt, dass eine Verringerung der Dichte an Grazern und die Einbeziehung gemischter Herbivoren und Browsern die Stabilität und Widerstandsfähigkeit von Ökosystemen fördern kann. Die Überschreitung von Kipppunkten kann so verzögert, oder gar vermieden werden.

Zusammenfassend lässt meine Forschung den Schluss zu, dass die Nutzung einer vielfältigen Herbivoren- und Pflanzengemeinschaft in Strategien zur Bewirtschaftung von Savannen-Weideländern die Resilienz von Ökosystemen verbessern, das Risiko einer irreversiblen Degradierung minimieren und die mit dem Klimawandel verbundenen Unsicherheiten besser bewältigen kann.


Louis Tatschke

1

General Introduction

Savannas provide a wide range of ecosystem services that are essential for human well-being, such as carbon sequestration, biodiversity conservation, and water regulation (Sala et al., 2017). However, changing climatic conditions and unsustainable rangeland practices, such as intensive livestock grazing, are threatening these ecosystems worldwide (Asner et al., 2004; Criado et al., 2020; Cipriotti et al., 2019; Stevens et al., 2017). In many African savannas, intensive grazing has contributed to shrub encroachment and widespread degradation of savanna systems (Nacoulma et al., 2011; Olbrich et al., 2012). Climate change poses a significant risk to savannas, exacerbating the challenges they already face. It particularly intensifies water scarcity and diminishes their resilience, ultimately affecting local communities who depend on these ecosystems for their livelihoods (Criado et al., 2020; Egoh et al., 2012). To ensure the continued provision of these critical ecosystem services, it is essential to implement sustainable land management practices that balance human needs with conservation goals. For example, shifting from livestock production to integrated wildlife systems can contribute to restoring degraded rangelands, recovering threatened wildlife populations, conserving biodiversity, and potentially providing higher economic returns than cattle production (Reid, 2007; Richardson, 1998). While the potential consequences of this shift on ecosystem properties and processes are unclear, it is known that the interaction between herbivores, vegetation composition, and climate plays a crucial role in the structure and resilience of savanna ecosystems (Asner et al., 2009; Knegt et al., 2008). Therefore, a shift to wildlife may be beneficial in promoting ecosystem resilience and maintaining crucial ecosystem services.

In this context, it is critical to understand the complex interplay between herbivores, functional vegetation composition, and climatic conditions in savanna ecosystems. However, there is a significant gap in knowledge as the combined impact of different rangeland management types, functional diversity, and climate change has not been extensively studied in modelling research. This thesis aims to contribute to this knowledge by investigating the effects of different rangeland practices on savanna ecosystem properties and processes under current and future climate using an ecohydrological simulation model. To achieve this, I developed new modelling tools to investigate how diverse herbivorous wildlife communities mitigate negative effects of climate change on savanna landscapes. The findings of this study can inform rangeland management strategies that aim to promote the long-term sustainability of savanna ecosystems and the well-being of local communities that depend on them.

1.1 Savanna ecosystems

Savanna biomes cover about 20% of the Earth's surface (Sankaran et al., 2005) and are found in a range of climates, from tropical to subtropical, primarily in Africa, South America, Australia, and India (Figure 1.1a, Beck et al., 2018).

Among these regions, southern Africa stands out due to its extensive savannas, which cover approximately 60% of the land surface (Lehmann et al., 2011; Scholes and Archer, 1997), encompassing the countries of South Africa, Namibia, Botswana, Angola, Mozambique, Zimbabwe, and Zambia.

The savannas of southern Africa experience a high degree of variability in rainfall, with most of the precipitation occurring in the summer months (November to April) (Scholes and Archer, 1997). This strongly influences ecosystem processes and leads to strong seasonal cycles in plant growth and primary productivity, which determines the distribution of plant and animal species (D'Odorico and Bhattachan, 2012).

Southern African savannas are characterised by their high species richness, with over 5,000 plant species identified in the region (Rutherford et al., 2006). Savannas are dominated by two vegetation types: woody and herbaceous plants. Woodland savannas are characterised by a discontinuous layer of trees and shrubs, with grasses forming the understory. Grassy savannas are dominated by grasses, with few trees present (Scholes and Archer, 1997). The region supports a diverse range of wildlife, including large herbivores such as elephants, giraffes, and zebras, as well as predators like lions, hyenas, and cheetahs. These animals play important roles in shaping the structure and functioning of savanna ecosystems, through their effects on vegetation, nutrient cycling, and ecosystem processes such as fire (Knegt et al., 2008). Vegetation, in turn, fulfils vital ecosystem functions by stabilising dryland ecosystem dynamics through various mechanisms (Tietjen et al., 2017), including erosion prevention (Browning et al., 2012; D'Odorico and Bhattachan, 2012), impacts on soil structure and microorganisms (Srikanthasamy et al., 2022), and regulation of the water cycle (Scheffer et al., 2005; Tietjen et al., 2010).

In savannas, the relationship between climate, vegetation and herbivores is complex and interdependent. Grazing herbivores can benefit trees by reducing grass competition and limiting fire, while browsing herbivores consume trees and limit their recovery from fire (Staver et al., 2021). Herbivore feeding decisions are influenced by risk and resource trade-offs, such as the trade-off between accessing high-quality food resources, which may be located in areas with high risks, such as increased exposure to predation or reduced access to water. This trade-off influences the spatial patterns of herbivory, where herbivores may select areas with lower risks but lower-quality resources, or areas with higher risks but higher-quality resources. These trade-offs ultimately shape the distribution and composition of vegetation and herbivores in the savanna ecosystem (Donaldson et al., 2022).

Changes in vegetation composition due to herbivores can have significant implications for the value and usability of savanna ecosystems for human populations, particularly in Africa, where many rely on agriculture and livestock production as a primary source of income (Ryan et al., 2016). In fact, many savannas are used as rangelands, which are defined as areas of potential native vegetation primarily composed of grasses, grass-like plants, forbs, or shrubs that serve as a source of forage for domestic grazing or wild animals (Eldridge and Beecham, 2018; Kaufmann and Pyke, 2001). Although rangelands produce a wide range of ecosystem services, only a small number of them are commercially valuable (Sala and Paruelo, 1997). For instance, rangeland products like meat and wool have a market value, but other ecosystem services like regulating, cultural, and sustaining services typically do not (Figure 1.3), even though it is possible to infer an estimate of their value indirectly (Sala et al., 2017).

1.1.1 The threat of savanna degradation

While herbivores and climate variability have a consistent impact on savannas, these biomes are becoming increasingly vulnerable to human activities, including agriculture, urbanisation, and mining, as well as the impacts of climate change (Criado et al., 2020; Dougill et al., 1999; Egoh et al., 2012).

Unsustainable Rangeland Management: Impact on Vegetation and Ecosystem Functioning

Unsustainable rangeland practices, such as overgrazing and conversion of savanna lands to agriculture, have led to widespread degradation and loss of biodiversity (Pfeiffer et al., 2019; Pringle et al., 2007; Scholes and Archer, 1997). Shrub encroachment, the change in vegetation community composition from perennial grasses to shrubs and trees, has affected 10-20% of drylands globally, with regional variations depending on the methods used for assessment (Eldridge et al., 2011). In South Africa, shrub encroachment has impacted 25% of rangelands (O'Connor et al., 2014), and research suggests that significant changes in tree cover will continue to occur throughout Africa (Buitenwerf et al., 2012; Moncrieff et al., 2014). Similarly, the loss of biodiversity and ecosystem services corresponds to a value exceeding 10% of the annual gross products worldwide (IPBES and Willemen, 2018).

Shrub encroachment is a major trend in livestock-dominated savannas globally, particularly where fire is suppressed (Stevens et al., 2017; Zeidler et al., 2002). Cattle's preference for grasses and other herbaceous plants can cause shrub encroachment by releasing woody species from competition for water and light (February et al., 2013). Furthermore, grazing cattle can benefit woody plants by distributing their seeds and lowering the fuel burden, reducing fire frequency and intensity and increasing woody plant recruitment (Briske, 2017). This change towards shrubland is typically accompanied by a shift from perennial to annual grasses (Schlesinger and Jasechko, 2014; Seely and Jacobson, 1994) or from palatable to less palatable species (Milton et al., 1994; Schlesinger and Jasechko, 2014). Grazing has a significant impact on vegetation composition and diversity and on how well a semi-arid savanna ecosystem functions (Eldridge et al., 2013; O'Connor, 1998). Grazing intensification is associated with a loss of taxa, functional traits and within-trait diversity (Chillo et al., 2017). In addition to removing biomass, grazers have the potential to influence ecosystems through a range of mechanisms. They reduce soil porosity through trampling, which reduces soil water infiltration or percolation (Eldridge et al., 2022). Additionally, grazer faeces can change soil carbon and nitrogen storage as well as nutrient availability (Metzger et al., 2005). The reduction in grass biomass in combination with altered soil structure and nutrient composition can result in more bare and unstable dry soil surfaces (Washington-Allen et al., 2010) with negative consequences for plant diversity and ecosystem services such as soil conservation, water regulation, and carbon sequestration (Maestre et al., 2022; Sala and Maestre, 2014).

Climate change: Impacts on vegetation and water availability

In addition to being vulnerable to rangeland management practices, savannas are particularly sensitive to significant fluctuations in water availability which makes them highly vulnerable to the impacts of climate change.

While temperatures are expected to rise with high certainty, the direction of precipitation change remains uncertain (Figure 4.1) due to the limitations of current climate models and challenges in accurately representing complex processes such as land use change and land-atmosphere interactions (Schulze, 2011). Climate forecasts indicate that regions that are already arid or semi-arid, such as Namibia, Tanzania and Zambia, are projected to experience even greater aridity with an increase in the frequency and intensity of extreme weather events, such as droughts (Dai, 2013; Tadross et al., 2017). In contrast, more humid areas are expected to experience increased precipitation, which could lead to more floods or longer dry spells (IPCC (2022), Figure 1.1b). The resilience of savannas is expected to be affected by climate change, as it increases the frequency and intensity of extreme weather events, such as droughts (Dai, 2013; Tadross et al., 2017). The unpredictability of future water availability is a major concern, as the timing and magnitude of precipitation events have a significant impact on soil moisture and important processes such as growth, mortality, and establishment (Lohmann et al., 2012). Climate change is already leading to changes in temperature and precipitation patterns that in most cases result in increased aridity, decreased soil moisture, and altered groundwater recharge rates in savannas (IPCC, 2022). Variations in temperature and precipitation directly impact the amount of evapotranspiration and quantity of runoff. As a result, changes in temperature can considerably modify the spatial and temporal availability of water resources or the water balance (Kusangaya et al., 2014).

These changes, in turn, have significant impacts on the vegetation cover and structure, as well as the overall ecosystem productivity and biodiversity (Li et al., 2021). For example, prolonged droughts lead to severe dieback of grasses and reduced vegetation cover, which

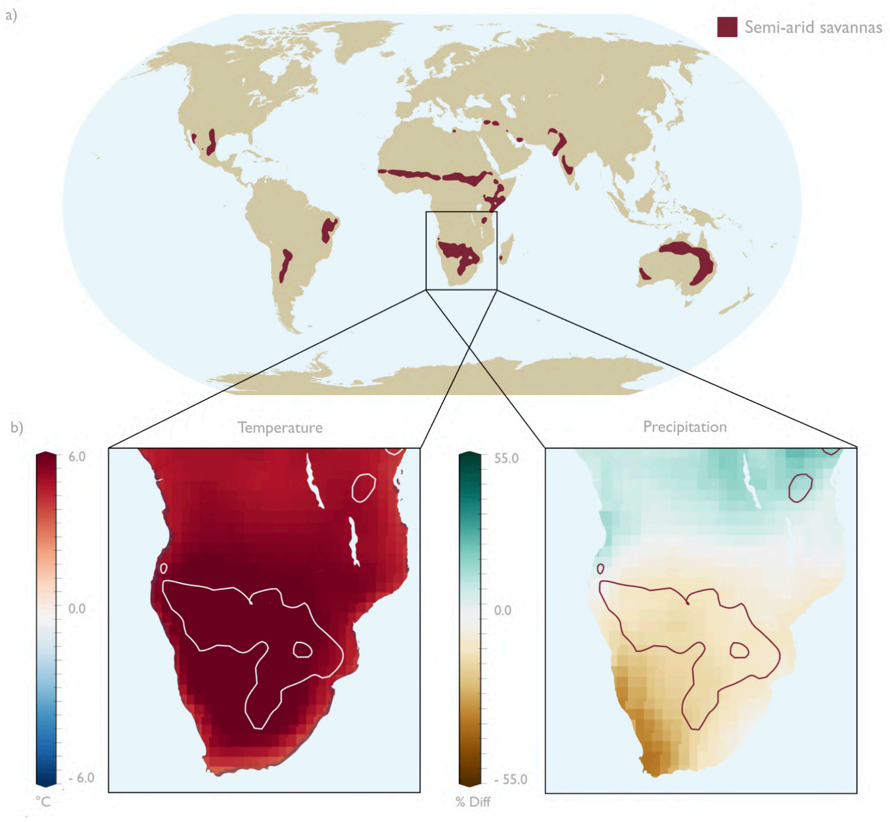


Figure 1.1: Semi-arid savannas and projected climate change. The top panel (a) presents the global distribution of semi-arid savannas (in red), which are also highlighted in the middle panels, representing southern Africa. The middle panels (b) demonstrate the projected changes in temperature (left, in °C, projected by 34 models) and precipitation (right, in %, projected by 33 models) under the SSP5-8.5 scenario with 2°C warming for 2080-2100 in southern Africa. Adapted from: IPCC Interactive Atlas (Gutiérrez et al., 2021).

can increase soil water losses, soil erosion rates and decrease soil nutrient availability (Dai, 2013; Derner and Augustine, 2016; Dong et al., 2019). As a consequence, juvenile shrubs and seedlings may benefit from reduced grass cover and above-average precipitation in consecutive years, which can lead to episodic mass recruitment of woody species (Buitenwerf et al., 2011; Joubert et al., 2008).

In periods of intense rainfall, the soil texture, structure, and roughness can determine the amount of water lost through runoff or deep infiltration (Fensham et al., 2005; Tietjen et al., 2010). Besides, increased rainfall variability leads to altered plant species and functional composition and changes in the timing of plant growth and reproduction, potentially affecting the food webs and interactions within the ecosystem (Inouye, 2022). These changes will have far-reaching consequences in the future, including decreased functional diversity and the potential extinction of plant species. Since plant functional diversity is associated with higher resilience to disturbances or environmental change (Pettorelli et al., 2019), a decline can cause severe impacts on ecosystem health, necessitating the implementation of additional and costly management interventions.

Climate change can cause changes in savanna vegetation, but poor grazing management can increase the likelihood of transitioning to an undesirable and irreversible state. Previous research has overlooked the combined effects of rangeland use and climate change or droughts of varying durations, despite their potential impact on savanna ecosystems (Smith et al., 2013; Wigley-Coetsee and Staver, 2020). This knowledge gap is concerning because understanding how these factors contribute to savanna decline is crucial for preventing further degradation.

1.2 Wildlife-based management strategies in savannas

Conservation efforts are necessary to protect savannas and the many ecosystem services they provide to both humans and wildlife. As land management plays a crucial role in preserving the health and resilience of savanna ecosystems, alternative and sustainable land use strategies must be explored. One promising approach is to explore the potential of wildlife as a valuable resource in these regions. In response to the widespread environmental degradation and challenges posed by climate change, many southern African countries are shifting from livestock production to integrated wildlife systems (Brodie et al., 2013; Richardson, 1998). The shift towards wildlife management is driven by its potential ecological and economic value (Figure 1.3). For example, the integration of wildlife into management can aid to restore degraded rangelands, recover threatened wildlife populations, and conserve biodiversity (Adeel

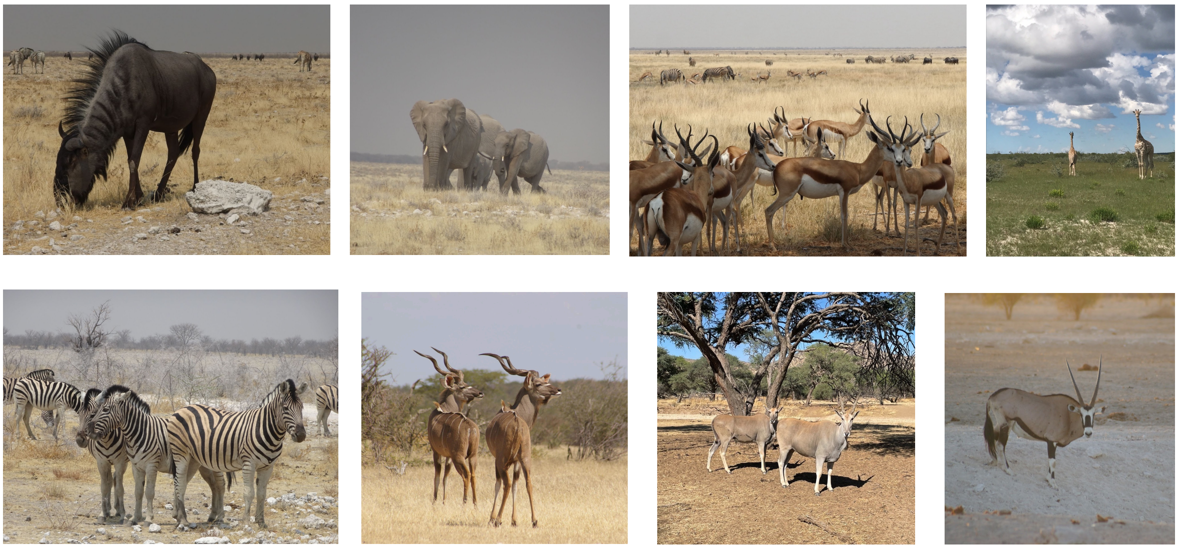


Figure 1.2: Common wildlife species found in southern African rangelands.

et al., 2005; Holechek and Valdez, 2018). Moreover, wildlife is better adapted to unfavourable climatic conditions and resistant to endemic diseases compared to cattle, making it a more lucrative option (Cleaveland et al., 2009). The diversity of wildlife in savanna ecosystems is not only ecologically important but also economically valuable due to its attractiveness for tourism-related activities (Richardson, 1998). Furthermore, managed wildlife can be used as a tool for vegetation management and fuel load reduction (Egoh et al., 2012; Briske et al., 2017), making it a potential alternative to traditional grazing methods. Native herbivores, in contrast to domestic cattle, exhibit greater diversity (Figure 1.2) and have co-evolved with savanna vegetation, resulting in a variety of feeding behaviours such as grazing, mixed-feeding, and browsing (Kartzinel et al., 2015). The flexibility and balance in the utilisation of biomass by mixed herbivore communities can improve ecosystem functioning by promoting the survival of a more diverse range of plant species and, as a result, maintain a functionally important composition (Bothma and du Toit, 2016; Veblen et al., 2016). Therefore, shifting from livestock to wildlife-based land management is a promising approach to preserve savanna ecosystems and their ecosystem services, restore degraded rangelands, and offer economic and tourism-related benefits.

Nevertheless, further research is needed to understand the long-term effects of reintroducing wildlife on rangelands on savanna plant communities, especially the role of browsing herbivores in altering plant communities' composition and abundance. Recent studies demonstrated that reducing grazer densities and using mixed or browsing wildlife increased habitat use and enhanced ecosystem resilience (Brodie et al., 2013; Wells et al., 2022). For instance, decreasing livestock densities has been shown to contribute to faster recovery after extended droughts (Tommasino et al., 2023). Given these findings, further exploration of the role of wildlife in maintaining ecosystem functioning under climate change is particularly promising.
In light of the changing environmental conditions, it is imperative that we develop effective conservation strategies for the future. One useful tool to test different management and climatic scenarios is through models.

1.3 Rangeland ecology and simulation models

Process-based models are a type of simulation model that incorporate detailed mathematical representations of the biological, physical, and chemical processes that govern ecosystem dynamics. Such simulation models are a valuable tool in rangeland ecology because they can test various management scenarios, climate conditions, vegetation composition, and different

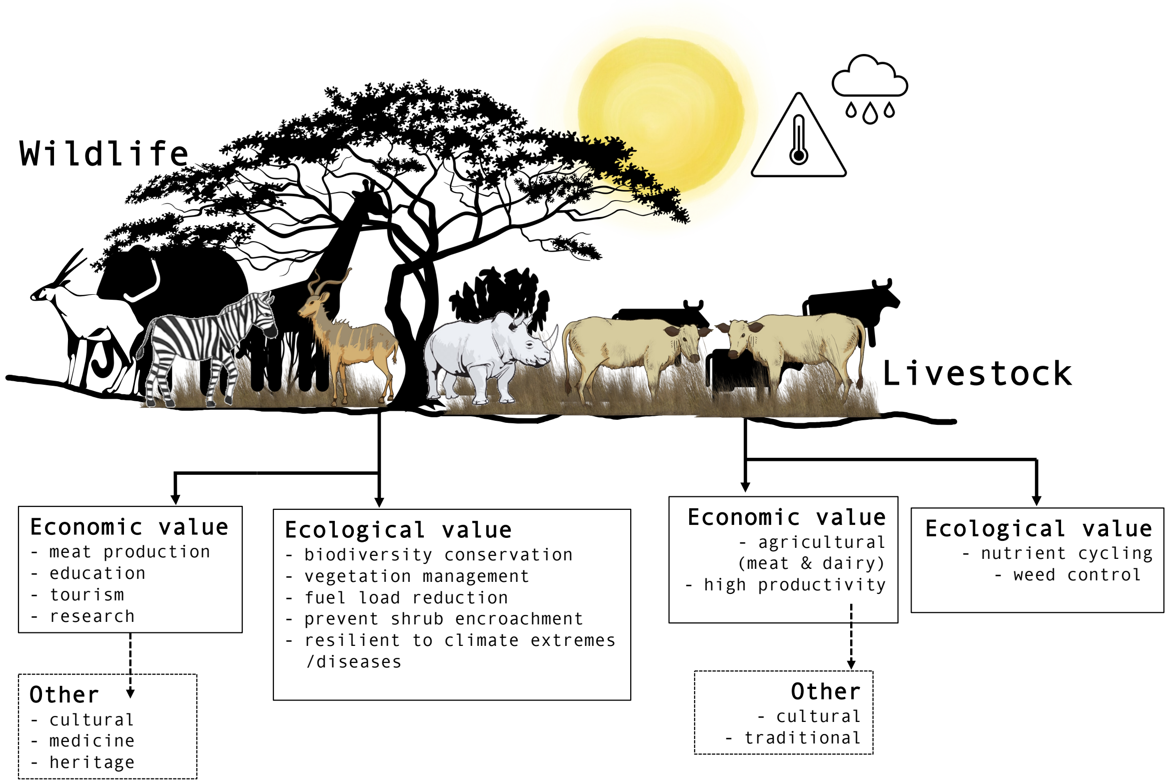


Figure 1.3: The economic and ecological value of different rangeland management types in savanna ecosystems.

temporal scales (Cuddington et al., 2013).

First, simulation models can provide a way to predict how different management strategies, such as grazing intensity (Guo et al., 2016; Holdo et al., 2009; Petz et al., 2014) or the use of prescribed fires (Lohmann et al., 2014; Langevelde et al., 2003) will impact rangeland ecosystems over time, before implementing them in the field, especially under different climatic conditions (Scheiter et al., 2019). This can help managers make more informed decisions and avoid unintended negative consequences, which is particularly important for developing adaptation strategies under future climate conditions. Second, simulation models can be used to explore different vegetation composition scenarios. By modelling the impacts of different plant species on rangeland ecosystems, researchers can assess the potential benefits and drawbacks of introducing new species or removing existing ones (Laughlin and Laughlin, 2013). This can be especially relevant for identifying functionally important species, managing invasive species or restoring degraded rangelands (Lavorel et al., 2013). Lastly, simulation models can help researchers investigate how rangeland ecosystems respond over long time frames. Looking at different temporal scales can be useful for understanding how rangeland ecosystems might evolve in response to slow natural or human-induced changes over time, such as climate change.

While process-based models have advanced our understanding of rangeland ecosystems, there are still gaps and limitations in our current models that need to be addressed. Firstly, although many modelling studies have investigated the impact of livestock grazing on several ecosystem parameters of drylands (Guo et al., 2016; Kiker and Scogings, 2019; Koomen and Borsboom-van Beurden, 2011; Metzger et al., 2005; Müller et al., 2007; Pachzelt et al., 2013; Pfeiffer et al., 2019), very few also analysed the impact of browsing animals (Holdo et al., 2009; Knegt et al., 2008; Langevelde et al., 2003). In this context, no modelling study has directly compared the effects of rangeland use by grazer, browser, or mixed-feeding herbivores on plant functional composition and associated ecosystem processes and properties, particularly related to soil hydrology. Second, many studies have incorporated broad vegetation classifications known as plant functional types (PFTs), such as the grouping of woody and herbaceous vegetation into single functional groups, that fail to capture the variety within each group (Pappas et al., 2016). Finally, no study has combined a small-scale hydrological model with vegetation dynamics to examine the impact of various regional climate change projections on the entire ecosystem, particularly under different rangeland management options to support the development of regional climate change adaptation plans, such as possible drought mitigation.

1.4 Objectives and structure of the thesis

Modelling studies play a crucial role in developing sustainable management plans and can inform decision-making by identifying knowledge gaps and providing insights into the complex interactions between vegetation, soil, and climate. The aim of this thesis is to mechanistically understand the effects of wildlife management on plant composition, ecosystem functions and services under a range of climatic conditions in a Namibian savanna using an ecohydrological model. (Figure 1.4). This will serve as an example for semi-arid savannas worldwide, both under current and future climates. Specifically, this thesis aims to identify strategies that promote the provision of multiple ecosystem functions and services in semi-arid savanna ecosystems in the face of changing climatic conditions, by:

1. investigating the effect of herbivore types and densities on plant community structure and composition (Chapter II)
2. identifying the impact of plant diversity on the resilience of semi-arid savanna ecosystems (Chapter III, IV)

3. evaluating the combined potential of herbivore communities and plant diversity in enhancing the resilience of semi-arid savanna ecosystems in the face of current and future climate challenges (Chapter IV)

4. developing recommendations for practical management applications (Chapter V).

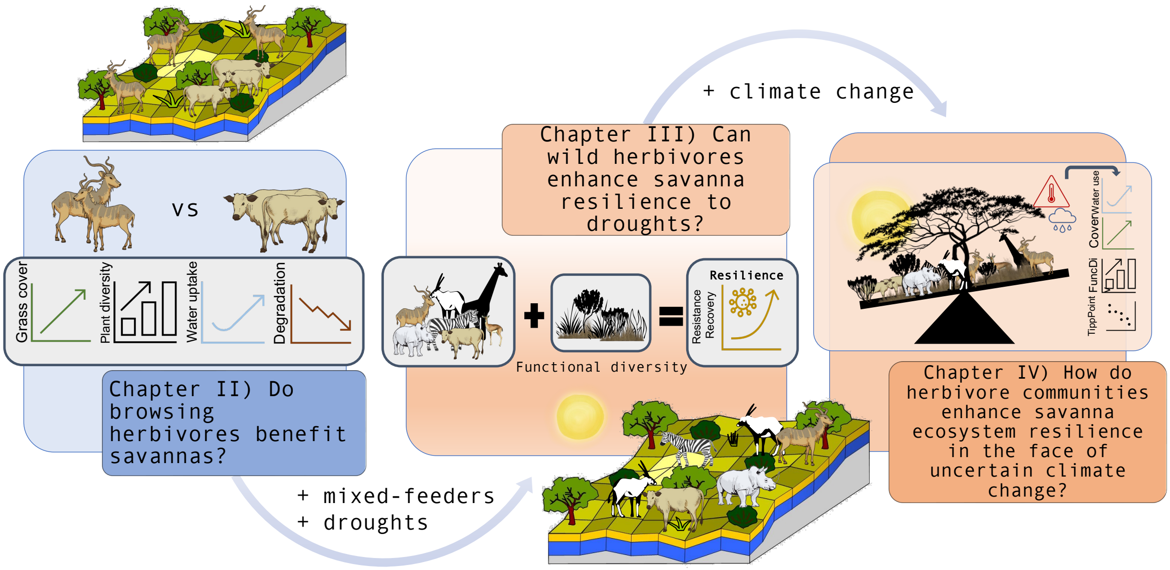


Figure 1.4: The three studies presented in Chapters II-IV explore various ecosystem functions in relation to different herbivore management strategies under current (blue, Chapter II), extreme (orange gradient, Chapter III) and future climate conditions (orange, Chapter III and IV). The regarded outputs were related to different aspects of ecosystem functions, in II) cover, composition, biodiversity and plant water use; III) cover, resistance and recovery of grass cover, vegetation composition and functional diversity; IV) cover, functional dispersion, water use efficiency and tipping points.

In Chapter II, I investigated how different herbivore grazing and browsing strategies affect plant functional diversity and ecosystem functioning under current climate (published as Irob et al., 2022 in *Ecology & Evolution*). My results revealed that herbivore grazing has a negative impact on both plant diversity and water availability. Specifically, I found that rangelands dominated by browsing herbivores could sustain higher total vegetation cover under the same amount of rainfall, which has positive implications for plant water use.

Despite the promising findings regarding the benefits of browsing herbivores, there remain knowledge gaps in understanding the effects of more diverse wildlife animals that exhibit a wider range of feeding behaviours. Therefore, the outcomes may vary under different herbivore communities, as well as under expected climate changes and extreme events, such as prolonged droughts.

In Chapter III (published as Irob et al., 2023 in the *Journal of Applied Ecology*) I investigated the potential impacts of droughts on the negative effects of grazing in savanna ecosystems. Specifically, I examined how droughts affect the resilience of these ecosystems and the role of a dynamic range of herbivore composition and plant functional diversity in promoting resilience. To achieve this, I extended an existing herbivory algorithm to incorporate a more diverse range of herbivores, each with a certain degree of dietary flexibility. The study revealed that high grazing intensity can significantly reduce the ability of perennial grasses to withstand drought-induced loss of plant cover and recover afterwards. However, maintaining a diverse herbivore population, including a high proportion of browsers and diverse plant strategies increased resistance and recovery even under extended droughts.

To capture the full picture of the impacts of climate change on savanna ecosystems, it is important to recognise that droughts are only one aspect of a much larger problem. Addressing climate change as a whole, including changing precipitation patterns, temperature increases, and droughts, is essential for ensuring the long-term resilience and sustainability of these ecosystems. In Chapter IV (currently under revision in the *Journal of Applied Ecology*), I investigated the potential of using wild herbivore communities as a local management strategy to adapt to uncertain climate change projections, such as alterations in precipitation, temperature, and droughts. My research revealed that climate change in combination with unsustainable rangeland management often results in reduced vegetation cover, lower functional diversity, reduced water use efficiency, and faster tipping points. However, I demonstrated that these effects can be mitigated by diversifying animal populations and reducing animal densities. This highlights the potential for effective rangeland management strategies to enhance ecosystem resilience and minimise the risk of irreversible degradation, even in the face of high uncertainty in climate.

Lastly, in the general discussion, I synthesise the information presented in Chapters II to IV. Specifically, I will address the following questions:

1. How do herbivore communities shape plant communities in semi-arid savanna ecosystems?
2. What positive effects does plant diversity have on the functioning of semi-arid savanna ecosystems?
3. How can wildlife management and plant diversity enhance the resilience of semi-arid savanna ecosystems in the face of current and future climate challenges?

2

Browsing herbivores improve the state and functioning of savannas: A model assessment of alternative land-use strategies

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Abstract Changing climatic conditions and unsustainable land use are major threats to savannas worldwide. Historically, many African savannas were used intensively for livestock grazing, which contributed to widespread patterns of bush encroachment across savanna systems. To reverse bush encroachment, it has been proposed to change the cattle-dominated land use to one dominated by comparatively specialised browsers and usually native herbivores. However, the consequences for ecosystem properties and processes remain largely unclear. We used the ecohydrological, spatially explicit model EcoHyD to assess the impacts of two contrasting, herbivore land-use strategies on a Namibian savanna: grazer- versus browser-dominated herbivore communities. We varied the densities of grazers and browsers and determined the resulting composition and diversity of the plant community, total vegetation cover, soil moisture, and water use by plants. Our results showed that plant types that are less palatable to herbivores were best adapted to grazing or browsing animals in all simulated densities. Also, plant types that had a competitive advantage under limited water availability were among the dominant ones irrespective of land-use scenario. Overall, the results were in line with our expectations: under high grazer densities, we found heavy bush encroachment and the loss of the perennial grass matrix. Importantly, regardless of the density of browsers, grass cover and plant functional diversity were significantly higher in browsing scenarios. Browsing herbivores increased grass cover, and the higher total cover in turn improved water uptake by plants overall. We concluded that, in contrast to grazing-dominated land-use strategies, land-use strategies dominated by browsing herbivores, even at high herbivore densities, sustain diverse vegetation communities with high cover of perennial grasses, resulting in lower erosion risk and bolstering ecosystem services.

2.1 Introduction

Savannas are woodland-grassland ecosystems that provide multiple ecosystem services, including the provision of food and clean water, sequestration of carbon, preservation of biodiversity, and recreational opportunities (Sala et al., 2017). Due to highly variable rainfall and low water availability in semi-arid savannas, agriculture is not feasible; therefore, commercial livestock are a major source of income (Adeel et al., 2005). Extensive livestock production offers some flexibility to adapt to demanding and variable environmental conditions and provides household security in drought years (Barrett, 1992; Olbrich et al., 2012). Nevertheless, farmers must balance economic sustainability and ecological capacity of a rangeland (Smet and Ward, 2005), and unsustainable land use has caused severe and widespread degradation. A major pattern in livestock dominated savannas (especially those where fire is suppressed) is bush encroachment, the undesirable change in vegetation community composition from perennial grasses to woody shrubs and trees (Zeidler et al., 2002). Bush encroachment is thought to result from cattle's preferential feeding on grasses and other herbaceous plants, which releases woody species from resource competition. Additionally, grazing livestock can benefit woody plants by dispersing their seeds and by removing the fuel load, thereby reducing fire frequency and intensity, enhancing woody plant recruitment (Briske, 2017). This shift toward shrubland is usually accompanied by a shift from perennial to annual grasses (Schlesinger and Jasechko, 2014; Seely and Jacobson, 1994) or from palatable to less palatable species (Milton, 1994).

The bush encroachment within savanna systems also implies changes in important ecosystem functions. Reduced cover of herbaceous vegetation leads to increased water losses and consequently accelerated soil erosion (Archer et al., 2017), as surface water runoff is enhanced due to the lower surface roughness and reduced infiltration in such areas (Tietjen et al., 2010). In general, the water cycle can be strongly altered, as woody species extract water from deeper layers (Case et al., 2020) and at the same time alter infiltration, soil water storage, transpiration, interception, and subsurface pathways that affect groundwater recharge (Acharya et al., 2018). The resultant reduced water availability puts further pressure on the performance of grasses and leads to decreases in forage quality and productivity per unit area (Egoh et al., 2012; Schlesinger and Jasechko, 2014).
Furthermore, climate change is projected to exacerbate the impact of unsustainable land use and is likely to exert a strong impact on ecosystem functions of savannas (Criado et al., 2020; Hoffmann et al., 2002; Jackson et al., 2002; Reid, 2007). The projected cooccurrence of more frequent and intense climatic extremes (i.e., droughts) and warmer climate (Shukla et al., 2019) with heavy grazing might lead to a decrease in overall rangeland productivity and biodiversity to an extent that is economically unsustainable and cannot be ecologically reversed without interventions (Abraham et al., 2019; Milton et al., 1994; Polley et al., 2017).

Responding to widespread environmental degradation and in anticipation of future challenges imposed by global change, many southern African countries have started to shift from livestock production to integrated wildlife systems, such as game hunting or conservancies, as the use of wildlife can contribute to restore degraded rangelands, lead to recovery of (threatened) wildlife populations, and conserve biodiversity (Adeel et al., 2005; Holechek and Valdez, 2018; Langholz and Kerley, 2006; Richardson, 1998). Moreover, native wildlife potentially lead to higher yield in economic returns, given that they are better adapted to unfavourable climatic conditions and more resistant to endemic diseases than cattle (Cleaveland et al., 2009). Furthermore, wildlife does not only offer an alternative for red meat production and other consumptive uses, but its unique diversity is also attractive for tourism-related activities (Richardson, 1998). Despite the current trend toward more wildlife-based land management, there are still major research gaps on the effects of managed wildlife on vegetation composition, resulting plant functional diversity and related ecosystem functions, specifically compared to the impacts of cattle. In the past, large browsers have been shown to be a successful management tool, especially when combined with other management measures, such as prescribed fires, because they reduce the competitive effect of trees on grasses and affect fuel load (Holdo, 2007; Holdo et al., 2009; Langevelde et al., 2003). Compared to domestic cattle, native herbivore communities include a broad range of animal species of different sizes and feeding preferences. Their ability to feed on various parts of herbaceous and woody plant species can result in an overall more flexible and also balanced use of primary production and might have important implications for vegetation cover and its plant functional diversity as well as resulting feedbacks with ecosystem functions and services. However, the long-term effects of rewilding on savanna plant communities, and in particular the role of browsing herbivores, remain unclear (Butt and Turner, 2012; Gitau, 2009; Richardson, 1998). Hence, the question arises whether native herbivores that have co-evolved with savanna vegetation and that feature a variety of feeding behaviors can alter the composition and abundance of plant communities, which could also potentially have positive impacts on ecosystem functioning (Holechek and Valdez, 2018; Polley et al., 2017; Volder et al., 2010).

With this study, we aimed to compare impacts of two different herbivory types (grazing and browsing animals) on total plant cover, functional composition and diversity, and selected ecosystem functions. For this, we evaluated both extreme ends of the grazing-browsing gradient within herbivore communities to span the widest possible range, but also allowed for some intake of the other vegetation type to account for some flexibility in herbivory diet under unfavourable conditions, when the preferred fodder type is limited.

We parameterised our simulation model using a Namibian savanna. This question is particularly relevant to Namibia because transitions from livestock to wildlife are being incentivized by governmental initiatives (Government of the Republic of Namibia, 2014; Jones, 2015; Lindsey et al., 2013).

Modelling land use by grazing livestock and its effects in drylands is a very common practice (Kiker and Scogings, 2019; Koomen and Borsboom-van Beurden, 2011), but only very few studies included also the removal of woody vegetation by browsers (Holdo et al., 2009; Knegt et al., 2008; Langevelde et al., 2003).

So far, no modeling study has attempted to directly compare the effects of land use by grazer- with land use by browser-dominated animal communities on plant functional composition and related ecosystem processes and properties, especially related to soil hydrology. Another limitation of many of these studies is that they only included broad vegetation categories, so called plant functional types based on broad plant functional groups (PFTs), without considering the great diversity within these groups (e.g., by implementing distinguishable subtypes) (Pappas et al., 2016). However, ecosystem responses to altered drivers cannot necessarily be adequately captured when plants are grouped into very broad types, without recognising that plant communities respond to local environmental conditions by adapting their traits, as existing simulation studies on ecosystem responses toward grazing could show (Guo et al., 2016; Lohmann et al., 2018).

Here, we built on the approach of the aforementioned studies and use the ecohydrological model EcoHyD (Guo et al., 2016; Lohmann et al., 2012; Tietjen et al., 2009, 2010) to compare the effects of grazing and browsing herbivores on the plant community composition of a savanna system and on selected resulting ecosystem properties and functions. For this, we applied a range of grazing and browsing scenarios (either dominated by grazing or browsing herbivores) to a Namibian rangeland that has been transformed from a livestock farm to a private game reserve. Our grazing scenarios allowed almost no browsing, whereas feeding in the browsing scenario occurs more selective but with a strong preference on woody vegetation. We implemented several subtypes of three broad PFTs, namely shrubs, perennial grass vegetation, and annual grass vegetation, which followed different plant life strategies (in the following called strategy types) that are characterised by specific adaptations to environmental conditions and their trade-off.

In particular, we addressed the following three questions: (i) How does plant functional abundance and composition respond to different land-use types and intensities and which plant life strategies prevail under specific herbivore pressure? (ii) How does this affect species richness and species evenness in the community? (iii) Do these changes affect water-related properties, in particular water availability, in the soil and water use by plants?

We hypothesised (i) that this approach would reproduce the well-known phenomenon of bush encroachment, (ii) that browser-dominated communities would maintain a balance between trees and grasses due to the reduced herbivory pressure on grasses, and (iii) that browsers would positively affect biodiversity and (iv) improve water uptake by plants, altogether supporting higher grass cover.

Altogether, this study illustrates the most sustainable land management strategies to avoid soil degradation and preserve crucial ecosystem services in the long term.

2.2 Methods

2.2.1 Study area

The private wildlife reserve Etosha Heights in Namibia (S19.1554° E15.1705°) was established in 2002 when the transformation of eight cattle farms took place, opening the farm boundaries and merging the farms into one entity, which is now the Etosha Heights Private Reserve. Since then, Etosha Heights was used as a game hunting lodge until 2016 when the management was changed to tourism activities and conservation research. It is now one of the largest private game reserves that offers robust conservation of wildlife (Nortjé, 2019).

Etosha Heights covers an area of 48,000 ha on the southwestern border of Etosha National Park for about 68 km in distance. The reserve lies at 1195 m and varies between hilly patches and open plains. The site selected for this study shows little variation in topography. Precipitation is highly variable and occurs mainly during the summer months from October to April. We retrieved mean climate data from a local station and could determine a mean annual precipitation (MAP) of 298.67 ± 30.20 mm and a mean annual temperature (MAT) of 26°C, with its lowest value in June (mean of 19°C) and its highest in October (mean of 29°C). Most of the soils at Etosha Heights can be classified as "Coega" soils or Petric calcisols (Nortjé, 2019). The soil type of our study site was loamy sand.

Etosha Heights shows a very diverse landscape with many different habitats. The eastern part is patched with hills covered by mopane trees (*Colophospermum mopane*), general mopane-veld, and open plains. The central part contains a hilly mountain range covered by a mixed habitat which is dominated by *Terminalia, Combretum*, and Commiphora species. In the west, the habitats consist of patches of mopane and acacia species.

2.2.2 Model description

We used the ecohydrological, spatially explicit dryland model EcoHyD, which is based on Tietjen et al. (2009, 2010) and was extended by a component for cattle grazing by Lohmann et al. (2012) and by a higher resolved description of plant diversity by Guo et al. (2016) and Lohmann et al. (2018). We simulated a total area of 2.25 ha consisting of 30×30 grid cells, with a 5×5 m^2 resolution. The model has been applied and validated to several dryland ecosystems in previous studies (Lohmann et al., 2012; Tietjen et al., 2009).

The model consists of two dynamically linked process-based submodels: a vegetation submodel and a hydrological submodel. These submodels and selected processes relevant to this study are briefly described in the following, while a comprehensive model description and model parameters can be found in Appendix A.1.

The vegetation submodel simulates the fate of various functional types (strategy types) that belong to one of three broad PFTs (meta-PFTs), namely shrubs, perennial grass vegetation, and annual grass vegetation. These strategy types differ in their traits, but follow the same processes defined by their respective meta-PFT. The fate of each strategy type is calculated with a biweekly resolution during the wet season, which starts and ends with the first and last rain event of 5 mm/day or more during summer. Vegetation dynamics are driven by processes such as growth, mortality, competition for water and space, dispersal and establishment of seeds and seedlings, and herbivory by grazing and browsing herbivores (see section "Grazing and browsing herbivory"). Although we acknowledge that fires can also be an important driver of savanna dynamics, we did not consider fires in this analysis, as they do not occur frequently at our study site and are usually suppressed. Plant dynamics are directly linked to soil water dynamics: growth is linked to transpiration; although dispersal is not directly linked to water, dispersed seeds can only translate into new cover given sufficient water availability; and plant mortality is caused by water scarcity or senescence and is updated at the end of a fixed growing season, which runs from October to April. For grass, we assume spatially uniform dispersal within a simulated area of 150 m^2, while shrub dispersal is restricted to a local dispersal kernel with individual larger dispersal events being facilitated by large herbivores.

The hydrological submodel simulates daily dynamics of surface water and soil moisture in two soil layers. Water dynamics are driven by precipitation, lateral water redistribution of surface water, infiltration, vertical fluxes, and water losses via evaporation and transpiration. Infiltration of surface water into the soil is linked to vegetation cover, as we assumed a positive effect of plant roots on soil porosity. Runoff decreases with increasing vegetation cover, first because of the higher infiltration facilitated by plant roots, and second because of a higher surface roughness delaying the water flow. Water losses are linked to plant root proportion in the two soil layers and to vegetation cover, which decreases evaporation but increases water use by plants and therefore transpiration. Annual grasses only have access to water in the upper soil layer, while perennial grasses and shrubs have access to water in both layers according to their root distribution (Case et al., 2020).

2.2.3 Model input

The model was parameterised to the environmental conditions of Etosha Heights Private Reserve, specifically topography and soil, climatic conditions, and plant species characteristics.

Topography and soil

We added a digital elevation map (DEM) corresponding to the position of the weather station to account for local differences in topography. We retrieved the DEM from the Shuttle Radar Topography Mission (SRTM) (Earth Resources Observation And Science (EROS) Center, 2017) and linearly interpolated it from a resolution of 30×30 m^2 to 5×5 m^2.

We parameterised the soil based on the standard data set of EcoHyD for loamy sandy soils (Rawls et al., 1992). We additionally calibrated selected soil parameters of the hydrological submodel fitted to a 1.5-year time series of soil moisture recorded at Etosha Heights (Figure A.1.4) using the corresponding data on temperature and precipitation of the weather station (coordinates of weather station: S19.245323° E15.1913950°). The station measured soil moisture at 5-minute intervals using sensors (SM150T, Dynamax, UK) in three depths ($10, 50, 100$ cm) under woody cover and in open plain. These soil parameters included residual water content and wilting points of soil and plants, as well as the evaporation constant accounting for reduced evaporative losses in the presence of soil crusts. We set vertical fluxes by diffusion to zero, as the measured data suggest that pore size is too high to allow for capillary transportation by suction (Nimmo, 2013). Furthermore, as the measured soil moisture data showed almost no response of soil moisture in the deeper soil to precipitation input and remained rather constant over time, we only allowed very little diffusion from the upper to the lower soil layer. Parameter values were chosen by determining the lowest root mean square error ($RSME$) when comparing measured and simulated soil moisture data after a local sensitivity analysis ($RSME = 1.092$).

Precipitation and temperature of the simulation experiment

As vegetation dynamics can be sensitive to rainfall conditions and savannas are exposed to highly variable precipitation events, we approached the resulting uncertainty by replicating simulation runs with artificial stochastic precipitation time series. We generated stochastic precipitation time series using the precipitation generator NamRain as described by Tietjen et al. (2010) and Lohmann et al. (2012). The time series were based on a precipitation time series from the Tropical Rainfall Measuring Mission (TRMM) (Huffman et al., 2010) measuring precipitation at a three-hourly rate from 1998 to 2014. We compared the time series to five-year long rain gauge data on site and concluded that they closely match. A comparison of monthly distribution showed a correlation coefficient of 0.98 (Spearman's Rho), but rainfall peaks were underestimated to some extent. Other studies using TRMM data for precipitation measurement also found out that TRMM data are a reliable estimation, but daily rainfall values are slightly underestimated compared to rain gauge recordings (Tarek et al., 2017; Yong et al., 2015). We therefore applied a calibration factor of 1.16 to the TRMM data to reduce the deviation from station data. Temperature was fitted according to MAT, yearly, and daily fluctuations. In total, 30 stochastic precipitation time series along with temperature with an hourly resolution were generated. The time series ranged from annual precipitation sums of 53.0 mm to 837.6 mm. The MAP of all climate repetitions was 291.3 mm, and they were highly correlated with the TRMM time series ($R^2 = 0.972$, Spearman's Rho = 0.986)

Assemblage of plant strategy types

Three major PFTs are represented in the model: woody vegetation, perennial, and annual herbaceous vegetation. In this study, these so-called meta-PFTs "woody vegetation" (hereafter referred to as shrubs) and "perennial herbaceous vegetation" (perennials) were further divided into subtypes representing particular life strategies to understand the effects of herbivory on a functionally more diverse plant community. As annual grasses (annuals) only dominate degraded systems (Archer et al., 2017; Case et al., 2020), we did not subdivide them further. We used the standard set of parameters of the meta-PFTs from previous studies (Guo et al., 2016; Lohmann et al., 2018) as starting point for parameterising the subtypes. The basic subtype of each meta-PFT (hereafter called "base type") had the same set of parameters as the original meta-PFT. We then derived additional subtypes (for shrubs and perennials) by defining individual life strategies that show trade-offs in two particular characteristics, but are otherwise the same as the base type. Based on major species found at Etosha Heights (Table 2.1), the simulated tradeoffs in this study include characteristics related to six processes (Tables 2.1 and A.1.1): (i) biomass production B (represented by parameter T_{veg} ; used in Equation A.6), (ii) mortality M (parameter mrd_{veg}; Equation A.8), (iii) palatability P (parameter herbivorePref; Equation A.3), (iv) defence D (parameter edibleFrac; Equation 3), (v) competitive strength for water C (parameter UptakeRate; Equation A.4-6), and (vi) resistance to drought R (parameter WiltingPoint; Equation A.8). A very drought-resistant subtype could for example show a very low biomass production as trade-off.

In order to generate comparable trade-offs for each strategy type, we used a sensitivity analysis, in which we separately determined for each of the six altered parameters, which parameter value led to a cover increase or decrease of 10% in subtype cover compared to simulations with the default parameter value (Figure A.1.4). For this, we evaluated the subtype cover of the last 20 years of 100-year simulation runs. The resulting parameter values were then used to parameterise strategy types with a beneficial value for one parameter and an adverse value for another parameter (Table 2.2).

In the following text and figures, we referred to these strategy types by their strategy name, which always consists of a capital and a lowercase letter, corresponding to the traits listed above. The first capitalised letter refers to the specialisation in a specific property, that is, the trait the plant benefits from by increasing its cover by 10%. The lowercase letter represents its trade-off, which results in a 10% cover decrease (Table 2.2).

Model parameterisation of plant species and sensitivity analysis

We performed a sensitivity analysis for perennial grass vegetation and shrubs to determine which parameter values of the above described strategies resulted in a 10% cover increase or decrease relative to the mean cover of the base type of the respective meta-PFT. However, as the performance of plants is highly dependent on their interactions with other plants, we ran these simulations in presence of other plants: For each parameter related to a specialisation, we have gradually changed its value in a range of up to ± 30 % relative to the default value of the respective base type. The performance (i.e., resulting cover) of this altered type was assessed in a simple plant community consisting of this altered type, the original base type of the same meta-PFT (both with dynamic cover) and the base types of the two other meta-PFTs (both with static cover). We assumed a linear relationship between the parameter value and resulting cover of the altered type. Based on this assumption, we used a linear regression analysis to determine which change in the parameter value results in a +10% or −10% deviation in cover. Only parameters with a significant slope were used for parameterisation.

Table 2.1: Plant life strategies of perennial grasses and shrubs and respective example species at Etosha Heights

Perennials	**Example species**	**Shrubs**	**Example species**
Bd	*Stipagrostis uniplumis*, *Oropetium capense*	Bd	*Grewia olukondae*, *Grewia villosa*

Bp	*Stipagrostis uniplumis*	Bp	*Acacia mellifera, Terminalia prunioides, Terminalia stuhlmannii, Colophospermum mopane*
Cb	*Eragrostis nindensi, Eragrostis trichophora, Bothriochloa radicans*	Bc	*Acacia kirkii s. kirkii v. kirkii*
Cp	*Eragrostis echinochloidea*	Cb	*Asparagus*
Pb	*Eragrostis trichophora, Oropetium capense*	Db	*Asparagus*
Pr	*Bothriochloa radicans*	Dc	*Acacia nebrownii*
Rb	*Eragrostis nindensis, Eragrostis trichophora*	Dr	*Acacia kirkii s. kirkii v. kirkii*
Rp	*Stipagrostis uniplumis*	Mb	*Terminalia pruniodes*
		Rc	*Acacia nebrownii*
		Rd	*Grewia olukondae*

Table 2.2: Parameter settings of perennial grasses and shrubs for the cattle and wildlife scenarios. The table lists the parameter name, how it is referred to in the text and figures, its default value, and the value used for trade-off (Parameter −10%) and specialisation (Parameter +10%).

		Land use by grazers			**Land use by browsers**		
Parameter	Short	Default	−10%	+10%	Default	−10%	+10%
Perennials							
Defence	D/d	0.15	0.125	0.175	0.95	0.944	0.956
Palatability	P/p	1	1.030	0.970	0.2	0.898	0.000
Mortality	M/m	0.54	0.557	0.523	0.54	0.556	0.524
Biomass production	B/b	0.5	0.484	0.516	0.5	0.482	0.518
Competitive strength for water	C/c	0.9	0.879	0.921	0.9	0.876	0.924

Table 2.2 continued.

		Land use by grazers			**Land use by browsers**		
Parameter	Short	Default	−10%	+10%	Default	−10%	+10%
Resistance to drought	R/r	0.077	0.0774	0.0766	0.077	0.0774	0.0766
Shrubs							
Defence	D/d	0.95	0.924	0.976	0.7	0.614	0.786
Palatability	P/p	0.2	0.243	0.157	1	1.291	0.709
Mortality	M/m	0.12	0.137	0.103	0.12	0.136	0.104
Biomass production	B/b	0.15	0.143	0.157	0.15	0.142	0.158
Competitive strength for water	C/c	0.5	0.479	0.521	0.5	0.471	0.529
Resistance to drought	R/r	0.076	0.077	0.075	0.076	0.083	0.069

The 100-year sensitivity analysis simulations were conducted separately for each meta-PFT. To minimise random effects during the initialisation process, shrubs and perennials were initialised with a fixed cover of 20%. All simulations were repeated for the thirty 100-year time series of stochastic rainfall to account for rainfall variability. We applied a medium animal density (stocking density = 40ha/LSU), allowing grasses and shrubs to coexist. One livestock unit is defined as a 450 kg live herbivore that ingests 2% of its body weight daily (Bothma & du Toit, 2016). We conducted the sensitivity analysis separately for the land-use type grazer-dominated and browser-dominated (Table 2.3), as the sensitivity of model results was highly dependent on the specific herbivore pressure.

This resulted in a total of 21 strategy types, of which 10 shrub and 8 perennial grass strategies each resulted from the analyses described above and, in addition, the base type of each meta-PFT was also included (Tables 2.1 and 2.2). Results of the sensitivity analysis can be found in Appendix A.4.

2.2.4 Grazing and browsing herbivory

The actual removal of biomass by herbivory was calculated at the end of the growing season. The herbivory algorithm can be divided into four main parts: estimation of above ground biomass (BM) from vegetation cover, calculation of the biomass demand and of edible biomass, removal of biomass by animals, and reconversion from biomass to vegetation cover.

As the model simulates vegetation cover rather than biomass, first, aboveground biomass has to be estimated from vegetation cover, calculated by multiplying cover with a conversion constant respective year and MAP (cf_{rain}) to predict plant growth depending on water availability (Lohmann et al., 2012).

$$\mathrm{BM}_{\mathrm{veg}} = C_{\mathrm{veg}} * \ \mathrm{conv\_c\_bm}_{\mathrm{veg}} * \mathrm{cf}_{\mathrm{rain}} \tag{2.1}$$

Biomass demand of the animals is calculated as a function of the density of animals in the landscape, which is given by the stocking rate (SR) in hectares per livestock unit (ha/LSU). This approach allows us to directly compare the effect of grazing and browsing animals that have the same overall biomass demand rather than their specific numbers or differences in per capita fodder uptake. The total needed BM consumed by animals of a certain density each year is thus defined as:

$$\text{Needed BM} = \ \text{animal bodyweight} \ \left(\frac{\mathrm{kg}}{\mathrm{LSU}}\right) * 365 \text{ days } * 0.02 \left(\frac{1}{\mathrm{day}}\right) * \frac{1}{\mathrm{SR}} * \ \text{gridarea (ha)} \tag{2.2}$$

In this study, we varied the density of animals (SR), resulting in different total biomass (BM) requirements for fodder. The lower SR, the more animals per area and the higher the total BM requirement and herbivory pressure.

Third, the edible BM (BM_{edible}) of each grid cell is calculated based on green and dry grass BM of the previous year that is still edible. The amount of edible BM is constrained by how much of a strategy type can be eaten, as specified in the properties of each strategy type (parameter edibleFrac/Defence). Thereafter, a random cell is drawn, and the amount of removed BM (RBM, Equation 3.3) is calculated based on local edible BM availability. Since several different strategy types can occur in a grid cell, the actual amount of BM consumed by each strategy type is determined by the relative palatability of each strategy type in that cell.

$$RBM_{type,veg} = \frac{herbivorePref}{\frac{\sum_{veg} herbivorepref_{veg}}{vegNr}} \times \left(\frac{BMedible_{type,veg}}{\sum_{veg} BMedible_{veg}}\right) [dimensionless] \tag{2.3}$$

If the BM demand of animals exceeds the amount of edible BM in this cell, all edible BM is removed; otherwise, BM removal happens selectively. This step is repeated until the total fodder demand is fulfilled. In the event that there is nevertheless a deficit of edible biomass, we assume that the animals are provided with enough fodder to survive, implying a constant SR throughout a simulation. However, when calculating seed dispersal, we adjust the SR in case of food deficits, which means that fewer animals disperse seeds that are translated into new cover. In the final step, the amount of remaining BM of each strategy type is converted back to cover using the inverse function of Equation 3.1.

Thus, depending on the relative feeding preference of animals for different functional vegetation types (parameter *herbivorePref*) and the ratio of edible to nonedible biomass of plants (parameter *edibleFrac*), we can use the same herbivory algorithm for the removal of grass and woody vegetation. Both parameters are crucial in determining how tasty or palatable a plant is and which biomass fraction of it can be eaten. Parameter variation can thus be used to simulate BM removal by grazing and browsing, but also plays a role in distinguishing between the attractiveness of strategy types within each meta-PFT group.

2.2.5 Land-use scenarios

We tested the effects of several land-use strategies by applying two land-use types, namely land use dominated by grazers, preferring grasses, versus land use dominated by browsers, preferring woody species in varying intensities. We decided to focus on browsing-dominated communities and not on an equal proportion of mixed feeders in order to have more direct and comparable effects between grass and shrub removal. In both land-use types, we nevertheless allowed some shrub/grass intake to allow adaptative herbivory in response to changes in food availability during very dry conditions. Furthermore, by parameterising strategy types, we additionally accounted for selective herbivory depending on the palatability and edibility of each type. The effect of land-use intensity was tested by varying the SR from very low to very high (Table 2.3).

Table 2.3: : Settings of different land-use scenarios in terms of herbivory pressure, animal density (SR), and plant parameters of the respective default PFT influencing biomass removal. Specific plant parameters can vary depending on plant life strategy.

Scenario	**Land-use type**	**Stocking rates [ha/LSU]**	**Feeding settings shrubs**	**Feeding settings perennials**	**Feeding settings annuals**
Grazing (very low, low, medium, high, very high)	Grazing dominated	50, 40, 30, 20, 10	herbivorePref = 0.2 edibleFrac = 0.95	herbivorePref = 1 edibleFrac = 0.15	herbivorePref = 0.6 edibleFrac = 0.05
Browsing (very low, low, medium, high, very high)	Grazing dominated	50, 40, 30, 20, 10	herbivorePref = 1 edibleFrac = 0.7	herbivorePref = 0.2 edibleFrac = 0.95	herbivorePref = 0.1 edibleFrac = 0.95

The simulation duration for every scenario was 100 years in order to identify long-term effects. All results are based on 30 repetitions using the previously described stochastic precipitation and temperature time series. Means were generally taken from the last 20 years of each simulation run. In this paper, we focused on the results of the low (40 ha/LSU) and high (20 ha/LSU) SRs as there was little variation in-between. The complete set of results can be found in Appendix A.5.

2.2.6 Data analysis

All results were analysed and visualised using R (R Core Team, 2019). For the statistical analyses, we evaluated the last 20 years of the simulation, in which a steady state for vegetation cover was reached.

Abundance and composition

To clarify the effects of different types of herbivory on abundance and composition (Question 1), total cover of all PFTs was compared by conducting a Scheirer-Ray-Hare nonparametric test for two-way factorial design looking at the factors: land-use type and intensity. The cover of strategy types was analysed as a function of strategy and land use. Factor levels were ordered from highest to lowest median for the post hoc analysis. To investigate differences between strategy-types in different land uses, the post-hoc Dunn test was conducted. To increase statistical significance, the "bh" method (Benjamini-Hochberg) was used to adjust the p-value. Furthermore, we calculated effect size using the nonparametric epsilon squared method (e^2), which determines everything below 0.08 as small, between 0.08 and 0.26 as medium, and above 0.26 as large effect size (Rea and Parker, 2014).

Biodiversity

To test the effect of herbivory on biodiversity, two biodiversity indices were calculated: richness of strategy types, counting the total number of strategy types present, and evenness (Pilou's J), which additionally accounts for the individual abundance and distribution of strategies. It is calculated by comparing the Shannon diversity (H) to the maximum possible diversity value (richness S):

$$J = \frac{H}{\ln S}$$

$$\text{and } H = -\sum_{i=1}^{k} p_i \log(p_i)$$

with k denoting number of groups and p_i denoting the proportion in group k. As plants are not represented as individuals, both measures were calculated using total cover in the whole simulated area as a proxy. Only strategy types with a total cover greater than 2.5% were included in the species richness calculation to remove residue or dead biomass of already near-to-extinct species.

We applied generalised linear mixed-effect models (GLMMs) to richness data using the R package "nlme" (Pinheira et al., 2021) to determine the response of richness to land use. We included climate repetition as a random effect to account for non-equal variances and to allow each repetition to have its own mean value. Richness is derived from count data, which is why we chose a Poisson distribution. To test the significance of random effects, we conducted a likelihood ratio test and compared the goodness of fit.

Evenness between land-use types was compared by conducting a nonparametric Kruskal-Wallis rank sum test and the post hoc Dunn test, including the "bh" p-value adjustment. Again, we calculated effect size using the nonparametric e^2 method.

Exploratory factor analysis

Furthermore, we conducted an exploratory factor analysis (EFA) to determine the clustering of strategy types based on factors for each scenario and to explore the underlying theoretical structural relationship between strategy types and degree of cover. Based on the factorisation, a cluster analysis was conducted. We calculated within cluster variance using the within-cluster sum of squares ($WCSS$).

Additionally, factorisation allowed to reduce the dimensionality of the data and the clear visualisation of functional dispersion (*FDis*). *FDis* served as an estimator of the dispersion in trait combination abundances by calculating the mean distance of all strategy types to the weighted centroid of the community in the multivariate trait space (Laliberté and Legendre, 2010). Each distance between species and centroid was weighted by the relative abundance of the respective species. Since within a functional plant group all cover differences were driven solely by trait differences, the total cover was used as the basis for determining the factor structure.

Latent factors were determined by choosing only factors with eigenvalues greater than 1 and those which were above threshold in the scree plot visual test. For the simplicity of presentation and because there was sufficient explanatory power, only two of three potential factors were extracted. The two-factor model was fitted and factor loads were determined for all PFTs. Based on the factors, two clusters could be identified which corresponded to the meta-PFTs. We plotted the strategy type loadings along the two-factor axes and combined this with *FDis* results by including the centroid and the distance axes to each strategy type representing *FDis*.

Water use and availability

In order to analyse the effects of different land uses on water fluxes, we first defined relative water use by plants as the ratio of transpired water to total water losses by evapotranspiration (T/ET). Since soil water was lost rapidly in our study area, we used T/ET to analyse the productive part of the water cycle in the plant. The water fluxes regarded in this study are all green water according to the classification by Falkenmark (1995). Green water refers to the precipitation input that is stored in the soil until part of it is consumed by plant transpiration which is directly related to their biomass production. T/ET is an important factor to investigate the relationship between vegetation growth and ecosystem water use that has gained increasing recognition in recent years (Fatichi and Pappas, 2017; Schlesinger and Jasechko, 2014; Wei et al., 2017).

We checked assumptions and performed a linear regression analysis and ANOVA tests to test differences between scenarios. Furthermore, we calculated the magnitude of the effect of land use on T/ET using Cohen's d (Cohen, 1988).

Second, for the comparison of soil moisture, we used mean moisture during the variable wet season, which we defined as the time between the first and last day with a rainfall of more than 5 mm during that respective season. Due to heteroscedasticity of the data, a one-way ANOVA with Welch correction was conducted.

2.3 Results

2.3.1 Plant composition

Abundance of meta-PFTs

Land-use type, intensity, as well as their interaction had a significant effect on total vegetation cover (Figure 2.1, $H = 153.5$, $p < .001$). Total cover differed between land-use scenarios ($p < .001$) with highest total cover for the browser scenario of high intensity (Browsing high). A power analysis revealed that land-use type (grazing vs. browsing) and intensity had a strong effect on perennial cover and thus on total vegetation cover ($e^2 = 0.48$).

All scenarios apart from those with a high grazer density (Grazing high, Figure 2.1c) resulted in a stable state where all three PFTs can coexist. Perennial grasses could not prevail under high grazing pressure as seen for high and very high grazer densities (Figure A.1.4).

The collapse of the perennial grass matrix resulted in an immediate increase of shrub cover and bush encroachment and allowed annual grasses to become more abundant. Shrubs were generally more dominant in grazer scenarios (Figure 2.1a, c) where they did not seem to be adversely affected by herbivory. Also, shrubs benefited from high SRs as there were more animals dispersing their seeds which was in turn translated into new cover. The sparse cover of shrubs in the browser scenarios (Figure 2.1b, d) suggested that browsing led to an increase in perennial grass cover and therefore reduced shrub cover.

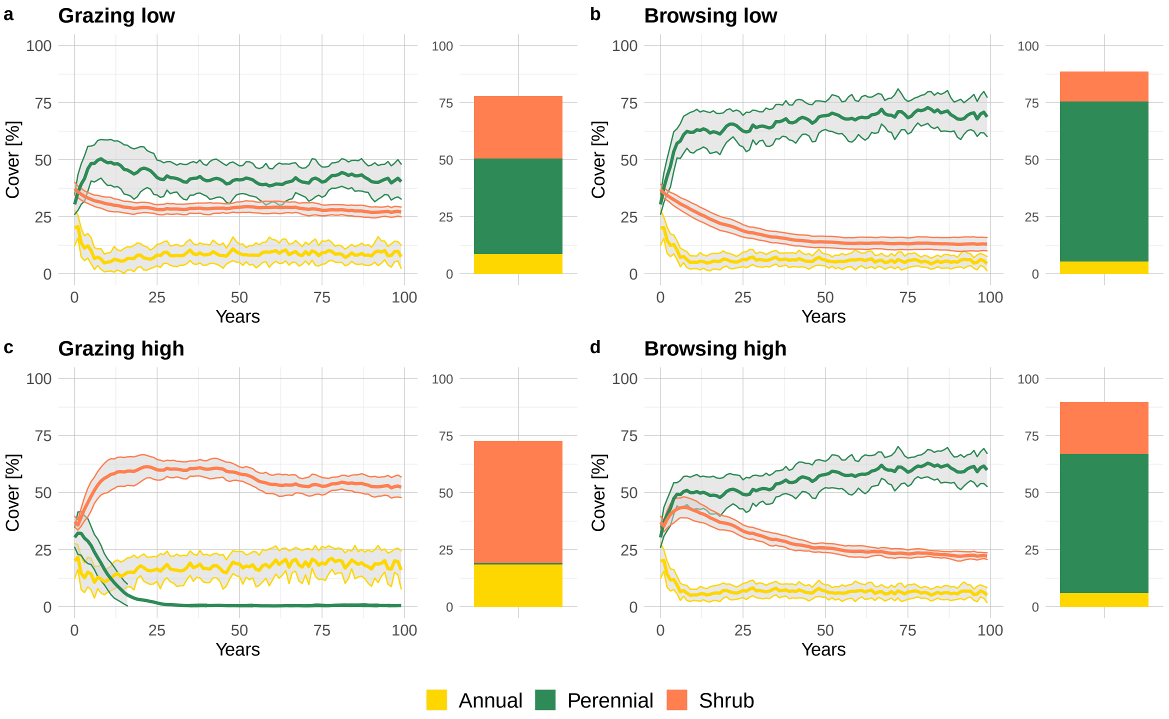

Figure 2.1: Predicted mean cover ± SD [%] for 30 climate repetitions of the three meta-PFTs for the whole simulation duration (lines) and the last 20 years of simulation (stacked bars) for all land-use scenarios.

Abundance of perennial grasses

Dominance of perennial grass species depended on herbivory type, intensity, and plant strategy (Figure 2.2a). Strategy and land-use played a significant role in determining the performance of a strategy type ($H = 19778.7$, $p < .001$). The scenarios with low grazer density (Grazing low) and high browser density (Browsing high) both led to similar abundances concerning successful strategies: The predominant plant types were the base-type, the highly water-competitive or drought-resistant plants with high palatability (Cp and Rp), but also the complementary strategy-type with low palatability and low drought resistance (Pr). Under lower browsing intensity (Browsing low), the latter strategy as well as the default type became even more successful, while the cover of the other strategies decreased.

Abundance of shrubs

Under grazing pressure, the cover of shrubs did not differ strongly between strategy types, suggesting that no specific strategy led to a higher abundance (Figure 2.2b). When perennial grasses increased under low cattle pressure, the amount of each shrub was reduced to the same extent. Nevertheless, the strategies related to high drought resistance (Rd and Rc) were slightly higher in their cover as their adaptation to water stress allowed them to survive longer under very dry conditions. The only strategy type that seemed to have a disadvantage was the generalist base type, which did not follow specific adaptations or trade-offs.Under browsing pressure, the variation in cover between shrub strategy types was higher than under grazing. Here, Rd and Rc became the dominant types, and the strategy types Bp and Bd were drastically reduced in their cover, indicating that either the increased BM production and/or the coupled trade-off that increased herbivory sensitivity was not advantageous under high browsing pressure. Also, the strategies with higher defence mechanisms, Db and Dc, had an advantage under high browsing as their defence mechanism reduced the amount of edible BM (Figure 2.2b).

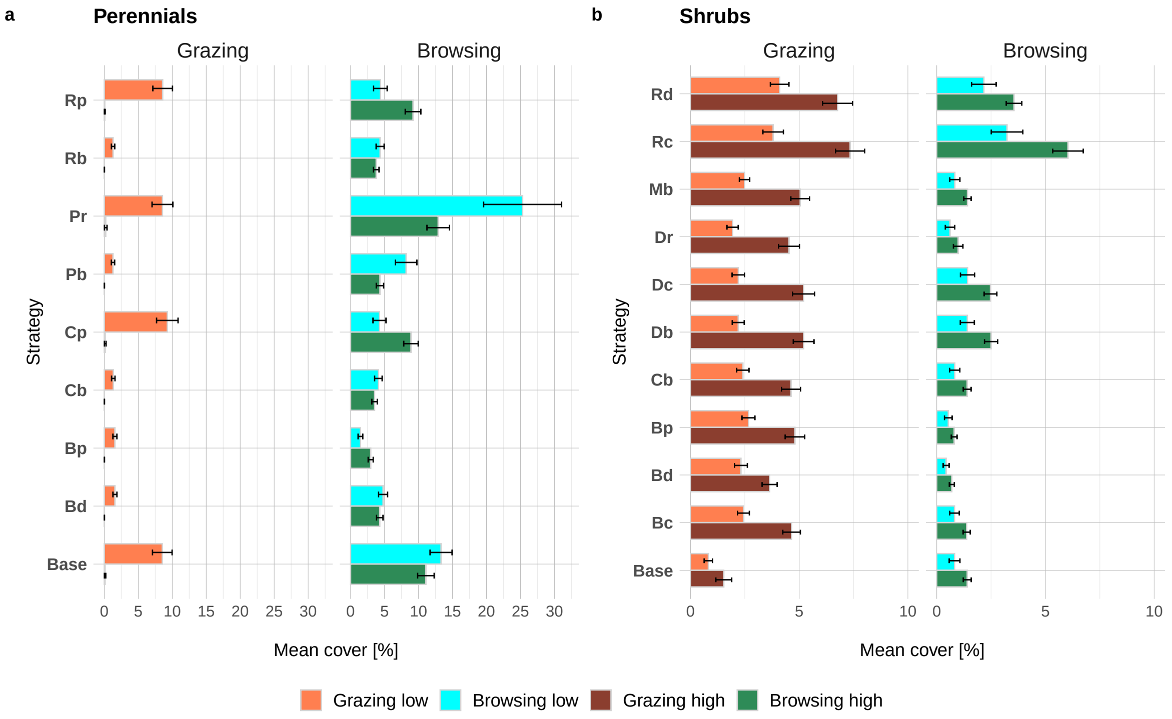

Figure 2.2: Mean cover ± SD [%] of perennial ($N = 9$) and shrub ($N = 11$) strategy types in different grazing and browsing scenarios, suggesting which strategy types dominate in a certain land-use scenario. Results represent vegetation cover of the last 20 years of simulation repeated for 30 climate time series. Note that x - and y-axes between perennial grasses and shrubs differ.

2.3.2 Biodiversity

Total richness varied slightly between scenarios, ranging from 9.49 ± 2.21 species under low grazing intensity (Grazing low) to 12.75 ± 1.54 under high browsing intensity (Browsing high). Land use in high intensity did either favour woody (grazer) or perennial grass species (browser) and led to high richness values. Both land use and PFT had a significant effect on total richness (GLMM, $p < .001$). Richness of each of the three meta-PFT indicated that perennial grass abundance was significantly higher in browsing scenarios and decreased in scenarios with decreasing grazing pressure (Figure 2.3, left). Browser-dominated land use could thus increase grass richness by a factor of 3.13 compared to grazing scenarios (GLMM, $p <.001$). Climate repetition as a random factor contributed significantly to the variation in richness (GLMM, $\text{Chi}^2 = 55.809$, $p < .001$), illustrating that land-use effects cannot always be separated from climate effects.

Evenness ($\text{Chi}^2 = 109.52$, $p < .001$) varied significantly between scenarios with a very strong effect of land use on evenness ($e^2 = 0.92$). As nearly all species surviving under high grazing belonged to woody vegetation, resulting evenness was lowest Browsers increased evenness, but it was still significantly lower than in the scenario with low grazing pressure, which can probably be attributed to the single dominance of strategy types and the drastic reduction in shrub cover. Evenness was highest for low grazing due to the relatively homogeneous distribution of plants and relatively high richness of species (Figure 2.3a, b).

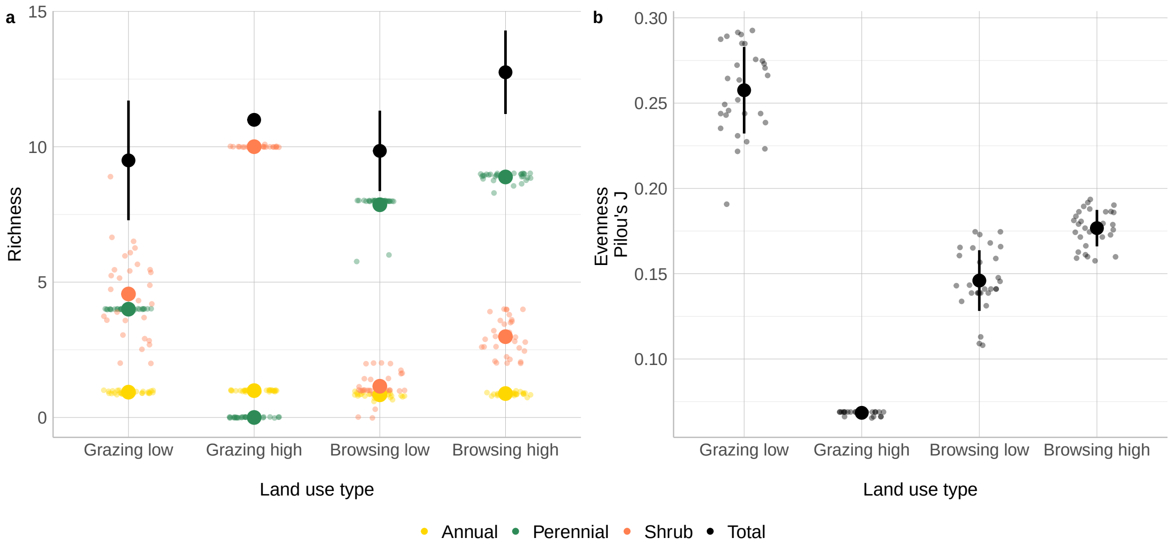

Figure 2.3: Mean ± SD of richness (a) and evenness (b) under all land-use scenarios for 30 climate repetitions. Every point represents one climate repetition. The left figure shows the total richness of all PFTs, as well as richness of each meta-PFT for every scenario respectively.

2.3.3 Implications of herbivory for plant diversity

Based on the factor loads, two clusters could be identified which separate the meta-PFTs (Figure 2.4). Generally, when plants in Cluster One dominated Cluster Two, vegetation abundance in Cluster Two generally declined, while conditions that favoured Cluster Two vegetation appeared to negatively affect vegetation in Cluster One. Plant functional trait composition responded to herbivory intensity in both community means and dispersion.

Factor one (x-axis) clearly separated shrubs from grasses while the second factor (y-axis) differentiated plants with high herbivory sensitivity versus plants with low herbivory sensitivity. Positive values of factor one included shrubs and annuals, and negative values included perennial grasses. Factor two included species with high sensitivity to herbivory at positive values and those not so sensitive at negative values. Thus, non-palatable or species with high defence or high recovery mechanisms were favoured under high herbivory pressure.

The species loadings were plotted along the two-factor axes and combined with *FDis* results by including the centroid and the distance axes to each species representing *FDis*. The centroid shifted from being near shrubs under high grazing pressure (Figure 2.4c) toward perennial grasses in the other scenarios (Figure 2.4a, b, d), suggesting which meta-PFT will dominate under which land-use type.

The clustering of species based on total cover of all scenarios showed to which extent and in which distance to the centroid they appear in the trait space. The annual grass type was categorised as having more shrub-like features and therefore appears in the woody cluster. These clusters indicate a smaller distance and hence fewer differences between the shrub species compared to distances between perennial grass species. The variance in the shrub cluster was therefore significantly lower ($WCSS = 0.33$) compared to the perennial cluster ($WCSS = 3.27$). Palatability seemed to be the driving factor in the variability within a cluster of perennial grasses. Generally, *FDis* was maximised under high grazing pressure (*FDis*: 2.62), when woody vegetation dominated, while it was minimised under low browsing pressure (1.19), when the cover was overall higher and more dominated by perennial grasses, suggesting that *FDis* increased with disturbance.

2.3.4 Water use and availability

For each scenario, relative water use by plants (T/ET) increased linearly with increasing total plant cover (Figure 2.5; $F_{7,2392} = 2655$, $p < .001$), but cover had no effect on soil moisture (Table 2.4; p>.05). Thus, cover increased transpiration and controlled T/ET over the long term. The lowest cover coincided with the lowest water used in the high grazing scenario.

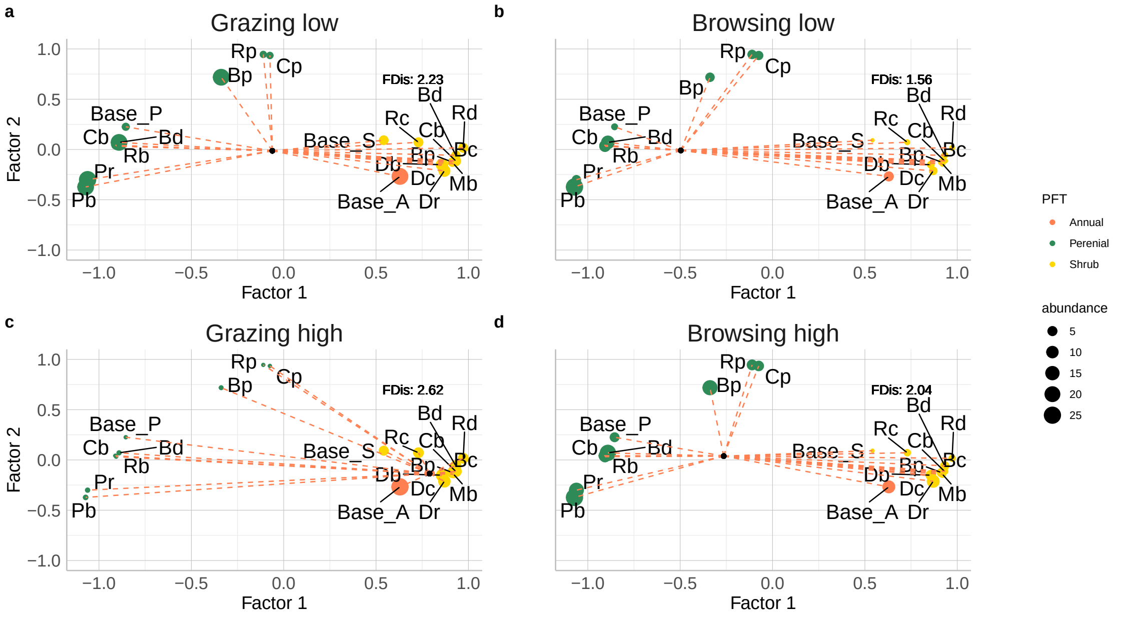

Figure 2.4: The relationship between factors correlating the occurrence of PFTs and functional dispersion (*FDis*). The x - and y-axes denote the two factors separating the distribution of strategy types. PFTs can be distinguished by color and the points are scaled by abundance. The black point depicts the centroid, representing the weighted centroid of trait combinations in the community, and the dashed lines the distance of the respective strategy type to the centroid, weighted by its relative abundance. The clusters suggest which species are similar and thus usually occur together.

Both were slightly higher in the lower grazing scenario. Remarkably, more water was available to plants in the browsing scenarios, with almost identical ranges in both, but slightly higher cover and T/ET in the low browsing scenario. In both browsing scenarios, there was almost no green water loss as almost all available water could be used for transpiration. In total, vegetation cover and land-use scenario could explain 88.6% of the variation in water use. Cohen's d predicted a very large effect size of land use on relative water use (2.73). Although total cover and soil moisture were significantly positively correlated ($p < .001$, Spearman's Rho = 0.56), land use did not have an effect on soil moisture as soil moisture levels were similar across all scenarios (Table 2.4; $F_{3,1331.1} = 0.84$, $p > .05$).

Table 2.4: : Mean values ±SD of total cover, relative water use by plants (T/ET), and soil moisture for each land-use scenario.

Scenario	**Total cover ± SD**	**T/ET ± SD [%]**	**Soil moisture ± SD [Vol %]**
Grazing low	77.96 ± 7.86	73.74 ± 7.33	11.41 ± 1.74
Grazing high	72.53 ± 8.37	62.37 ± 5.54	11.34 ± 1.75
Browsing low	88.60 ± 7.21	88.41 ± 6.20	11.48 ± 1.74
Browsing high	89.64 ± 7.14	88.84 ± 6.23	11.48 ± 1.75

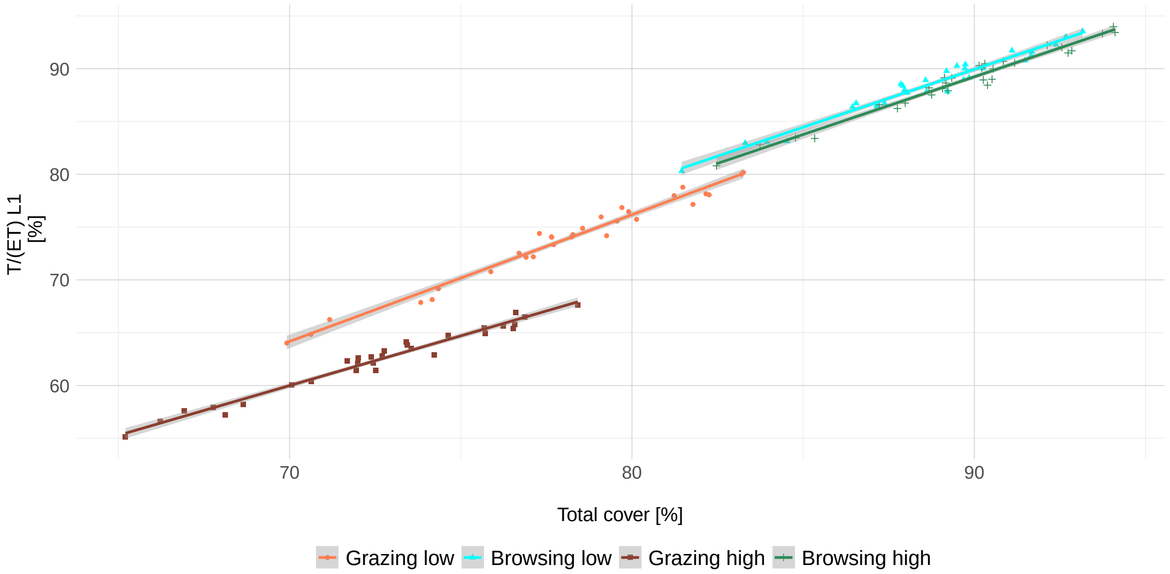

Figure 2.5: Correlation between the variation in the ratio of transpiration and evapotranspiration (T/ET) [%] as estimator for water use by plants and total plant cover [%], separated for the different scenarios of land use. Results refer to water dynamics in the upper soil layer of the last 20 years of simulation and 30 climate repetitions

2.4 Discussion

In this study, we examined potential effects of land-use types dominated by grazers or browsers in different intensities on grass and woody PFTs composition and resulting changes in total vegetation cover, biodiversity and water availability. Our modelling approach provides a new route for studying the effects of shifting land use from grazing to browsing herbivores on plant functional diversity and the link to ecosystem functions. In the following, we address our three major questions on the response of plant abundance, composition, and diversity on herbivory by grazing versus browsing as well as on water fluxes and discuss the implications for management. We also discuss whether we could confirm our hypotheses, (i) that we were able to reproduce bush encroachment under high grazing, that browser-dominated communities (ii) could reduce pressure on grasses and allowed a tree-grass coexistence, and (iii) had a positive effect on biodiversity and (iv) led to improved water uptake.

2.4.1 Plant composition

Abundance of meta-PFTs

The simulations showed that the choice of herbivores strongly affected plant community composition. High land-use intensities drove the vegetation to be more homogeneous and dominated by either woody (grazing) or herbaceous types (browsing).

Heavy grazing led to typical degradation patterns: a decrease in total vegetation cover, a shift in the plant community toward a higher proportion of woody vegetation, and the appearance of annual vegetation. These results, also referred to as bush encroachment, are in line with findings from previous studies (Meyer et al., 2007; Nacoulma et al., 2011; Pfeiffer et al., 2019). Heavy grazing led to an increase of bare ground due to selective removal of perennial grasses. Bare ground opened a window of opportunity for the establishment of woody species, but also provided space for annual grasses (Archer et al., 2017; Polley et al., 2017; Zeidler et al., 2002). We could also show that a decrease in grazing pressure allowed some perennial grass species to prevail, resulting in the coexistence of woody and grass species. Here, the increase of perennial grass species decreased the available space for woody vegetation and therefore their growth capacity.

In contrast, the perennial grass matrix could fully establish under browsing and reach its highest total cover with similar values for all animal densities. Our simulation results were in line with findings of empirical (Archer et al., 2017; Knegt et al., 2008; Staver et al., 2009) and other modelling (Holdo et al., 2009; Langevelde et al., 2003) studies in similar savannas: Browsing pressure allowed a high cover of perennial grasses, which in combination with reduced resource availability could reduce shrub cover. Resource availability has been previously documented as a large determinant of shrub cover (Acharya et al., 2018).
Also, shrub cover was higher under high browsing intensities compared to lower browsing intensities. The shrub increase can be attributed to the greater dispersal of shrub seeds due to the larger number of herbivores (Archer et al., 2017), which we accounted for in our simulations.

2.4.2 Composition of strategy types

The response of the PFT community to the intensity and type of herbivory was strong, leading to significant shifts within the meta-PFT composition. The simulation results showed that the variation of perennial grass strategy types between the land-use scenarios was much stronger compared to that of shrub strategies, which showed a rather homogeneous distribution of strategy types. The homogeneous distribution of shrub strategy types might indicate that the pursuit of a particular strategy had a greater impact on perennial species than on shrubs. However, we were able to identify strategies for both meta-PFTs that enabled them to dominate under specific herbivory pressure and to cope better with resource scarcity. We also detected a shift in dominance of specific strategies for an animal density between 30 and

40ha/LSU, explained by the combined effect of herbivory pressure and shrub seed dispersal and establishment, which we discuss in the following.

Composition of perennials grasses

Under low grazer and high browser density, the base type and strategies related to competitive water use (Cp), high drought resistance (Rp), as well as low palatability (Pr) were most successful in almost equal abundances. These strategies corresponded to species that were commonly found in the Namibian system studied here, for example, *Eragrostis echinochloidea* (Cp), *Stipagrostis uniplumis* (Rp), and *Bothriochloa radicans* (Pr).

In both browsing scenarios, woody and grass species coexisted and therefore competed for water (February et al., 2013; Tietjen et al., 2009). Not surprisingly, the strategies creating an advantage in dealing with the two main threats to the survival of grasses, herbivory and water limitation, were the ones that could prevail. When animal density was high, the trade-off leading to high palatability became less important, as the plant biomass demand by animals usually exceeded available edible biomass and thus all edible biomass got completely removed, regardless of the palatability of a certain PFT. However, plants with a more efficient resource use could recover quicker from grazing events, as they could allocate acquired water directly into new plant growth (Abraham et al., 2019; Roodt, 2015).

In the scenario with low browser and grazer density, the strategy with low palatability and low drought resistance (Pr) became the most common one besides the base type. Under low grazing pressure, grazing happened very selectively on palatable strategy types. Also, as less shrubs were present, belowground competition for water was reduced to an extent, where most perennial grasses had access to sufficient water and could hence survive. Interestingly, the base type seemed to generally be well adapted to varying environmental conditions in our model. This was in accordance with our initial aim that the base type acts as a generalist that is not subject to specialisation along specific trade-off axes and can therefore thrive in various environments, but with clear disadvantages if the stress level requires better adaptations.

Composition of shrubs

The results suggested that shrubs respond more strongly to changes in resource availability due to competition with perennial grasses than to browsing pressure or land-use intensity, irrespective of grazing/browsing pressure. When browsing pressure was marginal (grazing scenarios), the distribution of shrub strategy types was very homogeneous. For both land-use types, the strategy types with increased drought resistance (Rc, Rd) were clearly dominant in the community, but the strategies with high herbivory defence (Dc, Db) were also slightly more abundant. The increase of plant types with high defence mechanisms was in line with results of other studies: in regions with high animal densities, shrubs develop, for example, structural (spines) or chemical defences (tannins) in response to browsing animals (Kiker and Scogings, 2019; Owen-Smith, 1993).

While we reproduced the dominance of perennial grass strategy types in the model according to strategies used by common local species, the local shrub species corresponding to the dominant shrub strategy types are rather rarely found at our study site (e.g., *Acacia nebrownii* (Rc), *Grewia olukondae* (Rd)). Potential reasons for this are discussed in section Implications of herbivory for plant diversity.

In contrast to the perennial grass base type, the shrub base type performed the worst in every scenario, suggesting that the strategy types were better competitors irrespective of their trade-offs. With these results, we were able to answer how plant functional abundance and composition respond to different land-use types and intensities (Question 1). The results have shown that herbivory type and intensity were a main contribution in shaping vegetation structure in semi-arid African savannas. Grazing, especially at high intensity, has significantly reduced grass cover and confirmed our hypothesis (i) that bush encroachment would arise under these conditions. High (but common) SRs of grazers exceeded the capacity of savanna rangelands. Although the reduction of shrub cover in response to browsing was not as strong as the grass response to herbivory, browser-dominated communities reduced some pressure on grasses and allowed a coexistence of both vegetation types, confirming our second hypothesis. While the magnitude of grazing impacts was directly related to grazer densities, browsing impacts were less dependent on browser densities, which is in line with other studies (Holdo et al., 2009; Maron and Crone, 2006; Staver et al., 2021). Therefore, management decisions, especially for browser-dominated communities, should consider factors other than animal density, and implement a land-use strategy based on thorough studies with respect to soil, habitat composition, grazing and browsing capacity, and physical limitations (Bothma and du Toit, 2016; Briske, 2017; Stafford Smith et al., 2007).

Nevertheless, our study suggested several ecological and economic benefits of reducing SRs of grazing animals, such as the resulting increase in perennial grass cover leading to higher fodder availability and the reduction of woody vegetation, which can reduce or avoid costly supplementary feeding and mechanical removal of shrubs. Furthermore, empirical studies observed that native herbivore communities are also changing, with native grazers gradually being replaced by mixed feeders (Staver et al., 2021).

Our results have also shown that herbivory intensity can be a further important factor shaping the composition of plant communities. Under high animal densities, some trait specialisations, such as low or high palatability, become less important as herbivores feed on any plant they can to fulfil their biomass requirements. One consequence of this could be that undesirable plants benefit from herbivory disturbance. These plants, less desirable in terms of edibility, could then exploit the competitive advantage and replace palatable strategy types with less efficient recovery mechanisms. A common species in savanna systems taking advantage of high grazing intensities is *Tribulus zeyheri*, which is often found near waterholes where grazing intensity is particularly high (Van Rooyen et al., 1994).

In summary, the intensity of herbivory plays a critical role in determining vegetation abundance and composition and should therefore be determined with care.

2.4.3 Biodiversity

For both land-use types, total species richness was highest under high animal densities. However, total species richness in the scenario with high cattle density was solely driven by woody species, as all shrubs apart from the base type survived and all perennial grasses vanished. Browser-dominated land use could clearly increase survival of perennial grasses and therefore their richness, but also allowed some shrubs to prevail. In the scenario with low grazer density, shrubs and perennial grasses coexisted in almost identical numbers. Woody species richness always decreased to a lower level than grasses but for the scenario with high grazing intensity.

Hence, it is no surprise that evenness, which quantifies how equal a community is in terms of species numbers (Schwartz et al., 2000), is highest in the low grazer density scenario. Both browsing scenarios result in similar evenness values, with the high intensity scenario being slightly higher due to the higher number of shrubs in this scenario. Moreover, the high grazing intensity scenario, which resulted in the highest richness value, was the scenario with the lowest evenness. Such inverse pattern of evenness to richness with a species richness primarily driven by woody species is commonly found in studies linking land use to biodiversity patterns (Revermann et al., 2017; Rutherford and Powrie, 2013). For instance, in a similar *Colophospermum mopane* dominated savanna, heavy grazing did not affect species richness, but changed plant composition and decreased species evenness (Rutherford et al., 2012). Consequently, a high number of species that only comprises one functional group is not necessarily an indicator of high biodiversity.

Implications of herbivory for plant diversity

The two factors explaining the distribution of PFTs showed a clear separation between perennial grasses and shrubs and a separation between the sensitivity of species to herbivory. The factor loadings suggested that in scenarios where herbivory was particularly intense, non-palatable or species with high defence or recovery mechanisms were favoured.

The clusters indicated that the distances between shrub strategy types were smaller compared to the distances between perennial grass strategy types, although shrub strategy types were more diverse in their traits.

Although shrub abundance differed between scenarios, there were little differences between shrub strategy types. The homogeneous distribution of shrub strategy types across land-use strategies could either mean that traits did not exert a strong effect on their abundance or that we did not capture certain key traits in our strategies that are related to resource use. Accordingly, this could explain why the dominant strategy types in the model do not correspond to the dominant local shrub species. Another reason for this could be that shrubs respond more strongly to climatic conditions than to herbivory, as previous results suggested (Lohmann et al., 2018). However, we did not test for different precipitation frequencies and intensities in this study.

FDis was higher in the two grazing scenarios where shrubs dominated. Previous studies also linked higher *FDis* with disturbance although less grass strategy types were viable under high herbivory pressure (Costa et al., 2017). An increase of *FDis* with disturbance could mean that a high trait dispersion is not necessarily beneficial per se for the ecosystem and that certain traits have a greater impact than others. Indeed, higher *FDis* did not coincide with higher vegetation cover. The mismatch of higher *FDis* with high vegetation cover could indicate that a completely even distribution of traits within one meta-PFT might not be ideal, but rather a low level of *FDis* with grass-like traits dominating. Generally, lower levels of *FDis* coincided with higher levels of total cover, suggesting that savannas with a dense grass matrix may only be able to support trait variability up to a certain level. This is in agreement with results of other studies linking community weighted means and functional diversity (Costa et al., 2017; Wen et al., 2019).

These results show the response of species richness and evenness to the contrasting land use scenarios (Question 2): Herbivory was a key process affecting richness and evenness, with high grazing intensity in particular having a negative effect on grass diversity. The model suggested that low grazer stocking densities (>30 ha/LSU) enable long-term coexistence of trees and grasses. The results of a study comparing the response of plant diversity to the limitation of movement of both managed wildlife (with a high proportion of large browsers) and of grazing animals also found that high wildlife density reduces woody plant diversity and cover, while low grazer intensity allowed grasses and woody plants to coexist (Cassidy et al., 2013).

Unexpectedly, we found that browsers in all densities allowed for higher coexistence of plant species, which confirms hypothesis (iii). We conclude that biodiversity should not be evaluated by total species richness, but rather by focusing on the conservation value of particular species or functional traits. Therefore, we could only partly confirm our third hypothesis that browser-dominated land use would positively influence biodiversity, especially if total richness was regarded. Moreover, functional diversity and ecosystem services did not co-increase linearly, but it seemed that only some functional traits, that is drought resistance or palatability, improved the performance of a strategy type and allowed growth and survival under disturbance. This is confirmed by another study that investigated the trait distribution of a savanna community in a heavily grazed bush encroached savanna. The authors found little trait variability within this community, but noted that stress-avoiding and stress tolerance through efficient resource conservation were clearly the dominating processes determining community composition (Geissler et al., 2019). Therefore, high trait diversity was not necessarily a direct indicator of a healthy ecosystem if certain traits were not present in the community.

2.4.4 Water use and availability

Land-use type and intensity had a clear effect on total vegetation cover, which correlated strongly with water used by plants. We observed a distinct separation between the scenarios where T/ET increased with total cover. Previous studies linking T/ET to leaf area index (LAI) supported this result and also found vegetation growth properties to mainly determine water use in the absence of water stress (Kato et al., 2004; Ren et al., 2019). Although there was no difference in total ET between the scenarios, the higher vegetation cover increased the water used by plants, while reducing water loss by evaporation.

Under browsing, the reduction of evaporative loss due to higher vegetation cover promoted water use through transpiration and resulted in an increase in T/ET. Consequently, water was used more efficiently for plant growth instead of being lost through evaporation, which is supported by other studies considering vegetation and T/ET (Kato et al., 2004; Ren et al., 2019; Wei et al., 2017).

In contrast to plant water use, soil moisture was neither affected by land-use type nor by intensity. The constant soil moisture level in this study indicated that it was not affected by vegetation cover and type and depended thus solely on precipitation. This can be explained by two aspects: First, the precipitation intensity of single rainfall events was rather low, leading to almost full infiltration of the rain into the rather sandy soil and to very low water losses by runoff, independent of vegetation cover. Second, potential evaporation exceeded the available water by far; therefore, losses by evapotranspiration were very fast, no matter if losses occurred mainly by evaporation or by transpiration.

Overall, we conclude that browser-dominated when compared to grazer-dominated land use could sustain a higher total vegetation cover given the same rainfall and soil moisture, answering our third question and confirming our fourth hypothesis that browser-dominated communities can lead to an improved water uptake. With browsing animals, a higher perennial grass cover could be sustained, which had positive implications for plant water use, but also erosion control (Archer et al., 2017). More water was used by plants and less water was lost by evaporation, leading to a more efficient ecosystem water use. As water could be used more efficiently, these positive implications underline the benefits of browser-dominated land use in the face of extended drought periods under climate change.

2.5 Conclusion

We found several ecological benefits of shifting land use from grazing- to browsing-dominated herbivore herds, even for high densities. First, as the cover of woody species was less affected by herbivory compared to grass cover, land use dominated by browsers involved lower risks of degradation compared to grazers. Second, browsers could strongly decrease the pressure on grasses and therefore served as an organic and cost-efficient way to counteract woody plant encroachment. Furthermore, we found increased biodiversity across major plant functional groups and an overall increase in water uptake by plants in scenarios with browsers. Therefore, browsers could provide a buffer against adverse effects of climate change, such as decreased soil moisture and loss of vegetation cover, also implying a lower erosion risk.

As we aimed for extremes of herbivory to narrow the possible range of responses, we only included browsing animals into this study, although wildlife consists of a range of species with different feeding behaviour, including grazers, mixed feeders, and browsers. In addition, especially in Namibia, the importance of integrated wildlife systems where domesticated and native animals are kept together, such as in conservancies and nature reserves, is increasingly being recognised. In future work, the model could be expanded to incorporate (1) mixed feeders, (2) the effects of spatially and temporally varying animal density (e.g., due to seasonal migration), (3) non-consumptive impacts (e.g., trampling, tree removal), and (4) the combined impacts of animals and wildfires.

In summary, we provided a new route to examine direct effects of herbivory by browser-dominated compared to grazer-dominated communities and its impact on selected ecosystem functions, which may assist rangeland managers to make sustainable decisions in the future.

3

Savanna resilience to droughts increases with the proportion of browsing wild herbivores and plant functional diversity

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Abstract Maintaining the resilience and functionality of savannas is key to sustaining the ecosystem services they provide. This maintenance is largely dependent on the resilience of savannas to stressors, such as prolonged droughts. The resilience to drought is largely determined by the interaction of herbivores and the functional composition of vegetation. So far, our understanding and ability to predict the response of savannas to drought under different types of rangeland use and as a function of vegetation composition are still limited. In this study, we used the ecohydrological, spatially-explicit savanna model EcoHyD to determine if the resilience of a savanna rangeland towards prolonged droughts can be enhanced by the choice of rangeland use type (grazer-dominated, mixed-feeders or browser-dominated) and animal density. We evaluated the ability of a Namibian savanna system to withstand droughts and recover from droughts based on its perennial grass cover and the overall species composition. Generally, we determined a low resilience under high grazer densities. Most importantly, we found that functional diversification of herbivores and plants acted as resilience insurance against droughts, leading to greater resistance and recovery of perennial grasses. In particular, a higher proportion of herbivores allowed for higher resilience, probably also due to a short-term switch to more drought-resistant or unpalatable species. In this case, herbivore diversification was of high self-regulatory value by reestablishing trophic complexity, reducing the need for additional management interventions. Savanna systems will be more resistant to drought if (i) a dense perennial grass cover is maintained, protecting the topsoil from heat induced water losses and erosion, encompassing functionally important species that are particularly well adapted to water stress and that are palatable, if (ii) the grazing pressure is adjusted to the productivity of the system, and (iii) the herbivore community includes browsers.

3.1 Introduction

Extreme climatic events, such as droughts pose major challenges to the resilience of savanna systems and consequently the provision of important ecosystem services (Biggs et al., 2012; Zolli and Healy, 2012). Especially the combination of droughts with unsustainable rangeland management can decrease the resilience of savannas substantially by eliminating crucial self-regulatory mechanisms.

Since Holling (1973) introduced the concept of ecological resilience, numerous definitions have been proposed. Originally, resilience was defined as the recovery speed of the system after a disturbance (Pimm, 1984). This definition has gradually been replaced by a broader concept that recognises multiple stable states and the system's ability to withstand change while maintaining important ecosystem functioning (Gunderson, 2000). A recent definition of ecological resilience encompasses resistance to stress, recovery after stress, and persistence of the overall state (Weise et al., 2020). In this sense, we define resilience here as the degree of disturbance that an ecological system can accommodate without transitioning to a qualitatively different state (Gunderson and Holling, 2002), by either resisting change and/or recovering after the stress.

Savannas are woodland-grassland ecosystems that are subject to highly variable rainfall and low water availability with several qualitatively different ecological states (Sala et al., 2017).

Savannas exhibit several self-regulatory mechanisms through which they generate or maintain important ecosystem functions. For example, wildfires are of highly self-regulatory value because they alter the composition and structure of vegetation and reduce fuel loads, minimising the potential for subsequent fires until sufficient fuel reaccumulates (Parks et al., 2015). Since greater species diversity increases the resilience to environmental change (Pettorelli et al., 2019), it also contributes to self-regulation of a system by preventing the transition to a different ecological state and, thus, limits the need for additional land management. However, extreme events can stress a savanna to such an extent that the ability to self-regulate declines and the system transitions to a new state, often from grass- to-woody-dominated.

Applying the resilience concept to savannas, this means that self-regulatory, stabilising mechanisms increase the degree of disturbance that savannas can accommodate and prevent transitions among the multiple stable vegetation states. The latter include grass-dominated vegetation, a mixture of trees and grasses, or wood-dominated vegetation or potentially also bare soil (Jeltsch et al., 2000).

The ability of savanna vegetation to withstand extreme events such as droughts (periods of prolonged absence of precipitation or below-average precipitation amounts; Dai (2013)) is enhanced by two main mechanisms. First, drought-resistant species could increase and functionally compensate for decreased occurrence and health of less resistant species (Gonzalez and Loreau, 2009; Hoover et al., 2014). Second, during short-term droughts, plants may physiologically respond by reducing growth and redistributing available water and nutrients towards below-ground resources (Connell and Ghedini, 2015).

Grass species differ in their sensitivity to disturbance. Some can resist a higher degree of stress, i.e., they persist or recover quickly under drought and/or grazing, but recovery might still be slow, even after conditions have improved (Ludwig et al., 2001). The loss of these resistant species could open up colonisable space for shrubs to dominate the system. This shrub dominance likely shifts the ecosystem towards a degraded state marked by a decline of important ecosystem services (Dougill et al., 2010; Holling, 1996). The so-called shrub encroachment in response to heavy grazing is commonly accompanied by changes in taxonomic composition, an increase in unpalatable, trampling resistant and/or annual grasses (Milton et al., 1994; Tabares et al., 2020). A diminished grass layer increases the risk of soil erosion (Archer et al., 2017) and leads to altered productivity, nutrient cycling and water balance (Sankaran et al., 2004; Scholes and Archer, 1997). That is, a change in herbivory, fire or climatic conditions can lead to a savanna with a different dominant vegetation type and hence altered plant functional diversity, leading to implications for ecosystem functioning. Transitions in savannas are in most cases only measurable over years or decades (Oliver et al., 2015) and are therefore difficult to observe in shortterm field experiments. It is therefore crucial to unravel the complex interactions between climate and rangeland use in savanna systems to maintain the resilience of the system and thus meet the future challenges of savanna management. For this disentanglement, models are ideal as they enable the understanding of future developments by reproducing key processes and elements of the system.

Climate change is expected to affect the resilience of the savanna by exacerbating the intensity and frequency of climatic extremes such as droughts (Dai, 2013; Tadross et al., 2017). Drought alone can cause a change in vegetation, but combined with unsustainable grazing management, the probability of transitioning to a new and possibly undesirable state increases. In particular, the combined impact of different types of rangeland use and droughts of different duration has been largely neglected (Smith et al., 2013; Wigley-Coetsee and Staver, 2020). Some efforts have been made for grazing systems (Ruppert et al., 2015; von Keyserlingk et al., 2021), but neither empirical nor modelling studies have analysed alternative rangeland use types, such as mixed-feeding or browser-dominated regimes, and their possible mitigation or exacerbation of the effects of droughts. Since recent studies already pointed out that reducing grazer densities and using wildlife increases habitat use and benefits ecosystem resilience (Brodie et al., 2013; Wells et al., 2022), we expect that reducing the number of grazing animals by using mixed herbivore communities with more browsers will lead to a more balanced system and thus increase the resilience of savannas to droughts.

In this study, we used an ecohydrological savanna model to assess the resilience of savanna vegetation under three different types of rangeland use (grazer-dominated, mixed, and browser-dominated) at two animal densities exposed to drought periods of varying lengths (4 and 8 years).

We specifically addressed the following questions: (i) Is perennial grass cover resilient to extended droughts and does resilience vary with rangeland use type, rangeland use intensity, and drought length? (ii) What role does functional diversity play in post-drought resilience and does this role vary with rangeland use type, intensity, and drought length? (iii) What are the consequences for important self-regulation mechanisms within the ecosystem and (iv) hence the implications for land management?

3.2 Methods

3.2.1 Study site

Etosha Heights is a private wildlife reserve in Namibia's arid savanna (S19.1554° E15.1705°), established in 2002 by merging eight livestock farms and replacing the domestic stock with indigenous wildlife. The reserve covers an area of 492 km^2 bordering the southern boundary of Etosha National Park. It is within Namibia's arid savanna where precipitation is highly variable and occurs mainly in summer (October to April). The mean annual precipitation (MAP) is 298.67 ± 30.20 mm (retrieved from a local weather station from 2018 to 2021) and the mean annual temperature is 26°C. Topography (mean elevation: 1995 m, rather flat), soil (loamy sand), climate and vegetation characteristics are described in Irob et al. (2022) in detail. Much of the study area is already encroached by *Colophospermum mopane* and acacia species, but there are also mixed habitats and open plains. The corresponding parameters can be found in Appendix A.2. Dominant herbivores are springbok, oryx, giraffe and plains zebra. The grazer-to-browser ratio has ranged between 1.2:1 and 0.9:1 (Hauptfleisch, 2022). Game counts are not conducted regularly, but stocking rates range between 10 and 50 ha/LSU depending on field condition and recent droughts, but also on fence management.

3.2.2 Model description

We used the ecohydrological, spatially explicit dryland model EcoHyD (Guo et al., 2016; Irob et al., 2022; Lohmann et al., 2012; Tietjen et al., 2009, 2010). In this study, we extended the existing herbivory algorithm to allow for a more dynamic range of herbivory types (A1.2). We simulated a total area of 2.25 ha consisting of 900 grid cells, with a resolution of 5×5 m per cell. In the past, the model has been successfully applied and validated in different dryland ecosystems (Lohmann et al., 2012; Tietjen et al., 2010). The model comprises two dynamically linked process-based submodels: a vegetation submodel and a hydrological submodel. A comprehensive model description and model parameters can be found in the Appendices (A.1 and A.2). The life cycle of different plant functional types (sub-PFTs) belonging to one of three major plant functional types (shrubs, perennial grasses and annual grasses) are simulated in the vegetation submodel. The main processes determining vegetation dynamics are growth, mortality, competition for water and space, seed dispersal, seedling establishment, and herbivory. Fires have not been considered in this study as they are usually suppressed at our study site. Plant dynamics are directly related to soil water dynamics, as growth is coupled with transpiration. Plant death is caused by water scarcity or senescence.

The hydrological submodel simulates the daily dynamics of surface water and soil moisture in two soil layers. These dynamics are determined by precipitation, lateral water redistribution of surface water, infiltration, vertical fluxes and water losses through evaporation and transpiration. Water losses to the atmosphere are related to the proportion of plant roots in the two soil layers and vegetation cover. Vegetation cover reduces evaporation but increases the transpiration of plant water. Although perennial grasses and shrubs have access to water in both layers, the root distribution of annual grasses allows them to access water only in the upper soil layer (Case et al., 2020).

Model inputs and scenarios

The model was parameterised to the environmental conditions of Etosha Heights Private Reserve, specifically topography and soil, climatic conditions and plant species characteristics.

Temperature, precipitation and drought

We approached the uncertainty of highly variable precipitation conditions by replicating simulation runs with stochastic precipitation time series generated by the NamRain precipitation generator (see Lohmann et al. (2012)). All 30 rainfall time series have the same MAP on average, but with a large variability of yearly sums ranging from 100 mm to 800 mm that are distributed differently over the 100 years (Figures A.1.14 and A.1.14). In addition to the control scenario without induced droughts, we simulated droughts with a single drought period after 60 years with a duration of 2 to 8 years. We determined extreme drought years at our study site as yearly precipitation sums of less than 100 mm (one-third of MAP). Droughts of 2 years are relatively common, 4 years are based on the extreme drought of 2012-2015 in Namibia and 6-8years should reflect potential future droughts that fall outside historical norms (Cook et al., 2015).

Assemblage of plant sub-plant functional types

The model describes the fate of three major plant functional types (PFTs): woody vegetation (hereafter referred to as shrubs), perennial herbaceous vegetation (perennials) and annual herbaceous vegetation (annuals). The base subtype of each meta-PFT (hereafter referred to as "base type") had the same set of parameters as the original meta-PFT. We then derived additional subtypes (for shrubs and perennials) by defining individual life strategies that had trade-offs in two specific traits but were otherwise identical to the base type. Sub-PFTs were derived by defining individual life strategies based on the main species we found in

Etosha Heights that we categorised into trade-offs in two particular characteristics, related to processes defence D, biomass production B, mortality M, palatability P, competitive strength for water C and resistance to drought R (Irob et al., 2022). For example, a sub-PFT could be very drought resistant and show a very low biomass production as a trade-off (Table 3.1). As annuals only dominate degraded systems (Archer et al., 2017; Case et al., 2020), we did not subdivide them further. In total, we selected five sub-PFTs for perennials and four for shrubs from our local species pool that exhibit potential relevant adaptation mechanisms to herbivory and/or drought. We tested the role of plant functional diversity (an assemblage of sub-PFTs) on modelled outcomes by comparing results for simulations with one meta-PFT each (low diversity, referred to as single) and with the results of simulations with several sub-PFTs of perennials and shrubs (high diversity, referred to as diversity).

Table 3.1: Perennial grass and shrub plant life strategies in Etosha Heights. The two-letter code refers to the strategy name used in the text and figures, and adjacent to the two-letter code its description.

Perennials		**Example species**	**Shrubs**		**Example species**
Bd	High biomass production – Low forage defence	*Stipagrostis uniplumis, Oropetium capense*	Bm	High biomass production – High mortality	*Colophospermum mopane*
Cp	High competitive strength for water use efficiency – High palatability	*Eragrostis echinochloidea*	Cb	High competitive strength for water use efficiency – Low biomass production	*Acacia reficiens*
Pb	Low palatability – Low biomass production	*Eragrostis trichophora*	Db	High forage defence – Low biomass production	*Dichrostachys cinerea*
Pr	Low palatability – Low resistance to drought	*Bothriochloa radicans*	Rd	High resistance to drought – Low defence	*Boscia albitrunca, Grewia olukondae*
Rp	High resistance to drought – High palatability	*Stipagrostis uniplumis*			

Rangeland use scenarios

We analysed the effects of three types of rangeland use, namely rangeland use dominated by grazing, mixed feeding and browsing herbivores at two different intensities (animal density in hectare per livestock unit): 20ha/LSU (high) and 40ha/LSU (low). For rangelands dominated by grazing or browsing herbivores, we established a ratio of 80 : 20% between the diet preference of herbaceous vegetation and shrubs (and vice versa) with a flexibility of 15% to allow adaptive herbivory in response to changes in food availability. If there is not enough edible biomass of the preferred forage type available, the ratio is adjusted within the defined parameter range, and the animals can switch to a higher grazing/browse intake. This led to a minimum of 65% and a maximum of 95% herbaceous vegetation intake for the grazers. For mixed feeders, we set the ratio to 50 : 50%, again with a flexibility of 15%. This means that our communities do not represent specific animal species, but rather communities of different herbivore types that have on average the specified fodder demands described above. Depending on the density of the animal, the ratio of grazers to browsers then leads to an amount of biomass of a functional type of plant that can then be taken from the edible biomass. In addition, with this model setup, we do not account for the impact of large browsers, such as elephants.

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3.2.3 Data analysis

All simulated output was analysed and visualised using *R* (version 4.1.3, R Core Team, 2019). In the main part of this paper, we focus on the results of the 4- and 8-year long droughts. The complete set of results can be found in Appendix A.6. In all statistical evaluations, climate repetitions were included as a random effect.

Perennial grass cover

To analyse the effect of rangeland use, intensity and drought duration on post-drought perennial grass cover, we applied an aligned rank transform ANOVA (ART-ANOVA) using the ARTool R package (Wobbrock et al., 2011) and conducted post hoc pairwise tests using ART-C (Elkin et al., 2021). To investigate short-, medium-, and longterm plant cover recovery, we chose several points in time for this comparison: the year in which the drought ended (year 0), as well as 10 and 20 years afterwards. For the effect size statistic, we chose the partial eta-squared. The interpretations have been proposed by (Cohen, 1988) and consider an eta squared below 0.06 small, between 0.06 and 0.14 medium and above 0.14 as large.

Resistance and recovery

We defined resistance as the amount the perennial grass cover can resist cover loss compared with the identical scenario without the induced drought (control). We determined the maximum cover loss in response to drought and compared it with undisturbed control cover at the same time.

$$\text{Max. cover loss} = \frac{\text{cover}_{\text{control } i} - \text{cover}_{i}}{\text{cover}_{\text{control } i}} \tag{3.1}$$

We applied generalised linear mixed models (GLMMs) with beta regression and a logit link using the GLMMADAPTIVE R-package (Pinheiro and Bates, 1995) to analyse the ability of grasses to resist cover loss.

We defined recovery as the time until perennial grass regained 80% of the control cover in the identical no-drought scenario after the respective drought event. To determine the impact of rangeland use type, drought duration and plant diversity on recovery rate, we applied GLMMs using the R package NLME (Pinheira et al., 2021).

Plant functional composition

We decided to focus on functional composition instead of biodiversity indices to identify functions and services of specific types and how they can increase rangeland resilience. To determine how the functional composition of perennial grasses and shrubs shifted directly after a drought, we looked at the composition in the year the drought ended. We evaluated the cover of each sub-PFT and the cover relative to its control without drought. We conducted a structural equation modelling (SEM) approach using the package PIECEWISESEM (Lefcheck, 2016) and linear mixed regression models within the SEM. Direct effects assume that rangeland use and drought duration impact PFT cover and its cover relative to control directly. The indirect effect infers that intensity impacts cover by inducing changes in herbivory demand depending on the type of rangeland use. We encoded our questions into a conceptual path diagram (Figure A.1.12):

$$\text{Log\_cover} \sim \text{rangeland use} + \text{intensity} + \text{drought length} + \text{sub PFT} + \text{random} = 1 \;|\text{climrep} \tag{3.2}$$

$$\text{Intensity} \sim \text{rangeland use} + \text{random} = 1|\text{climrep} \tag{3.3}$$

$$\text{Cover\_ratio}_{control} \sim \text{rangeland use} + \text{intensity} + \text{drought length} + \text{sub-PFT} + \text{random} = 1 \;|\text{climrep} \tag{3.4}$$

We tested several model combinations for the best fit using Akaike's information criterion (AIC) and selected the model with the lowest AIC. Global goodness of fit of the final piecewise

SEM was assessed using the χ^2 distributed Fisher's C statistic and the log-likelihood-based χ^2 statistic. We used standardised coefficients to quantify marginal means for each path. We used ANOVA to identify the overall statistical significance of categorical predictors and to calculate marginal means for each level using the EMMEANs package (Lefcheck, 2016). Finally, we performed a pairwise post hoc test using the Tukey-Kramer method.

Cover-NDVI comparison

We related the simulated dynamics of vegetation cover to NDVI time series from Landsat and Sentinel2 in two different habitats at our study site and compared the quantitative changes after a four-year drought. We chose an *Acacia reficiens* shrubland (representing shrub cover) and an open plain (representing grass cover), both at a spatial resolution of 30 × 30 m. We compared the simulated drought scenario with high-density mixed animals to relate them to postdrought NDVI changes.

3.3 Results

3.3.1 Resilience of perennial grasses to droughts

Grass cover was always highest in browsing scenarios, followed by mixed feeding and then grazing (Figure 3.1, Figure A.1.8, Tables A.1.5 and A.1.7). Prolonged droughts, higher proportion of grazers and high intensity of rangeland use significantly decreased perennial grass cover. In the immediate response, the decrease in grass cover was more strongly controlled by the duration of the drought period. However, rangeland use (two-way interaction) and the intensity of this use (three-way interaction) altered this effect. Ten years after the drought, the impact of the duration of the drought on recovery decreased, making rangeland use the strongest determinant of recovery and current cover. Consequently, the combined impact with other factors also decreased. Again, intensity (two-way interaction) and duration of drought (three-way interaction) could enhance or decrease this effect (Tables A.1.6 and A.1.8). In long-term recovery, the impact of rangeland use and intensity increased, but the impact of drought length decreased.

3.3.2 Effects of plant functional diversity on resistance and recovery

In the regimes dominated by grazers, there was no resistance with almost a total loss of perennial grass cover, apart from the regimes with low intensity and no or only a short drought duration (Figure 3.2a, Table A.1.9). Vegetation cover losses were strongest during

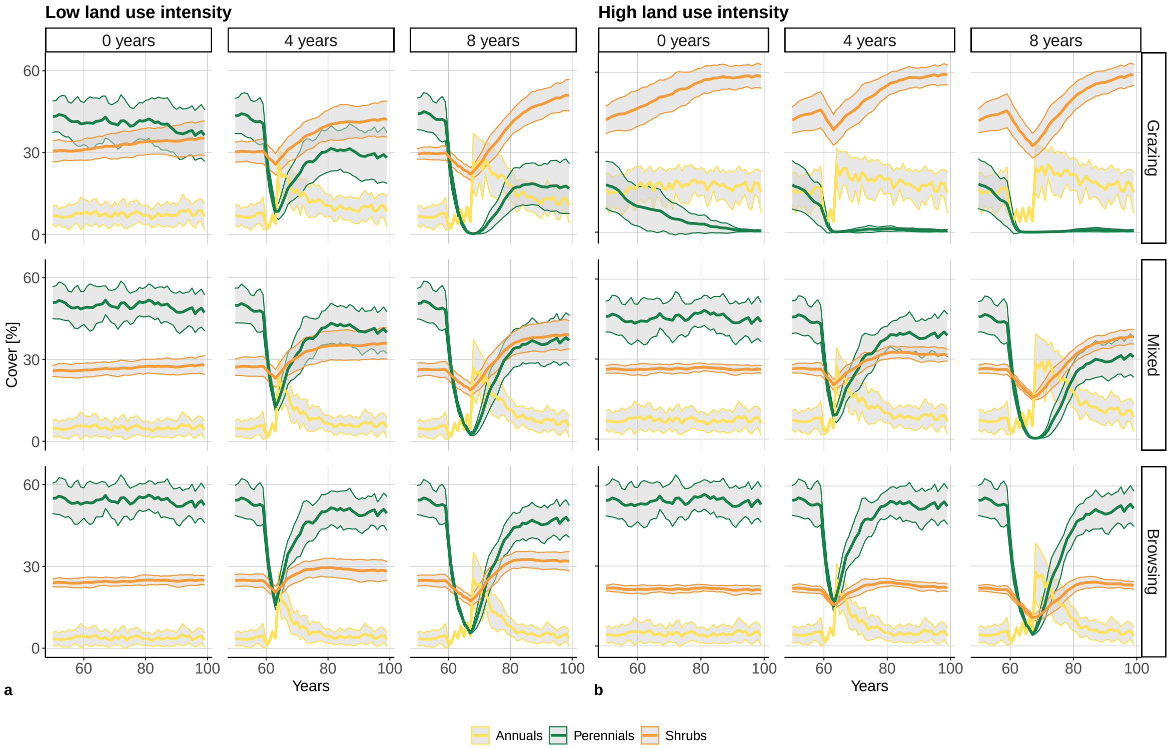

Figure 3.1: Change in vegetation cover over time and relating to rangeland scenario. Predicted mean cover ± SD [%] of the three metaPFTs (lines) under various drought period lengths for all rangeland use scenarios in two intensities (a, b). The numbers (0, 4, 8) at the top correspond to drought duration in years. All droughts began in the year 60 . The graphs are shown from year 50 onwards. All simulations were repeated 30 times with varying climates.

prolonged droughts in combination with high intensity of rangeland use. Independent of intensity, resistance was highest under browsing regimes. Plant diversity served as a buffer against losses during drought periods. Grazing, high intensity of rangeland use, prolonged droughts, and low plant diversity (single) prolonged the recovery time of perennial grasses (Tables A.1.10 and A.1.20, Figure 3.2b). Perennial grasses could not recover under high grazing intensity. We also found faster and more frequent recovery events for diverse plant communities and with more browsers in our climate replicates. However, in a mixed system, there was no significant difference in recovery between communities with high or low plant functional diversity.

3.3.3 Shifts in plant functional composition

In general, the shift of cover was positively influenced by mixed feeding and browsing (Figure A.1.12, Table A.1.11). Rangeland use intensity and drought duration had a negative effect on the extent of cover change (Tables A.1.12 and A.1.13, 83% explained variation, Table A.1.11). Grazing led to the highest deviation in the cover of each sub-PFT and browsing to the lowest

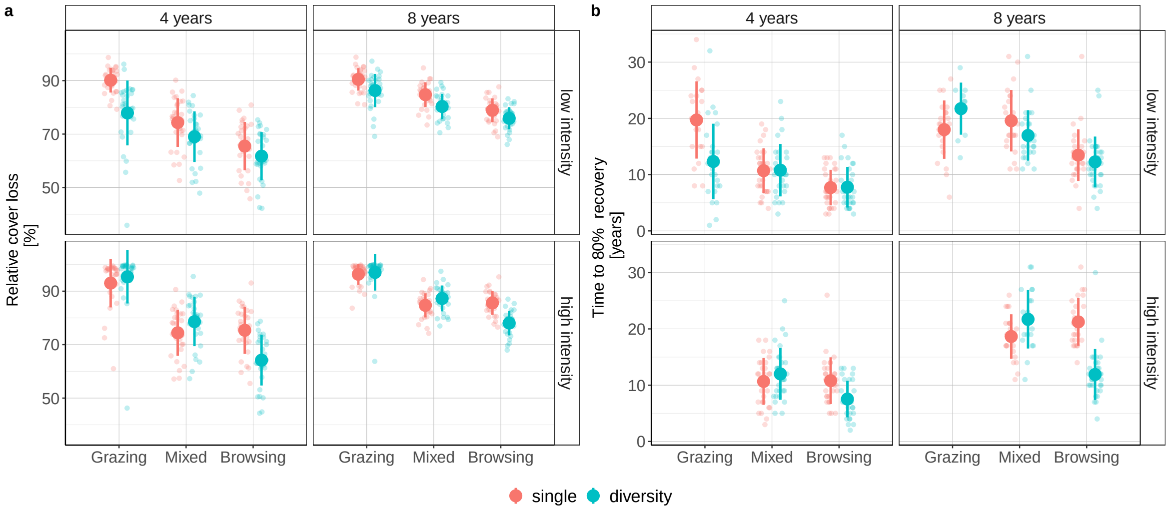

Figure 3.2: Resistance and recovery of perennial grasses in response to droughts. (a) Highest mean cover loss ± SD [%] (large points + range) of perennial grasses during the 4- and 8-year long drought periods compared with the cover in the no-drought control scenario for all three rangeland use types (x-axis). (b) Mean time ± SD [years] until 80% of the perennial grass cover in the control scenario was reached after the drought period ended (large point+range). Red indicates scenarios with a single FPT (single), and blue indicates scenarios with high plant functional diversity. Small points show each of the climate repetitions when 80% of the control cover was reach again (maximum of 30 repetitions per scenario).

(Tables A.1.14 and A.1.15, 53% of the variation explained).

Under a low intensity of grazing, the resulting perennial grass community was dominated by the PFT with low palatability and low drought resistance (Pr) and the highly water-competitive and high drought-resistant PFTs, but very palatable (Cp, Rp, Table 3.1, Figure A.1.10a). Water-efficient and low-palatable PFTs were more abundant than PFTs with high biomass production. The longer the drought lasted, the more dominant Pr and Cp were. As the number of grazers in the mixed feeder and browser-dominated scenarios decreased, the less palatable and drought-resistant PFT (Pr) became slightly less abundant and its dominance was replaced by PFTs of high palatability with efficient water use (CP, Rp, Table A.1.16).

At low herbivore densities, the type of rangeland use affected the shrub composition only slightly (Figure 3.3b). Rangeland use type and intensity, trait combination and duration of drought were the main drivers of each PFT cover (78% of the variation explained) and the respective change in cover compared with the control cover 59% of the variation explained, Table A.1.17). The PFT with high drought resistance and low defence (Rd) was predominant in all scenarios except when there was heavy browsing (Table A.1.19). The PFT with high defence and low biomass production (Db) increased with higher browser proportion and intensity. The longer the drought lasted, the more dominant the drought-resistant and low-defended PFT (Rd).

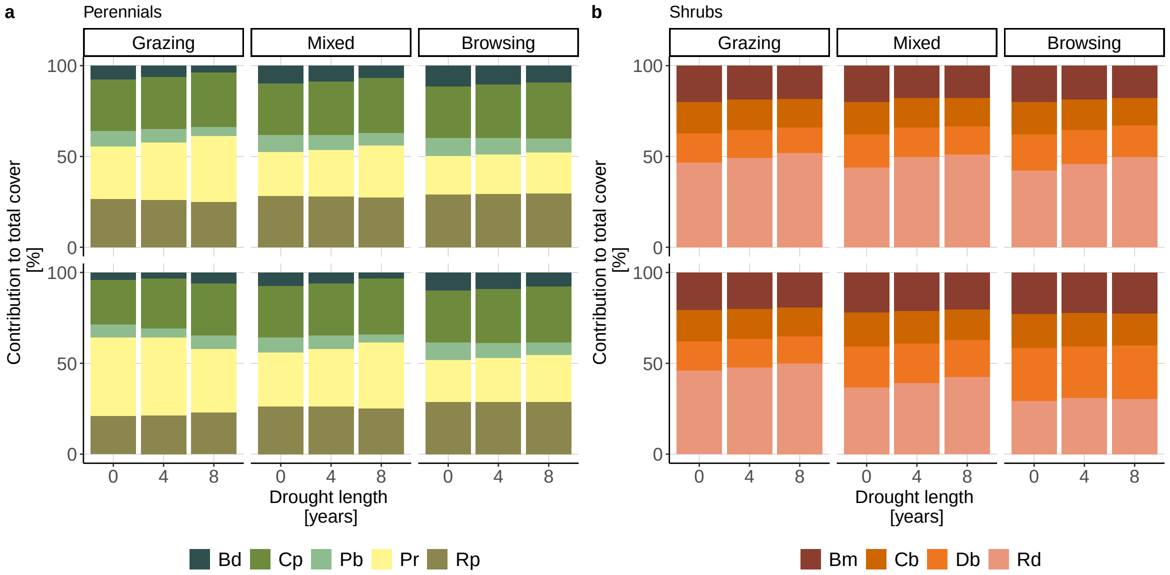

Figure 3.3: Mean relative cover shift of perennial (a) and shrub (b) sub-PFTs in all rangeland use scenarios and under different drought lengths (0, 4 and 8 years). Results represent mean vegetation cover of the first year post-drought repeated 30 times with varying climates.

3.3.4 Cover-NDVI comparison

We found that the mean loss of grass cover and the loss of NDVI were identical (37%, Figure A.1.15). The loss of shrub cover after the drought was 5%, while the loss of NDVI was 25%. Since NDVI loss directly translates into grass loss, the model seems to have done a good job. The loss of shrub cover was lower than the NDVI loss, which is probably because there was still non-green shrub biomass in the model, while in the real system the shrubs were no longer very green and, therefore, had a lower NDVI.

3.4 Discussion

We investigated the combined effects of rangeland use, drought and plant diversity on savanna resilience through modelling. Our findings provide insight into (i) the role of rangeland use type and intensity, drought duration and functional diversity for the resistance and recovery of perennial grasses cover, (ii) the change of vegetation composition in response to prolonged drought, as well as (iii) the importance of self-regulation in ecological processes and (iv) the implications for land management.

3.4.1 Resilience of perennial grasses to droughts

The ability of the perennial grass layer to resist drought-induced loss of plant cover and subsequently recover from these droughts varied greatly depending on the rangeland use type. Changes in perennial cover and subsequent shrub encroachment can be very abrupt (Lohmann et al., 2012; Stuart-Haëntjens et al., 2018), which we found already in single climate repetitions (Figure A.1.14). The dominant presence of grazers significantly reduced the grasses' ability to recover from droughts and suppressed recovery at high intensity of use. That is, when prolonged droughts occur in a savanna system already prone to severe herbivore-induced losses of perennial grasses, the system crossed a threshold that no longer allowed perennial grasses to recover. At the same time, the system degraded even further as shrubs encroached and annuals increased, leading to more bare ground during the dry season. In contrast, the difference in grass cover loss between high and low rangeland use intensity by browsers was only marginal. However, in the scenario with a high number of browsers and grazers, we found a reduction in competition for water. This reduction was caused by browsing limiting shrub cover and allowing higher grass cover (compared with the scenario with a low number of browsing and grazing animals), demonstrating a higher resilience of the system. Our results support the findings of Porensky et al. (2013), who found that more intense grazing by cattle had a greater effect on plant community dynamics than intense grazing by wild herbivores dominated by browsers. We found no differences in the recovery of low- or high-diversity vegetation communities in a mixed herbivore system, which suggests that the balanced effects of herbivory already mitigated some pressure on the vegetation.

The underlying processes determining the performance of perennial grasses are essential to better understand the causes of drought-induced shift of savanna vegetation from a grass-dominated state to a shrub-encroached state, it is necessary to closely look at the underlying processes determining the performance of perennial grasses. Savannas are frequently exposed to droughts, with low soil water content causing extreme stress to plants. Prolonged drought periods can lead to a strong reduction in net primary grass production (Gao et al., 2019) or even to the senescence of most aboveground parts (De Boeck et al., 2011). However, various adaptive physiological and reproductive mechanisms can still allow for a slow growth leading to some recovery (Gao et al., 2019). The speed of perennial grass recovery is highly variable: For example, while some studies found grasses to recover within weeks and a few years after the drought (Wigley-Coetsee and Staver, 2020; Wilcox et al., 2020), others found this to occur only after several years or even decades (Haddad et al., 2002; Ruppert et al., 2015). These contrasting findings show that the severity of a drought and its impact on grass recovery depend on many underlying processes and factors, such as competition for resources, impaired reproduction and ability to re-sprout (Ruppert et al., 2015), compositional shifts towards loss of dominant species (Sankaran et al., 2005) and post-drought rainfall (Stuart-Haëntjens et al., 2018). In our study, we focused on a subset of these factors and found that when perennial grass cover decreased significantly or recovered too slowly, shrubs used their competitive advantage in the acquisition of water from deep soil layers and shrub seedlings established on the available space hence limiting the regrowth of grasses. These results are also in line with previous findings showing that grass removal increased sapling growth and woody plant cover (LaMalfa et al., 2021). Additionally, our model showed the stabilising effect of reduced herbivory pressure on grasses initiated by the introduction of browsing herbivores. Notably, the simulated changes in vegetation are consistent with the remote sensed NDVI changes after a 4-year drought at our study site.

3.4.2 The role of plant functional diversity

Droughts in combination with rangeland use can affect the abundance and composition of savanna vegetation. In particular, drought exempts subordinate taxa from competitive exclusion facilitating their establishment (Porensky et al., 2013), which might partly compensate for loss-induced declines in ecosystem functioning.

In our study, the most dominant grass types always showed adaptations to resist one of the stressors, that is, grazing or drought. Low grazing intensity allows selective grazing with strong benefits for less palatable species. When grazing pressure increases, feeding is no longer selective and, therefore, being superior in the acquisition of resource water becomes more important. The increase in drought-resistant or grazing-tolerant grass species in response to heavy grazing and low rainfall is well known. In response to stress, Fynn and O'Connor (2000) and Wigley-Coetsee and Staver (2020) found an increase in annual grasses as well as weakly tufted perennial grasses, such as *Urochloa mosambicensis* (corresponding to the traits of Rp and Cp in this study) and *Bothriochloa radicans* (equivalent to our other dominant type Pr, Table A.1.4). Although these opposing strategies seem to contradict each other, they show that the importance of a particular adaptation in the recovery phase may be greater than its trade-off.

In stressful environments, short-lived plant species and species with higher persistence and faster recovery after disturbance become dominant (Connell and Ghedini, 2015; Wilcox et al., 2020), as seen by the increase in annuals in this study.

The observed shift in shrub composition resulted from the adaptation of certain shrub sub-PFTs towards severe disturbances. The duration of the drought had only a marginal effect on the shrub composition, as all shrub sub-PFTs benefited from sufficient access to water in deeper soil layers due to their deep rooting system (Joubert et al., 2012; Yang et al., 2021), as well as residual water in the upper soil layer due to low grass cover.

In general, a more diverse plant functional trait composition was more resilient to prolonged droughts and served as a buffer mechanism reducing plant cover losses (e.g. Smith et al., 2013; Wilcox et al., 2020) and supporting faster recovery. However, in some cases of the mixed feeder- and grazer-dominated scenarios, recovery times were prolonged since slow-growing types increased. The slightly slower recovery in the scenarios with more grazers was contrary to our expectations. Here, our approach of including only sub-PFTs with single trade-offs might be too simplified to capture the full picture. Nevertheless, when plant diversity accelerated recovery, we also observed an increase in drought resilient and palatable species. Nevertheless, the slightly slower recovery in the scenarios with more grazers was still contrary to our expectations.

3.4.3 Building savanna resilience through rangeland management

Many nature-based management measures (e.g. restoration, reintroduction, conservation) aim to restore an ecosystem to a previous state that was either "healthier", had a higher degree of "self-regulation" or an "important species composition". Although the management approaches are different, they commonly follow the same objectives: restoration of ecological processes and functions, species restoration and/or the reduction of management interventions (Lorimer et al., 2015; Naundrup and Svenning, 2015; Prior and Brady, 2017). However, to date, it is not clear which ecological processes or functions allow for an appropriate level of self-regulation. With our results, we could determine key factors that contribute to the self-regulation of an ecosystem by reestablishing trophic complexity.

First, we found that the maintenance of a dense perennial grass cover can protect the soil from hot and dry conditions, which decreases soil water losses. Limiting decreases the pressure on grasses by reducing competition for water and space, and thus the need for further management measures, such as fodder supplementation. However, here it is important not only to exclude grazers but also to implement some form of shrub control. As large-scale manual and chemical debushing is costly, and fires are often suppressed in rangelands, the use of browsing herbivores to suppress shrubs can serve as an alternative. Moreover, since wildlife cannot be forced to "debush" small-scale parts of the rangeland, rangeland managers should focus on keeping plains open by systematically removing shrubs before they encroach.

Second, a higher level of functional diversity in the plant community leads to greater resistance and recovery of grasses in response to drought. Although some species were lost, few functionally important species could compensate for their loss and maintain a productive system. In addition, reducing grazing pressure also resulted in a more resilient plant community. Therefore, we conclude that the use of a mix of animal types with more wild browsing herbivores can maintain the perennial grass cover, conserve important functional types and balance the competition between grasses and shrubs, and is therefore of high self-regulatory value. However, in our study, we did not vary the timing of the herbivory impact, which is a critical component of rangeland management. Stimulating grasses by grazing in the growing season can increase growth and enhance productivity (Oba et al., 2000). As animals in game reserves no longer migrate and feeding pressure on plants is high throughout the year, managers must take care of plants and ensure recovery. Feeding pressure can be minimised by effective fence management (Hering et al., 2022), or be reduced by rotation of water points. Consequently, the diversification of animals and plants and good management of the timing and intensity of herbivory have tremendous potential to mitigate climate change and allow for sustainable utilisation of natural resources. For conservation and restoration efforts, we highlight the importance of plant species that are adapted to different environmental stressors and take on appropriate functions. Conserving fast growing, water-efficient and palatable species can be essential to achieve conservation or restoration objectives in the long term.

We propose the following steps to increase the resilience of savannas:

1. Adjust the number of grazers to the system's productivity (Nott and Boys, 2022) and integrate browsers or mixed feeders. We propose that the coexistence of wildlife and livestock is possible in many rangeland types (e.g. conservancy, communal and commercial).

2. Identify plant species that are functionally important for the maintenance of the target ecological processes in the study system (e.g. drought resistant, palatable/nutritional) and include measures to conserve these.

3. Reduce animal stocking rates in anticipation of droughts, during drought conditions, and in the recovery phase afterwards, and manage the timing of high herbivore impact to stimulate plant growth.

4. Consider vegetation dynamics and soil conditions when evaluating changes in animal composition.

Furthermore, in anticipation of droughts, we suggest that rangeland managers diversify their incomes, that is, tourism, meat production, environmental education and fodder production to buffer potential losses within one source of income.

In this context, ecological or socioecological models are a useful tool to identify key factors that increase the self-regulation of ecological processes under different management regimes. Moving forward, we advocate integrating local managers early into the development of models and scenarios, as their combined knowledge of ecology, drought resistance and resilience of savannas will provide crucial guidance for climate-resilient management plans.

4

Navigating Uncertainty: Enhancing Climate Change Resilience in Savanna Ecosystems Through Herbivore Communities

submitted as **Irob, K.**, Blaum, N., Tietjen B (2023). Navigating Uncertainty: Enhancing Climate Change Resilience in Savanna Ecosystems Through Herbivore Communities. *Journal of Applied Ecology.*

Abstract Savannas are characterised by water scarcity and degradation, making them highly vulnerable to increased uncertainties in water availability resulting from climate change. This poses a significant threat to ecosystem services and rural livelihoods that depend on them. In addition, the lack of consensus among climate models on precipitation change makes it difficult for land managers to plan for the future. Therefore, savanna rangeland management needs to develop strategies that can sustain savanna resilience and avoid tipping points under an uncertain future climate. Our study aims to analyse the impacts of climate change and rangeland management on degradation in savanna ecosystems of southern Africa, providing insights for the management of semi-arid savannas worldwide. To achieve this, we simulated the effects of projected changes in temperature and precipitation, as predicted by ten global climate models, on water resources and vegetation (cover, functional diversity, tipping points). We simulated three different rangeland management options (herbivore community dominated by grazers, by browser and by mixed feeders), each with low and high animal densities using the ecohydrological model EcoHyD.

Our findings demonstrate that under high grazing intensity and decreased available water for plant growth, total cover was reduced, functionally important plant types were lost, and available water could not be used as efficiently, leading to earlier tipping points. In contrast, we found that mixed herbivore communities with more browsers had a positive effect on the resilience of the system with tipping points occurring significantly later if at all. This management strategy maintained a higher plant functional diversity and a more stable ecosystem, buffering against adverse climatic conditions.

The study highlights that effective rangeland management practices can enhance ecosystem resilience against the uncertainties and fluctuations of climate change. This is crucial for the sustainability of critical habitats and the communities they support.

4.1 Introduction

The impacts of climate change on semi-arid savannas worldwide are a significant concern, resulting in a decline in ecosystem functioning and services, and affecting the livelihoods of local communities (Hoegh-Guldberg et al., 2019; Osborne et al., 2018). Savannas, woodland-grassland ecosystems that are subject to highly variable rainfall and low water availability (Scholes and Archer, 1997), are expected to face higher uncertainty of water availability due to climate change, which will have consequences for agriculture, health, ecosystems, biodiversity, and energy Generation (Kusangaya et al., 2014). Climate change has already caused changes in temperature and precipitation in savannas reducing soil water availability, altering soil conditions, vegetation cover and composition, soil moisture, groundwater recharge and the entire ecosystem. Most climate change scenarios predict that these changes will only worsen and become more pronounced in the future. Impacts on a regional scale include a decline in vegetation productivity, range contraction and mortality of various plant species (Lawal et al., 2019). Tipping points, characterised by catastrophic and irreversible shifts from grass-dominated to shrub-dominated states are a global phenomenon in savannas. These shifts are already occurring under current climatic conditions, with an expectation for a more frequent occurrence in the future (Stevens et al., 2017). These tipping points can be triggered by various factors, including non-linear responses to precipitation (Hirota et al., 2011), fire intensity and timing (Staver et al., 2009), and grazing (Koch et al., 2023). Critical transitions like these can cause severe soil erosion, loss of biodiversity, and reduced soil fertility (Buisson et al., 2019; Gillson and Ekblom, 2009). While global efforts have focused on reducing carbon emissions to mitigate the impacts of changing climate, there has been less focus on regional climate change adaptation to prevent such transitions. Adaptation through changes in land management is an essential and realistic pathway to prepare humans and ecosystems for the impacts of climate change. Numerous approaches to adapt land management have been proposed, including research and monitoring, biodiversity conservation, education, and awareness raising (Wangai et al., 2016). Vegetation conservation is a crucial aspect of management aimed at preserving important grass and tree species, preventing shrub encroachment, and critical tipping points (Irob et al., 2022; Kapuka et al., 2022; Lohmann et al., 2012). That is, maintaining a dense grass cover can protect the soil from hot and dry conditions, reducing soil water losses and increasing plant water availability (Castellanos et al., 2022; Irob et al., 2022). Moreover, the significance of maintaining plant functional diversity for ecosystem functioning has gained increasing recognition in recent years. Here, specific plant functional traits have been identified as crucial indicators of ecosystem functioning in the face of unpredictable disturbances (Osborne et al., 2018; St. James and Mallik, 2021).

In addition, conserving wildlife is just as crucial as preserving vegetation for the overall protection of biodiversity and sustainable management of natural resources (Lunney and Hutchings, 2012). Wild herbivore communities offer two significant advantages for biodiversity conservation and natural resource management. Firstly, they can alleviate pressure on certain vegetation types, particularly grasses, as they exhibit diverse feeding behaviours, but also by foraging and shifting their diets in response to changes in vegetation patterns and availability. This approach has been found to be effective, as studies by Asner et al. (2009), Irob et al. (2022) and Scogings and Sankaran (2019) have demonstrated. Secondly, mixed wild herbivore communities play a crucial role in shaping the structure and function of savanna ecosystems, potentially enhancing their resilience to the impacts of climate change (Augustine et al., 2011; Knegt et al., 2008; Scogings and Sankaran, 2019). While vegetation and wildlife show promise for addressing conservation challenges, our understanding of their potential is limited by factors such as the intricate nature of wildlife, uncertainties surrounding climate change, and a dearth of regional climate studies.

The lack of science-based regional adaptation plans is reflected in the focus of climate change studies. Most studies are based on global vegetation models (Boone et al., 2018; Scheiter and Higgins, 2009) and/or on the projections by a single global climate model (GCM) (e.g. Mujere & Mazvimavi, 2012). While a global approach is essential for addressing global problems, we also recognise the importance of local solutions that are tailored to the needs of specific regions. Unfortunately, there is a significant lack of studies that downscale climate change projections to the regional level, limiting our understanding of how climate change may impact local ecosystems (Tadross et al., 2017). Regionally, climate projections are influenced by uncertainty in the representation of land use change, land-atmosphere interactions, and the modelling of precipitation and temperature patterns (Schulze, 2011). These uncertainties make it difficult to make precise predictions about the impacts of climate change on southern Africa that is already subject to huge climate variability (Mujere and Mazvimavi, 2012; Schulze, 2011; Tadross et al., 2017). Due to factors, such as the typology and number of models used, the time period and emission scenario considered, and the availability of data, there is an immense lack of consensus among studies on the likely impacts of climate change on water resources (Kusangaya et al., 2014). For these reasons, uncertainty in climate projections and the impacts on water resources requires a multidisciplinary approach that combines hydrological and vegetation models with local data and knowledge. Nevertheless, water resources planning and management decisions in savannas are often based on simulated information using hydrological models only and are therefore likewise subject to uncertainty. Furthermore, it is important to note that to our knowledge, no study has coupled a small-scale hydrological model with vegetation dynamics to examine feedbacks on the entire system, let alone under different rangeland management options.

The objective of our study was to examine the impact of climate change on grazing-induced degradation in the savanna ecosystems of southern Africa. We addressed how rangeland managers could adjust their management to best deal with the uncertainties arising from uncertain future climate conditions. We used an ecohydrological model for drylands (EcoHyD) to test various climate change projections. Specifically, we focused on a Namibian rangeland and assessed the projected temperature and precipitation regimes of ten global climate models under two climate change scenarios across different rangeland types, including grazer-dominated, mixed, and browser-dominated ecosystems in low and high intensity. Our study, focusing on the uncertainties in different regional climate change model projections, aims at answering two following questions: (i) What is the extent of uncertainty in vegetation cover, functional vegetation composition and water resources in different rangeland systems?

(ii) Can adapting the number and types of herbivores promote ecosystem resilience to foster a more stable savanna ecosystem, avoiding critical tipping points? Our findings can be used to develop effective regional adaptation strategies that account for the complex interactions between climate change, rangeland management, and ecosystem health. Such practices can protect the region's natural resources, support local livelihoods, and be applied to similar semi-arid savanna systems worldwide.

4.2 Methods

We model the temporal dynamics of soil water and plant growth using the ecohydrological model EcoHyD, depending on abiotic environmental conditions as present in a typical semi-arid savanna in Namibia. For this purpose, we use data from a specific savanna and corresponding climate data, and test their influence under different rangeland management strategies as described in detail below.

4.2.1 Study site

Etosha Heights is a private wildlife reserve in Namibia's semi-arid savanna, located at S19.1554° E15.1705°. The reserve was established in 2002 by merging eight livestock farms and replacing domestic stock with indigenous wildlife. It covers an area of 492 km^2, situated on the southern boundary of the Etosha National Park. The area is characterised by highly variable precipitation, mainly occurring in the summer months and a mean annual precipitation of 298.67 ± 30.20 mm, with a mean annual temperature of 26°C. The topography is relatively flat with a mean elevation of 1995 m, soil is loamy sand. The wildlife reserve is quite heterogeneous in soil conditions, leading to diverse dominance in plant species, but many parts are dominated by *Colophospermum mopane* and acacia species. Dominant herbivores are springbok, oryx, giraffe, and plains zebra with a grazer-to-browser ratio ranging between 1.2:1 and 0.9:1. More information can be found in Irob et al. (2022) and Hauptfleisch (2022).

4.2.2 Climate input data

In this study, we utilised the results of ten global climate models from the Inter-Sectoral Impact Model Intercomparison Project Research (ISIMIP) that have been bias-corrected for the study site (S19.25°E15.25°) within Etosha Heights (Lange and Büchner, 2021). Here we used daily temperature and precipitation model outputs from the Coupled Model Intercomparison Project Phase 6 (CMIP6). The detailed methodology for these models can be found in the ISIMIP3b group I, II, and III simulation protocol, which are based on historical and projected climate change, as well as observed and fixed socio-economic forcing. To enhance the precision of our analysis, we adjusted the precipitation resolution from daily to hourly values, as described by Tietjen et al. (2010) and generated hourly temperatures based on a daily temperature cycle using the chillR package according to Luedeling (2022). We used historical data from the period from 1970-2014 as the build-up phase to allow for vegetation stabilisation before modelling the future time series from 2015 to 2099. We selected one historical time series that was closest to our station data and used it for all models.

4.2.3 Climate change scenarios

The IPCC's Sixth Assessment Report (AR6) has introduced a new set of climate scenarios, the "Shared Socioeconomic Pathways" (SSPs), that provide better representation of different socioeconomic developments and greenhouse gas pathways. Based on our current climate trajectory, we are focusing on two main pathways: SSP3, a pathway of regional rivalry with rising nationalism and inequality; and SSP5, a fossil-fueled development pathway with a focus on global economic growth and reliance on fossil fuels (IPCC, 2022). The SSP370 scenario involves filling a gap in the CMIP5 forcing pathways with a medium to high radiative forcing trajectory by the end of the century that represents a common forcing level in unmitigated SSP3-7.0 baselines. The SSP585 scenario involves a high radiative forcing trajectory by the end of the century, following the SSP5 socioeconomic conditions and approximately matching the RCP8.5 global forcing pathway, which represents the high end of plausible future.

4.2.4 Climate model description

We described the ten global climate models by analysing mean annual precipitation (MAP), mean annual temperature (MAT) and minimum and maximum values of both precipitation and temperature. In addition, we identified both, meteorological droughts (precipitation below half of average annual rain, length of growing season) and ecological droughts (soil moisture below threshold, Figure A.1.17). The climate models in all figures are ordered by MAP of the SSP585 scenario from low to high.

4.2.5 Precipitation and temperature projected by ten GCMs

The ten climate models differ in their assumptions, climate forcings and historical measurements. We summarised the mean annual precipitation sums from 2070 - 2099 (Table 4.1). In the SSP585, CanESM5 projects the strongest precipitation decrease, with 203 ± 104 mm on average (compared to today 298 ± 30 mm) and IPSL-CM6A-LR projects the highest MAP with 331 ± 123 mm. CanESM5 is also the model projecting the strongest temperature increase, with 27.6 ± 1.2°C. In the SSP370 scenario, CanESM5 projects a similarly strong, and the highest decrease in precipitation (219 ± 119 mm) with a temperature increase 26.5± 1°C. On the contrary, IPSL-CM6A-LR SSP370 projects a precipitation increase to 339 ± 140 mm alongside a temperature increase to 25.1 ± 0.9°C.

Table 4.1: : Mean values of key climatic variables for years 2070-2099: Mean annual precipitation (MAP), mean annual temperature (MAT), number of meteorological drought years (MAP < 150 mm) and mean duration of growing season (GrowS) based on 10 different global climate models and two climate change scenarios (SSP370, SSP585). The models are ranked in descending order by MAP under the SSP585 scenario, ranging from the lowest to highest.

	SSP730				SSP585			
Model	**MAP** [mm]	**MAT** [°C]	**Drought** [years]	**GrowS** [days]	**MAP** [mm]	**MAT** [°C]	**Drought** [years]	**GrowS** [days]
CanESM5	220 ± 119	27 ± 1	8	181 ± 103	203 ± 105	28 ± 1	9	202 ± 96
CNRM-ESM2-1	269 ± 138	26 ± 1	9	207 ± 90	215 ± 113	27 ± 1	12	253 ± 66
CNRM-CM6-1	252 ± 85	26 ± 1	5	199 ± 92	230 ± 112	28 ± 1	7	218 ± 99
GFDL-ESM4	242 ± 108	25 ± 1	5	198 ± 77	244 ± 101	25 ± 1	5	212 ± 95
EC-Earth3	255 ± 97	25 ± 1	4	206 ± 85	252 ± 109	26 ± 2	6	206 ± 89
MPI-ESM1-2-HR	278 ± 108	24 ± 1	2	204 ± 107	264 ± 116	25 ± 1	5	225 ± 76
UKESM1-0-LL	298 ± 116	26 ± 1	3	216 ± 74	286 ± 126	28 ± 1	5	206 ± 84
MIROC6	306 ± 153	24 ± 1	7	181 ± 90	289 ± 106	25 ± 1	2	185 ± 89
MRI-ESM2-0	291 ± 106	25 ± 1	4	208 ± 88	294 ± 109	26 ± 1	2	232 ± 71
IPSL-CM6A-LR	339 ± 140	25 ± 1	2	185 ± 109	332 ± 124	26 ± 1	1	161 ± 101

Meteorological droughts

For each climate model and change scenario, we analysed the total number of years in which MAP fell below 150 mm during the last 30 years of the climate data, i.e., between 2070 and 2099. Our findings indicate that the CNRM-ESM2-1 and CanESM5 models projected the highest number of drought years under the SSP585 scenario, with a total of 12 and 9 years respectively. This represents approximately one third of the analysed 30 years. Conversely, IPSL-CM6A-LR and MIROC6 models projected only 1 and 2 dry years respectively due to their projection of increased precipitation. Additionally, we observed that the SSP585 scenario projected more droughts when compared to SSP370. Most models projected over 15% of drought years in the 30-year period studied.

Growing season duration

We defined the growing season as the period between the first and last day with rain above 5 mm. We determined the length of the growing season for every year and calculated the mean value for the years 2070 to 2099 for every climate model and climate change scenario.

4.2.6 Model description

We employed the EcoHyD model, an ecohydrological and spatially explicit model for dryland systems (Irob et al., 2023; Irob et al., 2022; Lohmann et al., 2012; Tietjen et al., 2010) to simulate an area of 2.25 ha, which consists of 900 grid cells with a resolution of 5×5 m^2 per cell. This model has been previously used and validated in different dryland ecosystems (Irob et al., 2023; Lohmann et al., 2012; Tietjen et al., 2010).

The EcoHyD model is a spatially-explicit, process-based model that simulates the dynamics of vegetation and hydrology in dryland ecosystems. It consists of two submodels: a vegetation submodel and a hydrological submodel. The vegetation submodel simulates the life cycle of different plant functional types (PFTs) including shrubs, perennial grasses, and annual grasses. It takes into account processes such as growth, mortality, competition for water and space, seed dispersal, seedling establishment, and herbivory. The hydrological submodel simulates the daily dynamics of surface water and soil moisture in two soil layers. It is based on precipitation, lateral water redistribution, infiltration, vertical fluxes, and water losses through evaporation and transpiration. The model also considers the impact of vegetation cover on evaporation and transpiration, and the root distribution of annual grasses which allows them to access water only in the upper soil layer. More details on the model's structure and parameters can be found in the appendices (A.1, A.2).

4.2.7 Assemblage of plant sub-PFTs

The model describes the fate of three major plant functional types (meta-PFTs): woody vegetation (hereafter referred to as shrubs), perennial herbaceous vegetation (perennials) and annual herbaceous vegetation (annuals). The base subtype of each meta-PFT (hereafter referred to as "base type") had the same set of parameters as the default meta-PFT in savannas. We then derived additional subtypes (for shrubs and perennials) by defining individual life strategies that have trade-offs in seven traits but are otherwise identical to the base type. Sub-PFTs were derived by defining individual life strategies based on the main species we found in Etosha Heights (Table A.4.1). We categorized these into trade-offs in seven particular characteristics, related to processes biomass production B, competitive strength for water C, defense D, establishment moisture need E, mortality M, palatability P and resistance to drought R (Irob et al., 2022). According to a vegetation survey carried out at our study site, species were assigned qualitative values for these traits that we translated into parameter values that resulted in a 10% cover increase or decrease according to a sensitivity-analysis conducted (A.4). For example, a sub-PFT could be very strong in competing for water resources with very little need for a lot of water to establish but exhibit a very low biomass production as a trade-off.

As annuals only dominate degraded systems (Case et al., 2020), we did not subdivide them further. In total, we parameterised each seven sub-PFTs for perennials and shrubs from our local species pool that exhibit potential relevant adaptation mechanisms to herbivory, water use and/or climate.

4.2.8 Management scenarios

We investigated the impacts of three types of rangeland use defined by animal composition and density, that we refer to in our figures as land use and intensity. The herbivore communities in our model are defined by a specific biomass demand that they have to fulfil by feeding on plant functional types. Accordingly, we defined three rangeland types based on their biomass demand: with mainly grazing herbivores, with mainly browsing herbivores or with mixed feeders. The animal density of each type was set to high (10 ha/LSU) or low (40 ha/LSU). Depending on the animal density, the ratio of the diet preference determines then the amount of biomass of a functional plant type that can be taken from its edible biomass. Large browsers, such as elephants, were not accounted for in this model setup.

For grazing-dominated rangelands, the ratio of the diet preference was set to 80% herbaceous vegetation and 20% shrubs (vice versa for a browsing-dominated preference). If the preferred forage type was not fully available, this ratio had a flexibility of 15% to enable meeting the feeding demand by adaptive herbivory. This allowed grazing herbivores to meet their feeding demand with $65 - 95\%$ herbaceous vegetation intake. For mixed feeders, we set the ratio to 50:50% with the same flexibility.

4.2.9 Analysis

In the results and discussion, we evaluate output using the concepts of resilience and stability. Resilience, as per Irob et al. (2023), refers to an ecological system's ability to withstand disturbance without significant state change, achieved through resistance or recovery from stress.

Cover

In order to evaluate the effect of climate and rangeland management on vegetation cover, we calculated the mean cover and standard deviation for each vegetation type in response to mean annual precipitation (MAP). To detect uncertainties resulting from management, we analysed the period from 2089 to 2099, for each climate and rangeland management scenario.

Functional diversity

To assess the combined effect of climate and rangeland management on functional diversity, we calculated various functional diversity indices (functional richness ($FRic$), functional evenness ($Feve$), functional divergence ($FDiv$), functional dispersion (*FDis*), Rao's Q (RaoQ) and community weighted means (CWM), Table A.1.22) based on the trait distribution and species abundance of the resulting communities. As most of the indices were highly correlated, we only present the distance-based multidimensional index of functional dispersion (*FDis*). This index, calculated using the 'dbFD' function in the FD R-package (Laliberté and Legendre, 2010), considers the trait distribution and species abundance in the communities, and measures the dissimilarity and evenness of trait distribution. It is weighted by the relative abundances of each species in the community. High values of *FDis* indicate a more diverse and evenly distributed set of traits, while low values indicate dominance by a few similar traits. We then determined the average *FDis* at low and high rangeland use intensity scenarios in the last 10 years of simulation.

Water use efficiency

To evaluate the ability of vegetation to utilise available water and the potential impact of rangeland management on this ability, we calculated water use efficiency (WUE). WUE was defined as the proportion of annual precipitation that plants can use for transpiration and growth. We quantified the mean WUE in low and high rangeland use intensity scenarios in the years 2089-2099.

Tipping points

In order to investigate the impact of rangeland type and climate change on critical vegetation transitions, we determined the time point when a transition occurred from perennial grass dominance to shrub dominance. As all simulations began with perennial grasses as the dominant vegetation type, we defined the tipping point as the year when shrub cover turned equal to or higher than perennial grass cover. To assess the long-term implications of this tipping point and to confirm whether a true transition had occurred, i.e. shrub dominated or complete loss of grasses, we also analysed the total shrub cover at the end of the simulation and how it relates to total cover.

4.3 Results

4.3.1 Cover

Our analysis distinguishes between two main sources of uncertainty affecting rangeland management: those associated with climate model predictions and the underlying scenarios, and those associated with animal type and density. For rangeland management with low animal densities, the cover of grass and shrub was relatively resilient over time (Figure A.1.18 and A.1.19), and with minimal variation between the three rangeland types at the end of the simulation. In terms of animal type and density, our simulations show that the SSP370 scenario with low browser density had the highest perennial cover (across all GCMs: 58.1 ± 4.8%), while the highest shrub cover was almost identical in both climate change scenarios with high grazer density (across all GCMs in SSP370: 41.6 ± 4.6% and SSP585: 42.6 ± 4.6%). Furthermore, high grazing intensity resulted in a significant decrease in perennial grasses and near-complete loss, leading to more barren soil. Our results suggest that maintaining low grazing intensity and receiving higher precipitation are critical factors in achieving a high perennial grass coverage.

However, the different projections of the ten GCM caused variation of $20 - 25\%$ in perennial grass cover within one rangeland type (Figure 4.1, Table A.1.21). In contrast shrub cover was relatively stable in response to different climate projections with biggest variations in the high grazing scenario, with differences of up to 12%. The SSP585 scenario showed slightly lower grass cover and higher shrub cover than SSP370 but exhibited similar trends.

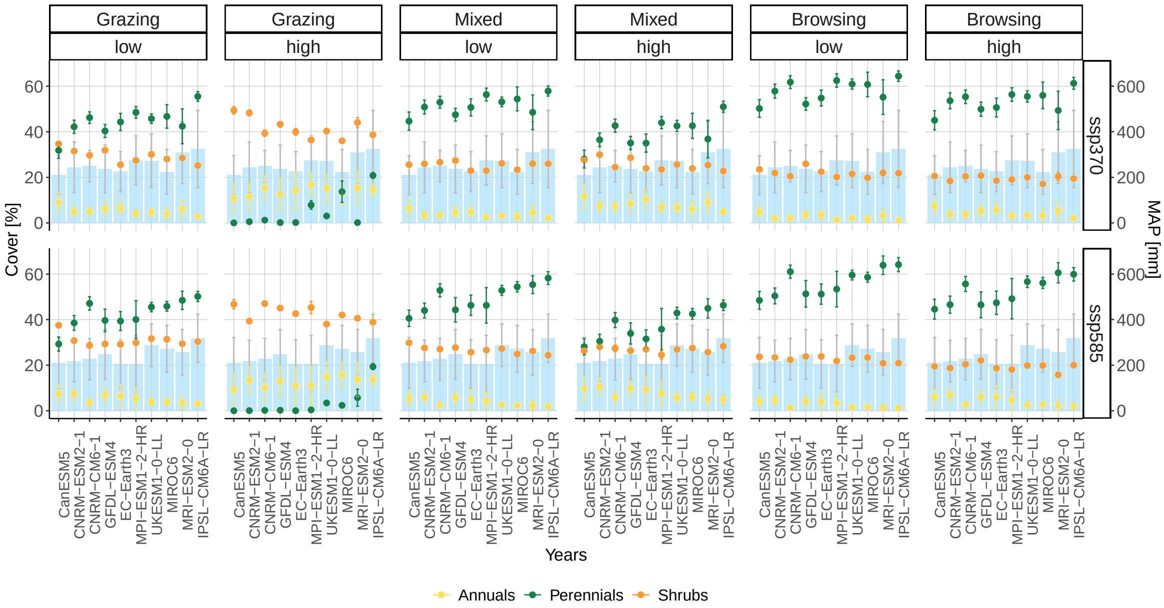

Figure 4.1: Discovering the relationship between precipitation and vegetation cover under different management. The blue bars represent the mean annual precipitation (MAP) ± SD, while points depict the mean cover ± SD of perennial (green), annual grasses (yellow), and shrubs (orange) averaged over the years 2089-2099. Changes shown across 10 different GCMs and 2 climate change scenarios under 3 rangeland types in two intensities.

4.3.2 Functional diversity

Our analysis of functional dispersion among different rangeland types and intensities revealed the importance of considering multiple sources of uncertainty, including climate scenarios and the respective model predictions and animal type/density factors. Our simulation showed that the resulting plant community was generally stable in response to different animal types, densities, and climatic conditions, indicating a high resilience of the ecosystem. However, for a high density of grazing animals we observed significant reductions in functional diversity and substantial uncertainties in response to climate projections (Figure 4.2, Table A.1.22). This highlights the vulnerability of high-intensity grazing systems and the importance of addressing these factors in rangeland management plans. In these cases, lower values of functional dispersion indicate that the system was dominated by species with few distinguishing characteristics. This trend was particularly evident in the SSP585 scenario, where functional diversity reduction was more pronounced. While the relationship between precipitation gradient and *FDis* was not clear in this analysis, we observed that IPSL-CM6A-LR - the climate model with the highest MAP - was the only one that did not show a reduction in *FDis* under high grazing.

Despite the negative effects of high-intensity grazing our analysis suggests that mixed herbivore and browsing scenarios are the most effective at maintaining species with a range of different traits regardless of animal density.

Figure 4.2: Differences in Functional Dispersion (*FDis*) in the last 10 years of simulation between low (grey) and high (red) land use intensity. All simulations were repeated for 10 climate models under 2 climate change scenarios for 3 rangeland types.

4.3.3 Water use efficiency

The analysis of water use efficiency (*WUE*) revealed that maintaining low animal densities resulted in similar *WUE* values across all rangeland types, averaging around 80% of precipitation that could be used by plants for growth (Figure 4.3). This low animal density helped to minimize uncertainty in the response to different climate scenarios, as the variation in *WUE* was lower compared to higher animal densities. Under high animal density, grazing scenarios had the lowest *WUE* values (65%), while browser-dominated scenarios had the highest (on average 79%), followed by mixed-feeder scenarios (on average 76%, Table A.1.23). The differences between climate models or climate scenarios were not significant, but differences in animal densities were evident, with lower *WUE* at high intensity. For instance, high grazing intensity in the SSP585 scenario resulted in a sharp decline of *WUE*, with a reduction of 19.5 ± 4% compared to low grazing. However, the difference in *WUE* within the other rangeland types and intensities was less strong, ranging between 4 and 7%.

4.3.4 Tipping points

We found that grazer density was the primary driver of vegetation transitions, resulting in a shift towards a shrub-dominated state with reduced cover of perennial grasses (Figure 4.4, Table A.1.24). For grazing-dominated scenarios, tipping points, i.e., strong and normally hardly reversible shifts from grass-dominated to shrub-dominated savannas, were observed

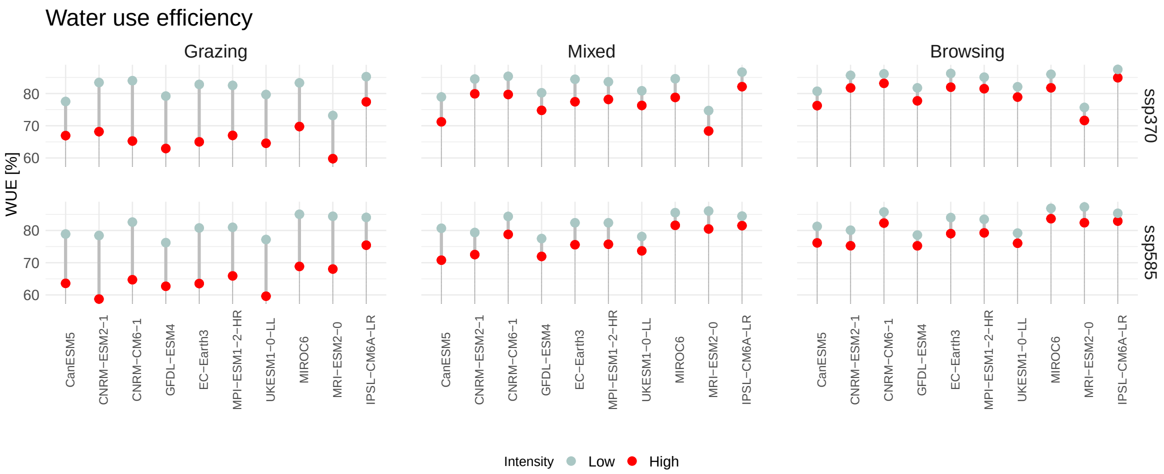

Figure 4.3: Comparison of water use efficiency (WUE) across three rangeland types with varying intensities, (low = grey, high = red) using data from 10 climate models under two different climate change scenarios. The WUE values are calculated as the ratio of transpiration to annual rainfall and are shown for the final 10 years of the simulation.

in all models and climate change scenarios within the first 10 years of simulations, with the highest probability occurring in the most arid models, CanESM5 and CNRM-ESM2-1. While no tipping occurred in browsing- dominated scenarios, tipping points were also detected in the mixed scenario at high intensity. This indicates that the intensity of grass removal has a greater impact on vegetation shifts than climate change alone. The timing of the tipping points showed a clear relationship with shrub abundance, with earlier tipping points resulting in higher shrub cover at the end of the simulation. The marginal difference in tipping point timing between climate change scenarios suggests that uncertainties related to animal type and density are more significant than those related to climate.

4.4 Discussion

The primary objective of this study was to investigate the impact of regional climate change projections on the vegetation and water resources of a savanna system, while exploring potential management strategies to mitigate uncertainties resulting from differences in climate projections. Through our modelling approach, we were able to comprehensively explore the interplay between savanna vegetation response to different climate scenarios and management practices, as well as the intricate relationships between vegetation cover, functional composition, and water resources.

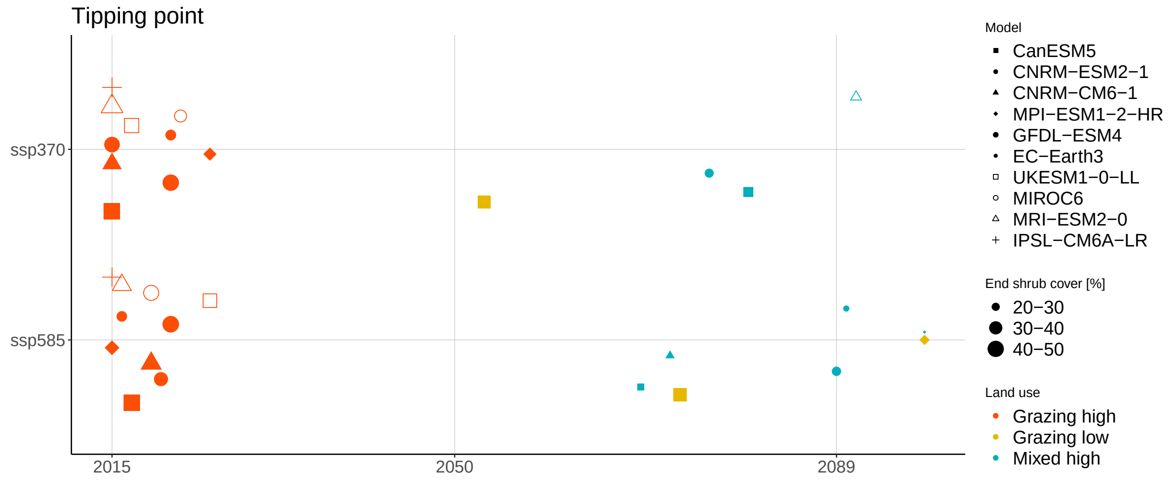

Figure 4.4: Time point (year) when a vegetation shift occurred from perennial grass to shrub dominance. Results are shown for two climate change scenarios (SSP370/SSP585) and 10 climate models. The figure only displays the cases where the vegetation shift occurred. The colour of the symbols represents the rangeland type (land use), their shape the indicate the model and the symbol's size indicates the shrub cover in the last year of the simulation. The number of points for a given climate and land use scenario provides information about the uncertainty of a tipping point, which is biggest for moderate numbers.

4.4.1 Climate change-related uncertainty in vegetation in grazing systems

Vegetation changes are influenced by a variety of factors, including both climatic conditions and management practices. However, the effect of management practices is heavily dependent on prevailing climate conditions. While the response of grasses to water availability is well understood and predictable - grass cover increases with increasing mean annual precipitation (MAP) - the response of shrubs to climate change is more uncertain. This is because shrubs are not directly responsive to rainfall and are instead strongly influenced by competition with perennial grasses, as also seen in February et al. (2013). Grasses are stronger competitors for surface water due to their extensive root systems in the upper soil layer, which can limit the growth and abundance of shrubs (Case et al., 2020). The competition between shrubs and grasses helps maintaining a balance between different plant species, ensuring the coexistence of diverse plant communities (Holdo and Nippert, 2023).

However, we found that the uncertainty in vegetation response was strongly correlated with grazing intensity. Overgrazing can lead to a reduction in grass biomass, which can result in more bare and unstable soil surfaces (Washington-Allen et al., 2010) with negative consequences for plant diversity and ecosystem services such as soil conservation, water regulation, and carbon sequestration (Maestre et al., 2022). Heavy grazing reduces grass cover, thereby increasing the amount of water available for shrubs, leading to a release from competition and expansion of shrub cover. This pattern was confirmed in this study and has been observed in many overgrazed savanna systems (Pfeiffer et al., 2019; Polley et al., 2017). The drastic reduction in grass cover in grazing systems in simulations with less precipitation may not be solely due to less rainfall. It could also result from other unpredictable water availability reductions, such as more frequent drought years, shorter growing seasons (Table 4.1), and less available water for plant growth (Figure A.1.17), with consequences for plant functional diversity.

The diversity of plant functional traits, as measured by functional dispersion (*FDis*) is a measure of the diversity of plant functional traits within a community, and it is an important indicator of ecosystem health and resilience in rangeland management (St. James & Mallik, 2021). We found that high grazing intensity had a negative effect on functional dispersion, as also found in Chillo et al. (2017), indicating that here, one or a few similar traits dominated the system. Low functional diversity can be a warning sign of declining ecosystem health, as it is often associated with reduced grass cover, increased shrub encroachment (Ford et al., 2018; Irob et al., 2023; Osborne et al., 2018) and low plant water availability (Castellanos et al., 2022; Irob et al., 2022). That is, the response of trait diversity to grazing pressure appeared to be considerably more uncertain when compared to the response to climate conditions.

While the response of vegetation to climate change-related uncertainty is complex and multifaceted, our findings suggest that understanding the interactions between climatic conditions, management practices, and plant competition can help improve our ability to manage vegetation and promote ecosystem resilience in the face of changing environmental conditions.

4.4.2 Navigating uncertainty: Best practices for vegetation and water management

In this study, we found that managing grazing intensity and animal populations can mitigate the negative impacts of climate change on ecosystems. Systems with mixed herbivores and browsers or low grazing intensity had a more stable cover of perennial herbaceous plants and functional diversity. Although the abundance of grasses and shrubs varied, the functional diversity remained constant, suggesting that different functional traits were present in the community, helping to maintain ecosystem functioning and services under changing environmental conditions. These findings highlight the importance of managing grazing intensity and promoting functional diversity to increase the resilience of savannas under climate change. The stable response to different climate projections suggests that plant communities can adapt well to climatic variations (Carmona et al., 2012).

Effective rangeland management is essential for maintaining water-related aspects impacted by climate and grazing practices. Reduced grass cover can increase the amount of bare soil, radiative heating and evaporation, which negatively affects water use efficiency (WUE, measured as the amount of precipitation that was used for plant transpiration), leading to less effective transfer of precipitation to soil moisture and resulting in landscapes with low WUE and heterogeneous vegetation patches (Abraha et al., 2016; Tian et al., 2011). However, by maintaining adequate vegetation cover and leaf area index (LAI), water loss through evapotranspiration are minimised, leading to increased water availability for ecosystem services, other purposes, and the restoration of degraded ecosystems (Irob et al., 2023; Tommasino et al., 2023).

High grazing intensity and increased aridity can lead to uncertain and negative outcomes for savanna ecosystems, including grass and functional diversity loss, as well as reduced water use efficiency (Chillo et al., 2017; Hirota et al., 2011; Pfeiffer et al., 2019). These outcomes can lead to degraded ecosystems that may not recover from environmental changes or disturbances. Rangeland management should be aware that high grazing pressure can cause tipping points, leading to dramatic and permanent changes in ecosystem functioning. Even in mixed-scenarios with both grazers and browsers present, high animal densities can still result in tipping points, albeit later than in scenarios with predominantly grazers. However, maintaining a balance of grasses and shrubs can be achieved by increasing the number of browsing animals, which remove shrubs and counteract shrub encroachment while allowing grasses to recover and grow. Managers should account for the potential for grazing animals to cause instability in savannas, particularly under hot and dry conditions. Research by Koch et al. (2022) highlights the risk of critical transitions to a state dominated by shrub encroachment when grazing is combined with other disturbances, such as drought. Therefore, managers should consider reducing animal densities to minimise the potential for ecosystem destabilisation. Managers should prioritise promoting a more diverse herbivore community to increase ecosystem resilience to changing conditions. Low animal densities and browser-dominated rangeland types can help prevent tipping points, whereas mixed rangeland types with high animal densities present uncertain risks for ecosystem stability. Due to the uncertain climate change impacts, managers should invest in further research and monitoring to improve understanding of ecosystem dynamics and inform effective management strategies. It is important to note that the tipping points we described are a local-scale phenomenon, and may not be applicable to larger landscapes or regions. Local managers hold a crucial role in the transition, as they possess the ability to either prevent or facilitate phase transitions (Gillson and Ekblom, 2009).

To manage ecosystems effectively in the face of uncertainty, it is essential to consider various adaptation measures that minimise negative impacts. Our research demonstrates that diverse herbivores and browsing species, are crucial for stabilising ecosystems, as confirmed by similar semi-arid savanna studies (Koch et al., 2023; Scogings and Gowda, 2019). Additionally, combining browsing herbivores and fire has a significant stabilising effect (Staver et al., 2009). Finally, several management tools have been identified, such as adjusting herbivore composition and densities, monitoring critical ecological variables (e.g. grass cover, functional vegetation composition and soil water), enhancing functional diversity, and promoting self-regulation factors, that can influence ecosystem transitions.

These findings underscore the potential for local managers to play a vital role in enhancing savanna resilience to climate change. By leveraging the right management instruments, managers can promote biodiversity and increase ecosystem resilience in the face of future disturbances.

4.5 Conclusion

Future climate change projections vary significantly, posing a challenge for developing effective rangeland management strategies to enhance savanna resilience and mitigate uncertainties. Thus, proactive and adaptive management approaches are necessary to account for the complexity and unpredictability of climate change.

Our research revealed that mixed or browser dominated herbivore communities can yield positive results associated with less uncertainties. We observed stable vegetation cover under various climate projections, such as low rainfall and droughts, with high functional diversity, and a high water use efficiency, highlighting the adaptability of the savanna plant community to different precipitation and temperature conditions. Our study confirms that the degradation of rangeland ecosystems is not solely driven by climate change, but rather by the interaction of climate change with unsustainable rangeland practices. In conclusion, our research has demonstrated that local managers have the power to prevent or facilitate transitions using various management tools at their disposal. We recommend the use of mixed herbivore communities as a means of maintaining a healthy, productive, and resilient ecosystem while mitigating the impacts of climate change induced disturbances.

5

General Discussion

Savannas are crucial for human well-being as they offer essential ecosystem services. However, they face threats from unsustainable rangeland practices and the challenges of climate change. The transition from traditional herding to farming, which involves confining livestock within fixed boundaries, has resulted in extensive degradation of semi-arid savannas. This degradation often leads to the ecosystem crossing a tipping point, with irreversible consequences.

This thesis aims to support rangeland management efforts that promote the long-term resilience of savannas and the provision of multiple ecosystem functions and services. To achieve this, I employed an ecohydrological simulation model to investigate the effects of various rangeland practices on the properties and processes of savanna ecosystems under current and future climatic conditions.

One of the significant contributions of this research is the evaluation of potential effects of various future climate projections on a regional scale, which is an important aspect of climate change studies that has been lacking in previous research efforts. Additionally, this research extends traditional modelling by incorporating rangeland types beyond grazing, such as browsers and mixed-feeding herds. This approach has yielded new perspectives on sustainable land management in savanna systems.

In Chapter II, I studied the effects of herbivore grazing and browsing strategies on plant functional diversity and ecosystem functioning. The results showed that intensive grazing lowered plant diversity and water availability. In contrast, browsing increased vegetation cover, plant diversity, and improved plant water use.

To have a better understanding of various management under climatic extremes, in Chapter III, I investigated the impacts of droughts of different lengths on savanna ecosystems under grazing, mixed and browsing herbivore communities. The results demonstrated that high grazing intensity reduces the resilience of perennial grasses during droughts. However, a more diverse herbivore population, with a high proportion of browsers, together with a higher level of plant functional diversity, enhanced the resistance and recovery of savanna vegetation, even during extended periods of drought. As a result, ecosystem functioning and resilience were preserved.

Lastly, in Chapter IV, I explored how wild herbivore communities can serve as a means in regional climate change adaptation plans to ensure resilience of savanna rangelands against the impacts of uncertain climate change. I found that intense grazing and low water availability can quickly push the system beyond a critical tipping point. However, management practices that reduced grazer densities and incorporated mixed herbivores and browsing animals increased vegetation cover, plant diversity, and water use efficiency. Such measures can delay or even prevent tipping points and promote ecosystem stability and resilience.

In the following discussion, I will present the theoretical and practical implications of my research findings from Chapters II to IV. First, I will explain how my findings demonstrate the effectiveness of wildlife management and plant diversity as tools for enhancing ecosystem functioning and resilience in savannas. My study provides insights into how herbivores shape plant communities and, in turn, how plant composition and diversity affect ecosystem functionality. Based on this, I will suggest how management strategies could be adapted to better address current and future climate challenges. Second, to enhance our understanding of savanna ecosystems even further, I will discuss the potential features to improve model predictions in future model development. Finally, I will outline practical steps that can be taken in real-world systems to ensure successful implementation of these tools. Overall, this discussion aims to provide a comprehensive outlook on how my research can contribute to improving the management and resilience of savanna ecosystems.

5.1 The role of herbivores in shaping plant communities

The abundance of plants is greatly influenced by herbivores, whose impact is determined by the density and diversity of these animals (Bakker et al., 2016). As rangeland management can control herbivore density and diversity, it is crucial to have a deep understanding of these interactions to ensure the long-term sustainability of plant communities and ecosystem functions.

By specifically modelling this in a savanna system, I could identify the following key processes to be considered in future rangeland management. High-density herds of grazers can shape the vegetation to be dominated by shrubs, with very few grasses present (Chapter II, Chapter III). This is because the removal of grasses creates unoccupied space, reducing competition for water and nutrients and allowing shrubs to thrive. Consequently, a window of opportunity arises for woody species to establish and encroach, as well as for annual grasses to thrive in the newly created open space. This commonly observed pattern (Eldridge et al., 2011; Maestre et al., 2022) is one of the main drivers of land degradation associated with overgrazing (Archer et al., 2017; Nacoulma et al., 2011; Pfeiffer et al., 2019). Besides, I found that intensive grazing homogenised the grass community composition, with only unpalatable and slow-growing types surviving, as also seen in DÍaz et al. (2007). Furthermore, my research revealed that moderate densities of herbivore communities of mixed-feeders resulted in an equitable utilisation of plant resources and shaped the savanna vegetation to be more balanced, with a variety of grasses and shrubs surviving (Chapter III and IV). Conversely, high densities of browsing-dominated herds led to lower shrub cover and a greater diversity of grass species thriving (Chapter II, III). Although browsing-induced reduction of shrub cover was less compared to the grazing-induced reduction of grass cover, it still created sufficient space for perennial grass to thrive and dominate (Chapters II, III, and IV). Besides, browsing also influenced shrub composition, as the dominant shrub shifted from a drought-resistant shrub to one with higher defence mechanisms against herbivores (Chapter III). Such increases in defence mechanisms are commonly observed in savannas as a response to browsing (Rooke et al., 2004; Scogings et al., 2011; Wigley et al., 2019).

Two key differences between grasses and shrubs explain the vulnerability of grasses to rangeland management and water scarcity. First, shrubs have a deep rooting system that provides them with an advantage in resource allocation and establishment over grasses, especially under periods of low water availability (Yang et al., 2021). Although grasses can quickly establish under new water input, their shallow root systems make them susceptible to grazing and limit their ability to compete with other plants in the long term (McSherry and Ritchie,

2013). Second, shrubs have developed several defence mechanisms, such as spines and tannins, that allow them to better cope with herbivory (Scogings et al., 2011; Wigley et al., 2019), while grasses rely on compensatory processes (Oba et al., 2000). As a result, grasses are more vulnerable to intense herbivory compared to shrubs.
With these features implemented in the model, shrubs could thrive under a variety of rangeland management scenarios, as evidenced by comparable cover and trait distributions (Chapter II, III and IV). These features allowed them to capitalise on opportunities such as the release from competition with grasses for resources like water and space. As a result, they could grow and spread rapidly, except in cases of intense browsing.

In addition to herbivore density and diversity, climate plays a crucial role in shaping plant communities. As the climate changes, competition for scarce resources such as water will increase, affecting the way herbivores shape plant communities. My research found that the negative impacts of high grazing intensity (Chapter II) were exacerbated under drought conditions (Chapter III) and even more so under future climatic conditions, such as lower precipitation, increasing temperatures, and droughts (Chapter IV). The combination of grazing with extreme climatic events triggered a loss of perennial grasses and, without management intervention, an irreversible shift to a shrub-dominated state (Chapter III and IV), a common phenomenon that has been observed in savannas worldwide (Cabral et al., 2003; Hirota et al., 2010; Lunt et al., 2010; Stevens et al., 2017; Van Auken, 2009; Wigley et al., 2009).

To maintain desirable grass cover and composition under challenging climate conditions, reducing grazing pressure is necessary (Chapter III and IV). Therefore, adequate herbivore management and climatic conditions should be considered in rangeland management to ensure long-term sustainability of plant communities and ecosystem functioning.

5.2 Positive effects of plant functional diversity on ecosystem functioning

In the following section, I will explore the effectiveness of several plant functional diversity measures as predictors for ecosystem functioning and discuss the relationship between plant functional types and ecosystem functioning.

Throughout my studies, I have explored various facets of plant diversity and their links to ecosystem functioning. One key observation I made was that species richness (in the following referred to as richness) as a stand-alone measure of biodiversity fell short in accurately assessing ecosystem functioning. I found that grazing pressure led to higher species richness compared to browsing, but this did not correspond to an increase in vegetation cover or productivity (Chapter II). The increase in species richness was primarily attributed to the proliferation of shrubs, which were able to thrive despite grazing pressure. In contrast, most perennial grasses were removed by grazers, and their space was taken up by annual grasses. On the other hand, browsing resulted in slightly lower richness, but the vegetation was more functionally diverse as it involved different functional types of both grasses and shrubs. This means that while grazing led to higher overall richness, browsing resulted in greater functional richness within and across different functional plant groups. This finding suggests that richness alone may not necessarily be beneficial for the ecosystem if it results from one functional group only. The poor predictive capacity of richness for ecosystem functioning has also been confirmed in other rangeland studies (Revermann et al., 2017; Rutherford and Powrie, 2013). I therefore focused on plant functional diversity and the value of particular functional types and traits. I linked plant functional diversity measures, such as functional richness ($FRic$), Rao's Q or functional dispersion ($FDis$) with ecosystem functioning (Chapter III, Chapter IV). I showed increased plant functional diversity was associated with higher perennial grass cover and therefore higher total vegetation cover. Maintaining a dense perennial grass cover protected the soil from hot and dry conditions, reduced soil water losses, increased plant water availability and water use efficiency, which displayed a better ecosystem functioning under disturbance (Chapter II, III and IV).

If a high vegetation cover was maintained, the savanna plant community demonstrated remarkable adaptability to different availabilities of water resources resulting changing precipitation and temperature conditions, droughts, and growing season lengths, as evidenced by high and stable functional diversity and cover, as well as water use efficiency (Chapter IV).

Previous research has also identified multiple stabilising impacts of grass cover on ecosystem functions, including the prevention of erosion (Browning et al., 2012; D'Odorico and Bhattachan, 2012), modulation of soil structure and microorganisms (Srikanthasamy et al., 2022), and improved water uptake and retention (Scheffer et al., 2005; Tietjen et al., 2010). While increased functional diversity has positive effects on ecosystem functions, a reduction in this diversity can lead to a loss of such functions. For instance, a decline in grass diversity and cover resulted in increased evaporation and lower soil moisture in the upper layer, and eventually pushed the system beyond a tipping point where the changes in vegetation composition became irreversible. Ultimately, this led to a complete loss of grasses and encroachment by shrubs (Chapter IV). Similar vegetation shifts and tipping points have been found in various studies linking decreases in functional diversity to decreases in productivity, decomposition, and hydrological services (Chillo et al., 2017; Costa et al., 2017; Wen et al., 2019).

My research supports the common expectation that plant traits are crucial in determining the functioning of an ecosystem. Clearly, a plant community with high functional diversity can have the potential to withstand environmental changes, but the exploitation of this resilience may be limited and contingent upon the distribution of functional traits within the community and the type of disturbance. Therefore, relying solely on plant traits as predictors for long-term ecosystem functioning could be misleading, and it is essential to consider the abiotic conditions under which specific plant traits are advantageous (van der Plas et al., 2020).

Recent studies have pointed out the importance of specific plant functional types in determining ecosystem properties (Hagan et al., 2023; Osborne et al., 2018). It appears that plant functional types that have direct mechanistic connections to ecosystem characteristics can be effective predictors of ecosystem properties if employed judiciously (Hagan et al., 2023). For instance, in moderate grazing scenarios, a functionally diverse plant community led to higher resistance and recovery of grasses after drought, despite the loss of other plant functional types (Chapter III). Functional types with efficient water use, drought adaptation, and grazing resistance, played a crucial role in maintaining ecosystem functioning because they could functionally compensate for the loss of others. This finding is consistent with empirical studies that have identified species, which are functionally equivalent to the model plant types, to dominate after droughts (Fynn and O'Connor, 2000; Tommasino et al., 2023; Wigley-Coetsee and Staver, 2020).

Furthermore, my results showed that these diverse plant communities, which include species adapted to water scarcity and herbivory, exhibited higher vegetation cover and water uptake under a range of future climatic conditions and contributed to ecosystem stability (Chapter IV). This illustrates that a functionally diverse plant community can only increase savanna resilience if it contains species which fulfil important functions relevant to the disturbance context of the ecosystem (Gross et al., 2017).

My results demonstrate that the relationship between functional diversity, ecosystem functioning and resilience is complex and must be considered with caution. Several factors, such as the timing of measurements, functional diversity indices used, plant functional groups considered, and disturbance context, can lead to significant differences in outcomes (Cadotte et al., 2011; Martin et al., 2010; Petchey et al., 2004). Despite these complexities, my findings suggest a strong association between functional diversity and ecosystem functions, particularly when the community comprises plant functional types adapted to different types of disturbances (Májeková et al., 2016; Hagan et al., 2023).

Although my research demonstrates the ability of some plant species to endure multiple stressors such as drought and grazing, it underscores the need to identify and preserve species that are essential to maintain important ecological processes. These species include those that contribute to nutrient cycling (Ndagurwa et al., 2014), soil stabilisation, and water regulation (Hartnett et al., 2013), among others. This may involve implementing targeted conservation and management strategies that prioritise the protection and restoration of key plant species and their habitats.

5.3 Strategies for sustainable wildlife management and conservation of plant diversity

Functionality of semi-arid savanna ecosystems depends on the long-term survival of many wildlife species and plants. However, these savannas face several challenges due to poor land management practices and increased aridity that threaten their resilience. This section aims to examine the potential risks associated with traditional management practices and the benefits of transitioning towards more diverse management practices that include the integration of various herbivores and the maintenance of plant diversity. The ultimate objective is to enhance ecosystem resilience and address challenges posed by climate change. Additionally, I will discuss practical methods for implementing these findings into management regimes, with a particular emphasis on the role of browsing herbivores and their interactions with the surrounding environment.

Rangeland managers are currently faced with the task of preserving the resilience of the ecosystems they manage, but they will likely face even greater challenges in the future as the climate continues to change. This study has confirmed the risks of traditional management practices, such as intensive livestock production (Koch et al., 2023; Nacoulma et al., 2011; Pfeiffer et al., 2019). I showed that high grazing intensities are problematic under current conditions (Chapter II), but even more so under future climate (Chapter III and IV). Climate change projections indicate that decreased water availability will result in more frequent droughts, limited soil water availability, and shorter growing seasons (Chapter IV). The unpredictable nature of climate change projections necessitates a proactive and adaptive approach to management that can account for a range of possible future scenarios (Eldridge and Beecham, 2018), such as measures to conserve grasses and soil water availability (Grillakis, 2019).

This thesis revealed several ecological benefits of shifting rangeland management from grazing-dominated to mixed- or browsing-dominated herbivores. I found that in rangelands dominated by browsing herbivores, there was a lower risk of degradation (Figure 5.1) compared to those dominated by grazing herbivores under current (Chapter II and III) and future climate (Chapter III and IV). This is because woody vegetation, which is less susceptible to herbivory than grasses, can serve as a food source for herbivores without being completely removed or outcompeted by grasses (Chapter II, Scogings and Gowda, 2019). As a result, the presence of browsing herbivores in mixed communities can help maintain plant cover and prevent the encroachment of woody species into grasslands organically and cost-effectively (Chapter II, Veblen et al., 2016). Additionally, rangeland types with browsing herbivores showed increased diversity across major plant functional groups which was associated with important ecosystem functions, such as higher vegetation cover and an overall increase in water uptake by plants. Other studies have highlighted similar ecological, but also economic benefits of shifting rangeland practices from domestic grazing to more wild native and browsing herbivore herds (Lindsey et al., 2013; Porensky et al., 2013; Wells et al., 2022).

To ensure the long-term sustainability of wildlife in rangelands, it is crucial to prioritise the maintenance of a stable vegetation community by managing the composition and density of the herbivore community. This can be achieved by imitating natural processes that promote self-regulation within ecosystems. Self-regulation is essential for achieving long-term conservation and restoration goals since it allows ecosystems to perform necessary functions with minimal additional management measures (Parks et al., 2015). One way to sustain self-regulation is to identify plant species that are adapted to specific environmental stressors and have corresponding functions, and protect them from herbivory (Lavorel et al., 2013; Pettorelli et al., 2019; Smith et al., 2013). These plants may include fast-growing, water-efficient, and palatable species. In my research, I found that the use of browsers and mixed-feeders maintained important functional types, increased functional diversity and promoted self-regulatory mechanisms (Chapters III and IV) that prevented the ecosystem from switching to another ecological state in response to disturbance. This reduced grazing pressure and maintained functional types adapted to drought and herbivory.

In fenced rangelands, where animal migrations are restricted, the high feeding pressure throughout the year is one of the biggest problems, as it can lead to vegetation degradation and loss of biodiversity (Cassidy et al., 2013). Effective fence management (Hering et al., 2022) and the rotation of water points can help minimise feeding pressure. To reduce the negative impact of herbivory on plants during critical times when they are particularly vulnerable, it is crucial to manage the timing and intensity of herbivory, especially grazing (Isbell et al., 2017; Oba et al., 2000; Porensky et al., 2013; Wilcox et al., 2020). Optimising grazing can enhance grass productivity and mitigate the impact of grazers on vegetation structure (Ritchie and Penner, 2020; Staver et al., 2021), especially in the face of changing climates and extreme events.

In the face of changing climates, decreasing precipitation and soil water can lead to lower productivity and animal densities (Abrahms et al., 2023). However, my research has shown that incorporating both browsers and grazers can help mitigate the effects of varying climatic conditions by promoting grass growth through self-regulatory mechanisms such as the conservation of functionally important grass types (Chapter III and IV). This approach can achieve the maximum sustainable number of animals, even under reduced precipitation conditions, without requiring additional management measures (Chapter IV).

Overall, my findings suggest that managing the diversity and composition of herbivore communities is essential for promoting self-regulatory mechanisms and enhancing ecosystem resilience in rangelands. In this context, I have identified several general management tools that can facilitate the preservation of self-regulatory mechanisms:

1. Diversify herbivores by integrating browsers or mixed feeders and adjust the densities of grazers to the system's productivity (Chapter II, Chapter III). I propose that the coexistence of wildlife and livestock is possible in many rangeland types (e.g. conservancy, communal, and commercial).

2. Promote plant functional diversity to minimise the impacts of climate change on the ecosystem by identifying and conserving functionally important plant species (Chapter III and IV). To promote the persistence of valuable plant species, actions can include reducing grazing pressure and excluding herbivores from key sites that can serve as sources for spreading important plants to other areas. Additionally, planting functionally

important specimens can help the ecosystem adapt to changing conditions and remain resilient over time.

3. Reduce animal stocking rates not only in anticipation of droughts and during drought conditions, but also during the recovery phase afterwards (Chapter III). This is particularly crucial because the recovery phase is often the most severe and vulnerable period, and at the same time the most applicable action. By proactively adjusting the number of animals grazing in the ecosystem, overgrazing can be avoided and the impact of droughts minimised.

Additionally, rangeland managers should consider vegetation dynamics and soil conditions when evaluating changes in animal composition (Fuhlendorf et al., 2012), and diversify income sources to buffer potential losses within one source of income (Achiba, 2018; Berhanu et al., 2007). Regular monitoring of the rangeland can help managers to detect changes in the ecosystem and respond proactively (Andreu et al., 2019; Herrick et al., 2005), while encouraging the use of fire management practices such as controlled burning can help reduce the risk of wildfire and promote the growth of desirable vegetation (Lohmann et al., 2014; Staver et al., 2009).

My research has clearly demonstrated that rangeland managers have a number of effective tools at their disposal to enhance the long-term sustainability of savanna ecosystems. By implementing evidence-based and practical management strategies, such as diversifying both animal and plant communities, managers can achieve long-term sustainability of these valuable ecosystems with minimal additional management intervention.

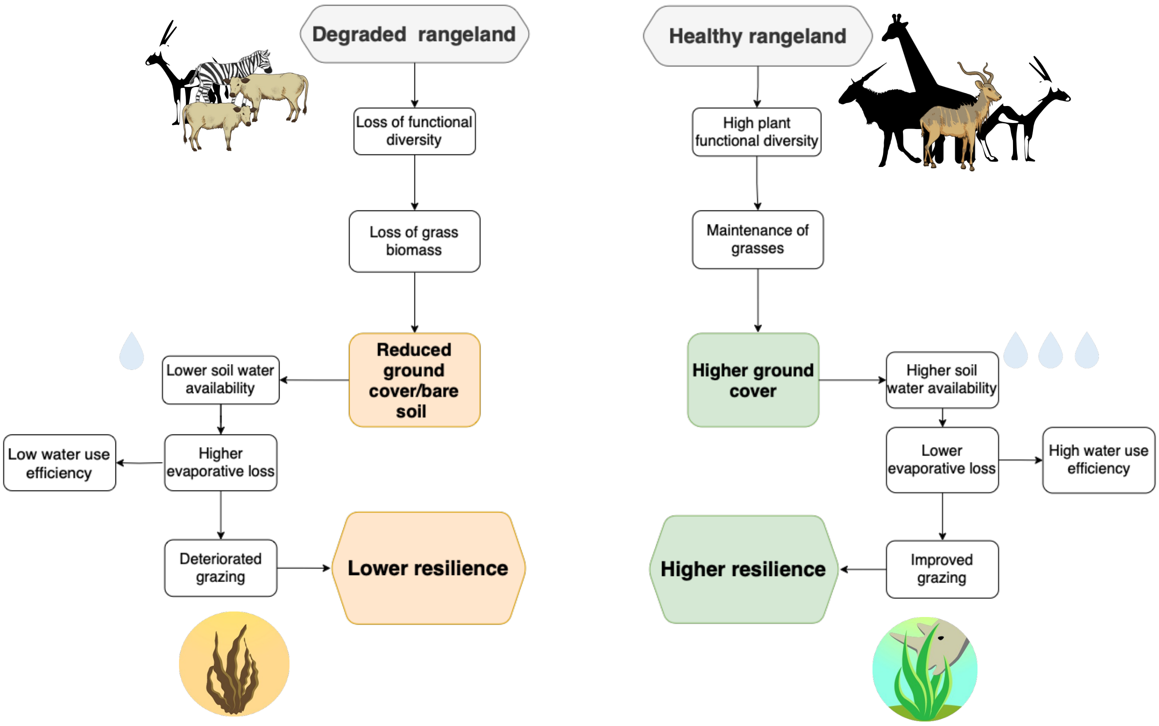

Figure 5.1: Exploring the synergy between rangeland condition, vegetation, and water availability: Unlocking the potential for resilience in natural habitats.

5.4 Moving forward in model development

While process-based models can provide mechanistic explanations for observed patterns and scale up field observations (Koomen and Borsboom-van Beurden, 2011), simulation combined with empirical research holds great promise for enhancing ecosystem understanding and providing management recommendations.

In this study, I calibrated the ecohydrological model EcoHyD to site-specific environmental conditions, such as soil moisture, topography, weather conditions and plant community assemblage. Moreover, I successfully matched the occurrence of modelled functional types after different disturbances with empirical research, and confirmed similar cover and NDVI after a simulated drought and a drought of the same length in the field observation. This coupling of EcoHyD with remote sensing and empirical data was a success as it increased the quality of the model predictions by better representing the system dynamics, validating outputs, while also enabling the identification of key management practices.

Nevertheless, potential new features could be incorporated into EcoHyD to further enhance the quality of predictions and the understanding of underlying processes:

One major improvement could be the implementation of a dynamic, temporarily and spatially varying, herbivory impact, which does account for fluctuations in animal populations in response to changes in vegetation resources, migratory opportunities, or health (Kiffner et al., 2017; Ogutu et al., 2014). This inclusion is significant, as fluctuations in animal populations are prevalent in both wild and managed rangelands and can have a significant impact on vegetation dynamics (Owen-Smith et al., 2020). Furthermore, it allows for the analysis of feedback loops between vegetation and herbivores and provides insights into the optimal timing of grazing.

Implementing plant physiology and phenology more accurately, and to implement adaptive plant traits that account for intraspecific variation in real species (Helsen et al., 2017) is promising. It enables a better understanding of plant species distribution in different environments and vegetation response to changing environmental conditions (Dickman et al., 2023; Seifan et al., 2013). To address this, novel tools like machine-learning-based approaches could account for trait adaptations in response to changing conditions (Dai et al., 2019).

Moreover, fires are a critical factor in shaping the structure of savannas (Staver et al., 2009). By modelling different fire intensities and frequencies, we can gain a better understanding of their role in shaping savanna vegetation (Lohmann et al., 2014; Langevelde et al., 2003) while minimising harm to natural systems. This can support the development of better fire management strategies that balance the preservation of ecosystem health with the need to mitigate the risks of wildfires.

Integrating dynamic herbivores, plant stress responses, and fire feedback loops into ecosystem models such as EcoHyD can provide valuable insights into plant and herbivore communities. The combined approach of simulations and empirical research holds great promise for gaining a deeper understanding of savanna ecosystems, which in turn will enable the development of evidence-based and practical management strategies that are critical for successful ecosystem management.

5.5 Perspectives for ecologically based management applications

While simulation models have become essential tools in ecological management, it is important to recognise that real-world ecosystems are complex and dynamic. In this section, I suggest additional factors that rangeland managers should consider, but I will also emphasise how models are useful complements that can carefully guide decision-making.

To ensure sustainable herbivore use for animal production, rangeland managers must balance various factors such as herbivore behaviour impacts, ecological roles, ethical and animal welfare concerns, and human-wildlife conflicts (Bischof et al., 2012; Gupta, 2013; Hering et al., 2022; Ogutu et al., 2014; Osipova et al., 2018). They are also challenged to determine the maximum number of animals that can be supported without damaging the ecosystem, while taking into account weather patterns to determine the best time for grazing or browsing (Ebrahimi et al., 2010; Holechek, 2013; Pilliod et al., 2022). Continuous monitoring of animal populations and habitat conditions is important to ensure grazing and management practices remain within the land's ecological carrying capacity (Ileri and Koç, 2022; Mörner et al., 2002). Additionally, rangeland managers are expected to reconcile ecological and economic factors when determining stocking densities (Teague et al., 2009). However, finding the optimal balance can be challenging depending on the rangeland's purpose and priorities.

Simulation models can assist rangeland managers in making informed decisions about herbivore composition, densities, and timing of herbivory, as well as vegetation dynamics, weather, and economic viability. However, there is an urgent need to combine these models (Derner et al., 2012), feed them with empirical data, and develop user-friendly applications. These applications will aid managers in making well-founded decisions during complex processes and accurately forecast the consequences of their actions in the future.

EcoHyD, the model used in my studies, focuses primarily on determining components of ecosystem health such as vegetation cover and soil water, but it could be improved by coupling it with animal models to reflect the health and behaviour of the herbivore community. Developing models that integrate water-soil-plant feedback loops with animal movements and that are regularly calibrated with current conditions through remote sensing, soil sensors, animal counts and movement data could provide important decision support to rangeland managers (Fust and Schlecht, 2018). In addition, managers can use economic models in conjunction with animal models (Subhashree et al., 2023) or ecohydrological vegetation models, such as EcoHyD, in order to achieve optimal economic output on an ecological basis (Martin et al., 2014).

An integrated approach that combines empirical research and simulation modelling can serve as a powerful tool for unravelling the complex relationships between environmental factors affecting rangeland viability. Such tools can facilitate outcome-based, adaptive decision-making with economic considerations and optimise conservation practices (Derner and Augustine, 2016). Approaches of this kind are crucial for attaining a sustainable, long-term balance between ecological and economic goals, thereby ensuring the achievement of all targets in rangeland management.

5.6 Conclusion

In conclusion, this thesis provides strong evidence for the benefits of shifting rangeland management practices from grazer-dominated to mixed-communities to improve the functioning and stability of savannas under a range of environmental conditions.

Such increased trophic complexity, characterised by a higher proportion of browsers, allows more sustainable utilisation of natural resources in the ecosystem, resulting in the preservation of plant types important for ecosystem functionality. In this context, I demonstrated that not plant functional diversity per se, but rather the presence of functional types that are adapted to multiple stressors, enhance ecosystem functioning and resilience to environmental disturbances.

By using a model, I could disentangle the impacts of climate change and management, and determine that climate change alone does not solely lead to ecosystem degradation. Instead, good management practices can lead to a stable response, while poor management, such as intensive grazing, can exacerbate the challenges faced by the ecosystem. Future research should continue to engage stakeholders to identify research priorities and needs to jointly assess the impact of adaptive management techniques in combination with environmental changes, such as weather and climate, on ecosystem functions.

The results of this thesis emphasise the potential of effective rangeland management strategies such as using mixed-feeders and browsers, in enhancing ecosystem resilience and in preventing irreversible ecosystem degradation, particularly in the face of the high uncertainty and challenges posed by climate change.

6

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A

Appendix

A.1 Model rules, parameters, calibration & sensitivity analysis

The model we used for this study is based on the ecohydrological dryland model EcoHyD (Tietjen et al., 2009; Tietjen et al., 2010; Lohmann et al., 2014; Guo et al., 2016). The model includes two sub-models: a hydrological and a vegetation sub-model (Fig. A.1.1). In the hydrological sub-model daily soil moisture in two layers (upper: 0-30 cm; lower: 30-80 cm) is calculated (Tietjen et al., 2009). The current version separates the actual evapotranspiration into soil evaporation and plant transpiration. Thus, we explicitly describe the process of evapotranspiration here while we do not describe other processes of the hydrological submodel and a full description thereof can be found in Tietjen et al. (2009). The vegetation submodel calculates biweekly growth of three plant functional types (PFTs), namely shrubs, perennial grasses and annual grasses (Tietjen et al., 2010; Lohmann et al., 2012; Guo et al., 2016).

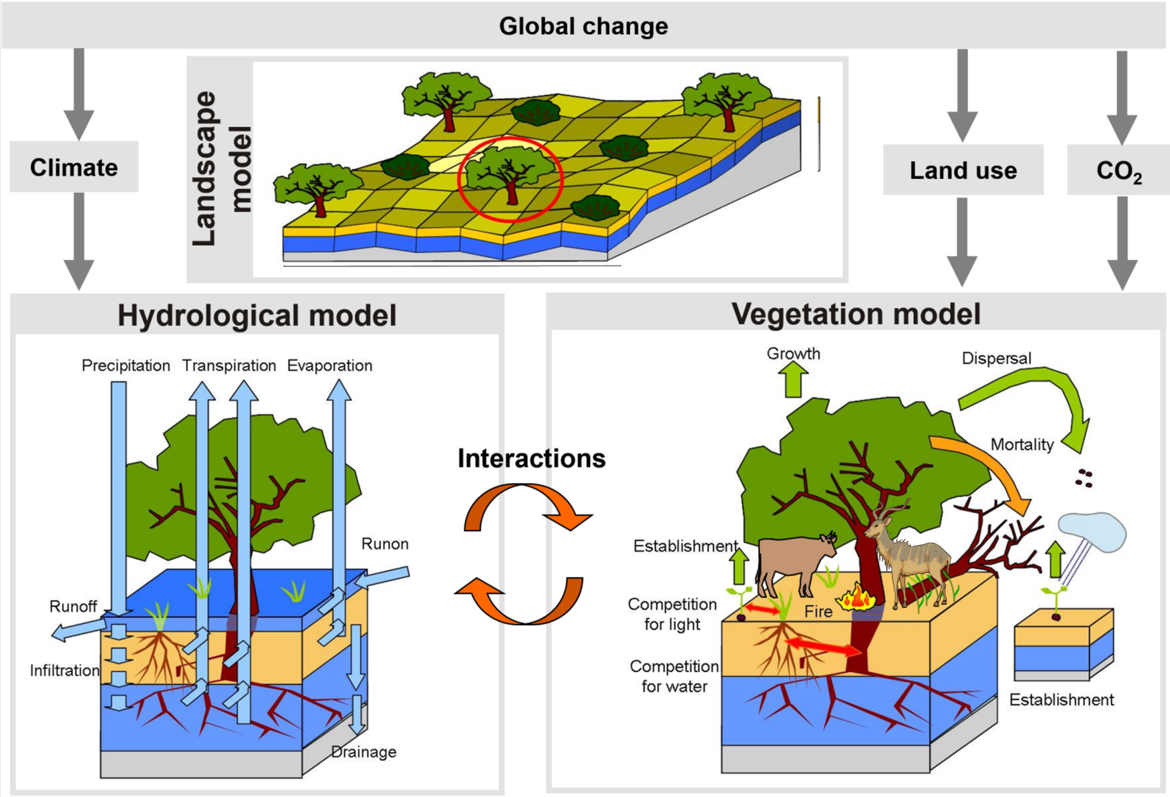

Figure A.1.1: Overview of the hydrological and vegetation processes in the model EcoHyD, after Guo et al. Description, value and source of all model parameters are given for the hydrological (Table A.1.1) and the vegetation sub-model (Table A.1.2), respectively. Parameter and variable names directly relate to the description in Tietjen et al. (2009, 2010), Lohmann et al. (2012), Guo et al. (2016) and Irob et al., (2023).

Hydrological model

Evapotranspiration

The assessment of potential evapotranspiration (ET_{pot}) follows the original description in Tietjen et al. (2009), in which ET_{pot} is calculated based on the Hargreaves approach, which involves daily mean, minimal and maximal temperature (T, T_{min} *and* T_{max} [°C], extraterrestrial radiation (R_a), slope (sl) and aspect effects (af). The potential evapotranspiration function is (according to Tietjen et al., 2009):

$$ET_{pot} = 0.0023 \times (T + 17.8) \times (T_{\max} - T_{\min})^{0.5} \times R_a \times af \times \cos(sl) \tag{A.1}$$

Actual evapotranspiration is then calculated by applying the conceptual HBV model (Hundecha and Bardossy, 2004) to calculate the actual evapotranspiration from the surface (ET_surf), the upper and the lower soil layer (ET$_L$1 and ET$_L$2) using the volumetric soil moisture (W_{Lx}) [m^3/m^3], stomata closing point, the cover of annual grasses, perennial grasses and shrubs ($c_t_{total}ag, c_total_{pg}, c_t_{total}$) and the cover of each sub-PFT (c_{veg}) (Tietjen, 2009). As in the version of Lohmann et al. (2012), annual grasses have only access to the upper soil layer, while perennial grasses and shrubs have access to water in both layers according to their root fraction ($\text{root}_{veg,Lx}$). The calculation functions of surface, upper and lower actual evapotranspiration are (according to Tietjen et al., 2009):

$$\begin{aligned}
ET_{surf} &= ET_{pot} \times (1 - 0.5 \times \sum_{veg} c\_\text{total}\ _{veg})\ [\text{mm/d}] \\
ET_{L1} &= ET_{pot} \times \left(\frac{W_{Ll}}{wsc}\right)^2 \times g_1\ [\text{mm/d}] \\
g_1 &= 1.2 - 0.2 \times \left(\sum_{veg} c\_\text{total}\ _{veg}\right) [\text{dimensionless}] \\
ET_{L2} &= ET_{pot} \times \left(\frac{W_{L2}}{wsc}\right)^2 \times g_2\ [\text{mm/d}] \\
\text{with } g_2 = \sum_{veg \text{ in perennial grasses,shrubs}} & \text{root}_{veg,L2} \times c_{veg}\ [\text{dimensionless}] \\
ET_{act} &= ET_{surf} + ET_{L1} + ET_{L2}\ [\text{mm/d}]
\end{aligned} \tag{A.2}$$

Evapotranspiration was separated into evaporation and transpiration (Guo et al., 2016), because plant dry matter production is directly linked to the water use, i.e. the transpiration of vegetation (Miller et al., 2012). A model assumption is that evaporation (E) is only relevant for surface water losses (E_{L0}) and water losses from the upper soil layer (E_{L1}), while transpiration (T) occurs in both soil layers. Therefore, actual evapotranspiration from the upper layer (ET_{L1}) is split into plant transpiration (T_{L1}) and soil evaporation (E_{L1}). We established the relationship between the fraction of transpired water $\left(\frac{T_{Ll}}{ET_{Ll}}\right)$ and total vegetation cover (c_total) in the upper soil layer (Guo et al., 2016). In contrast, actual evapotranspiration from the lower layer (ET_{L2}) is completely converted into transpiration (T_{L2}).:

$$\begin{aligned}
&E = E_{L0} + E_{L1} \\
&E_{L0} = ET_{\text{surf}} \\
&T = T_{L1} + T_{L2} \\
&ET_{L1} = T_{L1} + E_{L1} \\
&\frac{T_{LI}}{ET_{LI}} = \{1.05 \times c\_\text{total}\ - 0.04 \text{ if } c_{\text{total}} >\ \ 4\% \\
\text{else } &ET_{L1} = T_{L1} [\text{dimensionless}]
\end{aligned} \tag{A.3}$$

The next step is to determine how much water can be used by which plant functional type. This calculation did not change since the description of Tietjen et al. (2010) (Eq. A.4).

The relative uptake rate of each sub-PFT ($U_{veg,Lx}$) is calculated based on the potential water uptake rate per biomass (θ_{veg}) [mm$^\times$yr^{-1}], vegetation cover (c_{veg}) and the fraction of roots (root$_{veg,Lx}$) in the respective layer.

$$U_{veg,Lx} = \frac{\theta_{veg} \times \ \text{root}_{\ \text{veg}\ ,Lx}}{\sum_{\text{veg}} \theta_{\text{veg}} \ \times \text{root}_{\text{veg}\ ,Lx} \times c_{veg}} [\text{dimensionless}] \tag{A.4}$$

$$T_{veg,Lx} = T_{Lx} \times c_{veg} \times U_{veg,Lx} \ [\text{mm/d}] \tag{A.5}$$

Vegetation model

Plant growth

After the estimation of the fraction of transpired water in total evapotranspiration, we related the plant growth directly to transpiration instead of linking it to soil moisture as it was done in the original model version (Tietjen et al., 2010). In our model plant growth is implemented as an increase in the vegetation cover calculated in intervals of 14 days during a defined growing season. Growth of perennial grasses and shrubs (Eq. A.6) is hereby based on a logistic behavior and calculated separately for each 5 m × 5 m grid cell. It depends on its own maximum cover (cmax$_{veg}$), its own current cover (c_total$_{veg}$) and on the total cover of other vegetation formations (c_total$_{veg}$) representing competition for space and light, meanwhile assuming a potential cover overlap between woody plants and grass (lap). The growth of annual grasses differs from the growth of perennial plants. Growth of annual plants (Eq. A.7) does not include any competition for soil available water but exclusively depends on the size of empty space, potential growth rate (r_{ag}) and general water availability in the upper soil layer ($avW_{ag,L1}$), as annual grasses are not assumed to invest resources in deep soil layers. However, the transpiration of annual grasses in the upper soil layer and its shading effect on evaporation from the surface are accounted for in the hydrological sub-model in the same way as is implemented for perennial grasses and shrubs. The growth functions for perennial grasses, woody plants and annual grasses are (according to Tietjen et al., 2010; Lohmann et al., 2012):

$$gr_{veg,Lx} = T_{veg} \times r_{veg} \times \left(1 - \frac{c\_\text{total}_{\ \text{veg}}}{\text{cmax}_{\ veg} - (c\_\text{total}_{\ \neg veg} \times (1 - lap))}\right) \quad \left[yr^{-1}\right] \tag{A.6}$$

$$\begin{aligned} gr_{ag} = {} & \min\left(1 \times avW_{ag,Ll}, 1\right) \times r_{ag} \\ & \times \left(1 - c_{-}\ \text{total}_{pg} - c_{-}\ \text{total}_{s} \times (1 - \text{lap}) - c_{-}\ \text{total}_{ag} - c_{mor}\right) \quad [yr^{-1}] \end{aligned} \tag{A.7}$$

Plant mortality

Two types of mortality affect vegetation cover. First, drought induced mortality (md_{veg}) is calculated exactly as described in Tietjen et al. (2010). It is based on water availability and water uptake analogous to growth (see Eq. A.4) and depends on a drought mortality rate mrd_{veg}, the average available water content in both soil layers during the growing season ($avW_{veg,Lx}$) and the relative water uptake rate ($U_{veg,Lx}$).

$$md_{veg,Lx} = mrd_{veg} \times c_{veg} \times (1 - \min(U_{veg,Lx} \times \mathrm{av}\, W_{veg,Lx}, 1)) \times \frac{\mathrm{root}_{veg,Lx}}{\sum_i \mathrm{root}_{\mathrm{veg}\ ,Li}} \quad [yr^{-1}] \tag{A.8}$$

Second, we introduced stochastic age-based mortality (ma_s) for woody plants, referring to empirical data on Acacia mellifera L. from a semi-arid savanna similar to the one found in the study area (Meyer et al., 2009). This simulates a mortality that rather depends on the age of individuals than on water stress like for example infestation by fungi (Joubert et al., 2008). This senescence is applied to all cells with cohorts of shrubs older than the average age of death of individual trees (ScenAge) (Meyer et al., 2007). The age of a cohort is determined by the date of the last establishment event that occurred in the respective cell. Hence, cells where the last establishment event of woody vegetation has been more than ScenAge are completely cleared from woody vegetation with an annual probability (mp_{age}).

Plant biomass

While vegetation cover of different sub-PFTs is the basic unit used in most equations (see above), plant biomass is necessary for some of the calculations, too. Hence, biomass (BM) is calculated based on vegetation cover and precipitation, the latter being the single-most important driver of biomass production from a given vegetation cover in semi-arid savanna ecosystems (Snyman and Fouché, 1993). Specifically, biomass (b_{veg}) is deduced from cover (c_{veg}) and the average biomass produced per unit of cover given an average annual rainfall ($\mathrm{conv\_\ c\_bm}_{veg}$) depending on the following linear relation:

$$b_{veg} = c_{veg} \times conv\_c\_bm_{veg} \times cf \quad (\mathrm{rain}\ ) \tag{A.9}$$

The slope of this relation is adapted by cf (rain) to account for the dependence of biomass production on the precipitation in the current year (rain). The value of $cf(\ \mathrm{rain}\ )$ is 1 in case of an average annual rainfall, below 1 in case of lower and above 1 in case of higher annual rainfall amounts. It is given by a linear relation with a constant ($\beta_r \leq 1$) determining the strength of precipitation influence on the cover-biomass relation (Lohmann et al., 2012).

$$cf(\mathrm{rain}) = \mathrm{rain} \times \frac{1 - \beta_r}{MAP} + \beta_r \tag{A.10}$$

Herbivory (new algorithm)

The removal of biomass by herbivory is calculated at the end of the growing season. The main steps of the herbivory algorithm, calculation of edible biomass and of biomass, calculation of biomass to be removed, spatial determination of biomass removal, biomass removal and cover biomass conversion, are explained in the following.

Calculation of edible biomass

Each PFT has a proportion of edible biomass that can be consumed calculated from parameter *edibleFrac*. For grasses, this also entails dead biomass from the previous year. This means, the amount of total biomass of one PFT is reduced to be only the amount of edible biomass.

Calculation of biomass demand

The density of animals (stockingRate in ha/LSU) sets the biomass demand of herbivores and thus determines how much biomass is removed from the simulated landscape each year. One LSU is assumed to weigh 450 kg with a daily intake of biomass equivalent to 2% of its body mass each day. The total needed BM consumed by all animals in each year is thus defined as:

$$\text{NeededBM} = \text{ animal bodyweight } \left(\frac{\text{kg}}{LSU}\right) \times 356 \text{ days } \times 0.02 \left(\frac{1}{\text{day}}\right) \times \frac{1}{SR(ha/LSU)} \times \text{gridarea (ha)} \tag{A.11}$$

To simulate diverse communities with different proportions of grazer and browsers, we introduced a new parameter, graze_fraction_in_diet, which determines the ratio of grass to shrub intake in the diet of the animals. Considering this parameter, the total needed biomass to fulfil the demand is then calculated separately for grasses and shrubs:

$$\text{NeededBM}_{grass} = \text{NeededBM\_total}\times \text{ graze\_fraction\_in\_diet} \tag{A.12}$$

$$\text{NeededBM}_{shrub} = \text{NeededBM\_total}\times \text{ graze\_fraction\_in\_diet} \tag{A.13}$$

This way, in contrast to the old algorithm, no additional biomass of shrubs or grasses can be eaten beyond the defined grazing percentage in the diet, unless the grazing percentage in the diet is set flexibly, as explained in the following section. The required biomass of shrubs and grasses is then compared to their edible biomass. In case there is a deficit, it is recorded as fodder deficit for the whole community. Since we assume that deficits either result in moving them to other parts of the (non-simulated) landscape or in providing additional forage, this deficit is not translated into a reduction in stocking rate for the next year.

Flexibility in diet

To allow for diet flexibilities in cases of shortages of the preferred fodder type, we introduced the parameter graze_fraction_flexibility. This parameter sets boundaries in which the graze fraction in the diet can vary depending on the availability of either shrubs or grasses. The final graze_fraction is then adjusted in a way to cover the maximum biomass demand depending on available biomass and diet flexibility. This means, if the graze_fraction is 0.8 and the flexibility is 0.15 , and there are more shrubs available than grasses, the actual fraction of eaten grass might be reduced to as low as 0.65 , meaning 65% of their intake. The adjusted graze_fraction is then used to calculate the needed biomass for grass and shrub intake.

Removal of biomass

The removal of biomass can be divided into two steps. First, the BM fraction that will be removed from each PFT is calculated. It depends on the palatability values (*herbivorePref*) of each sub-PFT relative to the palatability of other sub-PFTs. The graze_fraction_in_diet already defines the preference of the simulated herbivore communities, thus the palatability of shrubs and grasses are only compared between sub-PFTs of each meta-PFT. Second, the previously calculated edible fraction of each PFT is randomly removed from each cell of the simulated landscape. The amount that is removed from each cell depends on the spatial heterogeneity parameter of biomass removal (explained below).

Calculation of fraction to be removed of each PFT

The calculation of the fraction to be removed of each PFT depends on the probability that the PFT is encountered (findProbability, Eq. A.13) and on the relative preference (Eq. A.14) of animals eating this PFT.

$$\text{findProbability}_{PFT} = \frac{\text{EdibleBiomassGrid}_{PFT}}{\text{EdibleBiomassGrid}_{\text{total}}} \tag{A.14}$$

$$\text{relativePreference}_{PFT} = \frac{\text{Palatability}_{PFT}}{\left(\sum_{i=1}^{\text{total}} \text{Palatability}_{i}\right) / \text{total}} \tag{A.15}$$

Animals are aware of each PFTs quantities in the simulated landscape and they memorize what they had eaten previously and in case they encounter the same PFT again, they only eat the residual edible part that was left after their previous visit. This avoids that a herbivore chooses the same cell multiple times based on previous availabilities within this cell. Therefore, the find probabilities are updated as soon as any edible biomass of a PFT is removed. We implemented a deterministic method to account for this by multiplying the amount of biomass removed in each step times the preference and findProbability looping through all PFTs (Eq. A.13)

$$\begin{aligned} EatenAmount_{PFT} = findProbability_{PFT} \times relativePreference_{PFT} \\ \times TotalAmountRemoved_{PFT} \end{aligned} \tag{A.16}$$

Removal of biomass

In the previous step, we determined the amount that will be removed from each PFT or subPFT. In this step, we determine how much of this amount will be removed from each cell. This is a new extension of the EcoHyD model which allows us to control the spatial variability of biomass removal. That is, a random fraction is drawn from a beta distribution.

Generation of beta distribution

For each PFT, a beta distribution is calculated, characterized by the two shape parameters alpha and beta, where the mean is the previously calculated proportion of biomass to be eaten. Whichever shape parameter is the smaller one is set to be the parameter for the spatial homogeneity of biomass removal. This means, the higher the homogeneity parameter is, the more homogenous the biomass removal and the smaller the variance becomes. At very high values, all random fractions will be identical to the mean.

Actual removal of biomass

In our simulated landscape of a grid of 30 x 30 cells (900 cells), 900 random fractions are generated for each PFT. The model loops through all grid cells and removes biomass until all cells are encountered. The amount of biomass to be removed from each cell is calculated by multiplying the randomly drawn fraction from each PFT's beta distribution by the amount of edible biomass of this PFT. Subsequently, the biomass is removed from the total biomass of this PFT in each cell. The total amount of biomass removed can only slightly deviate from the previously calculated fraction. Since the amount removed is determined by a percentage rather than absolute biomass, no homogeneity does not mean that the same amount of biomass is removed in each cell, but that the same percentage is removed. In this way, herbivores in cells with a lot of edible biomass also remove more biomass.

In the final step, the amount of remaining biomass of each PFT is converted back to cover using the inverse function of equation A1.9.

Dispersal and seedling establishment

Dispersal and establishment are simulated as addition to the cover of a respective growth form (ds_{veg}) to certain cells in the grid. Germination and seedling/juvenile survival are therefore rather implicitly included (Tietjen et al. 2010).

Dispersal and establishment of perennial grasses was implemented as described by Tietjen et al. (2010). We assume no dispersal limitation on the given spatial scales (Jeltsch et al., 1997), i.e. spatially homogeneous distribution of grass cover with the amount of cover depending on the mean perennial grass cover of the whole grid. Annuals are assumed to be always present as seeds and start off at every season without initial cover (i.e. no dispersal and establishment calculation, solely growth function determines occurrence). Woody plants are, in accordance with literature on regional typical shrub and tree species (i.e. Acacia species), assumed to be limited in dispersal, seed production and especially in establishment (Meyer et al., 2007; Joubert et al., 2008).

However, the establishment of shrubs was simulated in more detail compared to the model version of Tietjen et al. (2010). Dominant encroacher species in semi-arid African savannas are known to have relatively high requirements regarding water availability for seed production, seedling germination and successful establishment. Different studies showed, that at least two subsequent years of above average rainfall are needed for successful establishment of *A. mellifera* (Meyer et al., 2007; Joubert et al., 2008) and other woody plant species of semiarid savannas (Wilson and Witkowski, 1998). Hence, successful establishment of woody plants is only possible if the mean soil-water content in the upper soil layer during the growing season is well above the wilting point of plants during two subsequent years ($W_{Ll,\,\text{mean}} > m_{est} \times W_{wp,s}$). The factor m_{est} was calibrated so that establishment conditions at one location occur on average 5-6 times per century (Joubert et al., 2008). To account for positive impacts of grazing on dispersal and establishment of woody plants (Kraaij and Ward, 2006; Hiernaux et al., 2009), a grazing dependent factor was added to the function of Tietjen et al. (2010), so that amount and spatial extent of shrub establishment increases with increasing grazing pressure (Ward and Esler, 2011). This is achieved by linearly altering the parameters that determine the exponential decrease of "seedlings" (i.e. cover) with distance (distConst ($SR_{\text{dispersal}}$)) and the maximum dispersal distance (distmax dim$_s$ ($SR_{\text{dispersal}}$)).

The dispersal and establishment of shrub seedlings added as cover to a target cell (ds) is calculated for every source cell in the grid if the target cell had a sufficient water availability during the last and current growing season and its position was within the maximum dispersal distance according to the following term:

$$\begin{aligned} ds = c_{S\_\text{source}} \times \ \text{est}_s \times \ \text{dist}_0 \times e^{-\,\text{distConst}(SR)\times\ \text{dist}} \\ \times \max\left(1 - c\_\text{total}_s - c\_\text{total}_{pg}; 0\right) \quad [\text{dimensionless}] \end{aligned} \tag{A.17}$$

Establishment and dispersal consequently depend on shrub cover in the source cell (c_{S_source}), mean rate of seedling establishment (est_s), cover of grasses and shrubs in the target cell (c_s, c_{pg}) and the shape of an exponential dispersal decline (dependent on dist $_0$ and distConst) as well as on the distance of the target from the source cell (dist). Grazing affects the dispersal kernel by the following linear relation being a function of the dispersal stocking rate $(SR_{\text{dispersal}})$

$$\text{distConst}(SR) = dc_a + (dc_b * SR_{\text{dispersal}}) \ \text{[dimensionless]} \tag{A.18}$$

Here we assume a constant effect of herd migration carrying seeds from inside to the outside.

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A.2 Model parameters

Table A.1.1: Standard parameters and soil specific parameters in the vegetation sub-model (for further details see Tietjen et al., 2010; Lohmann et al., 2012; Guo et al., 2016).

Name	**Description**	**Value**	**Unit**
sclim	cover boundary for shrub (differentiate shrub and non-shrub)	0.001	-
scrlim	cover boundary for shrub (differentiate juvenile and adult)	0.1	-
lap	cover overlapping between grass and shrub	0.2	-
bm_c_rain	constant for impact of precipitation on the biomass per unit of cover	0.35	-
ga	constant for shaping quadratic function of grazing damage	0.8	-
gb	constant for shaping quadratic function of grazing damage	0.1	-
EnScov	cover boundary for shrub encroachment	0.4	-
$0_{BM,pg}$	relative uptake rate per perennial grass biomass	0.9	mm (yr * g)$^{-1}$
$0_{BM,s}$	relative uptake rate per shrub biomass	0.5	mm (yr * g)$^{-1}$
$0_{BM,ag}$	relative uptake rate per annual grass biomass	0.2	mm (yr * g)$^{-1}$
$root_{pgLI}$	fraction of roots in the upper layer for perennial grass	0.63	-
$root_{s,LI}$	fraction of roots in the upper layer for shrub	0.36	-
r_{ag}	potential growth rate of annual grass	1.5	mm^{-1} * yr^{-1}
r_{pg}	potential growth rate of perennial grass	0.5	mm^{-1} * yr^{-1}

Table A.1.1 continued.

Name	Description	Value	Unit	
r_s	potential growth rate of shrub	0.15	mm^{-1} yr^{-1}	*
mrd_{pg}	mortality rate dependent on soil moisture for perennial grass	0.54	mm^{-1} yr^{-1}	*
mrd_s	mortality rate dependent on soil moisture for shrub	0.12	mm^{-1} yr^{-1}	*
mrd_{ag}	mortality rate dependent on soil moisture for annual grass	0.8	mm^{-1} yr^{-1}	*
max_{ag}	maximum cover for perennial grass	1.0	-	
max_s	maximum cover for shrub	0.8	-	
$conv\_c\_bm_{pg}$	biomass at 100% cover for perennial grass	1.9*106	$\text{g} * \text{ha}^{-1}$	
$conv\_c\_bm_s$	biomass at 100% cover for shrub	2.1*107	$\text{g} * \text{ha}^{-1}$	
$conv\_c\_bm_{ag}$	biomass at 100% cover for annual grass	1.7*106	$\text{g} * \text{ha}^{-1}$	
$edibleFrac_{pg}$	non-edible biomass fraction for perennial grass	0.15	-	
$edibleFrac_s$	non-edible biomass fraction for shrub	0.7	-	
$edibleFrac_{ag}$	non-edible biomass fraction for annual grass	0.05	-	
$herbivorePref_{pg}$	grazing preference for perennial grass	1	-	
$herbivorePref_s$	grazing preference for shrub	0.3	-	
$herbivorePref_{ag}$	grazing preference for annual grass	0.6	-	
est_{pg}	rate of successful establishment for perennial grasses	0.05	yr^{-1}	
est_s	rate of successful establishment for shrub	0.005	yr^{-1}	

Table A.1.1 continued.

Name	Description	Value	Unit
$m_{est,pg}$	factor determining minimum mean soil moisture content for establishment for perennial grass	1.05	-
$m_{est,s}$	factor determining minimum mean soil moisture content for establishment for shrub	1.205	-
$dist_s$	constant for exponential dispersal decline with distance for shrub	0.5	-
dc_s	constant for exponential dispersal decline with distance for shrub	0.1	-
dc_b	constant for exponential dispersal decline with distance for shrub	0.0125	-
$Resbio\_L_{pg}$	fraction of reserved biomass that cannot be grazed for perennial grass	0.15	-
$Resbio\_T_{pg}$	fraction of alive biomass that is transformed into reserved biomass for perennial grass	0.25	-
$Resbio\_L_{ag}$	fraction of reserved biomass that cannot be grazed for annual grass	0.05	-
$Resbio\_T_{ag}$	fraction of alive biomass that is transformed into reserved biomass for annual grass	0.1	-
graze_fraction__in_diet	ratio grazing to browsing herbivory demand	0.2/0.5/0.80	-
diet_flexibility	diet flexibility outside of graze fraction in diet	0.15	-
spatial_heterogeneity_for__BM_removal	Spatial heterogeneity of herbivore biomass removal	0.4	-

Table A.1.2: Parameter settings of perennial grasses and shrubs. The table lists the parameter name, how it is referred to in the text and figures, its default value and the value used for trade-off (Parameter -10%) and specialisation (Parameter +10%).

		Perennial grasses			**Shrubs**		
Parameter	**Short**	**Default**	**-10%**	**+10%**	**Default**	**-10%**	**+10%**
Defense	D/d	0.15	0.125	0.175	0.7	0.60	0.797
Palatability	P/p	1	1.030	0.970	0.1	1.45	0.534
Mortality	M/m	0.54	0.557	0.523	0.12	0.15	0.09
Biomass production	B/b	0.5	0.484	0.516	0.15	0.14	0.16
Competitive strength for water	C/c	0.9	0.879	0.921	0.5	0.45	0.55
Resistance to drought	R/r	0.077	0.0774	0.0766	0.076	0.08	0.074

Table A.1.3: Hydrological parameters for the soil texture of loamy sand based on Tietjen et al (2009).

Name	**Description**	**Value**	**Unit**	**Source**
S_r	Effective suction	61.3	mm	Rawls et al., (1992)
K_S	Saturated hydraulic conductivity	59.8	mm h^{-1}	Rawls et al., (1992)
WP	Wilting point	8.8	Vol%	Calculated depending on rw
f_C	Field capacity	16.7	Vol%	Rawls et al., (1992)
sat	Water content at saturation	16.7	Vol%	Rawls et al., (1992)
Ef	Evaporation factor	0.16	-	Calibrated
rw	Residual water content	7.5	Vol%	Measured

Table A.1.3: Hydrological parameters for the soil texture of loamy sand based on Tietjen et al (2009).

Name	Description	Value	Unit	Source
$FL_{1,2}$	Infiltration rate into lower soil layer	0.1	-	Calibrated
$maxFL_2$	Maximum total infiltration into lower soil layer	1.5	mm h^{-1}	Rawls et al., (1992)
$diffConst$	Diffusion coefficient constant	0	-	Calibrated

A.3 Calibration

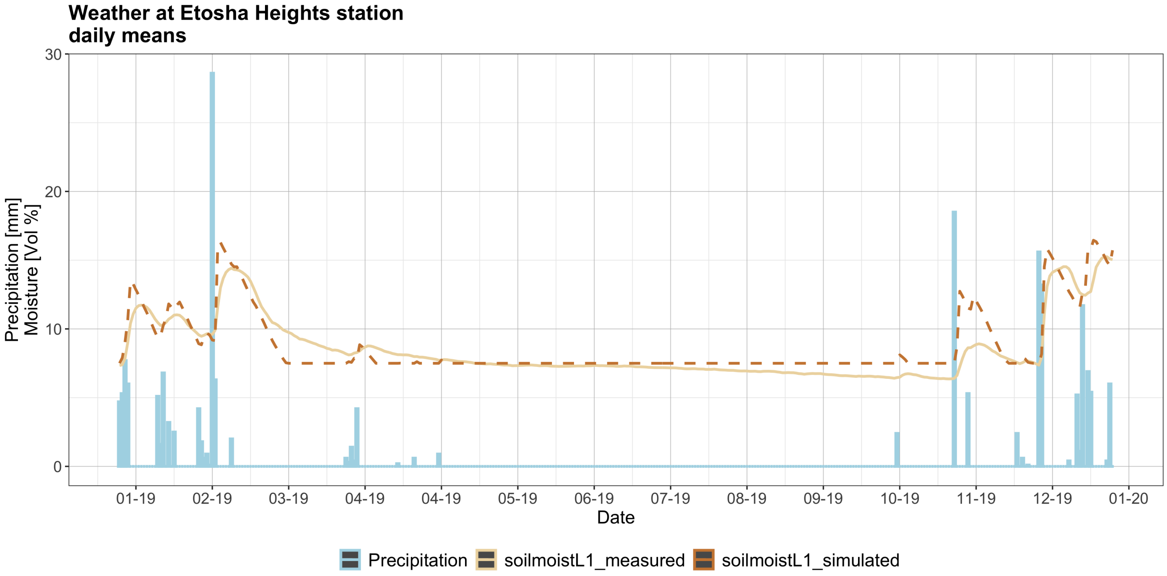

Figure A.1.2: Measured (yellow) and simulated (orange/dashed) moisture of the first soil layer with loamy sand, forced by precipitation events in 2019 (RMSE = 1.092).

A.4 Sensitivity analysis

We performed a sensitivity analysis for perennial grass vegetation and shrubs to determine which parameter values resulted in a 10% cover increase or decrease relative to the mean cover of the base-type of the respective meta-PFT. We gradually varied the range of the standard parameter by 20 – 30% and determined by linear regression which parameter value would result in a 10% cover change.

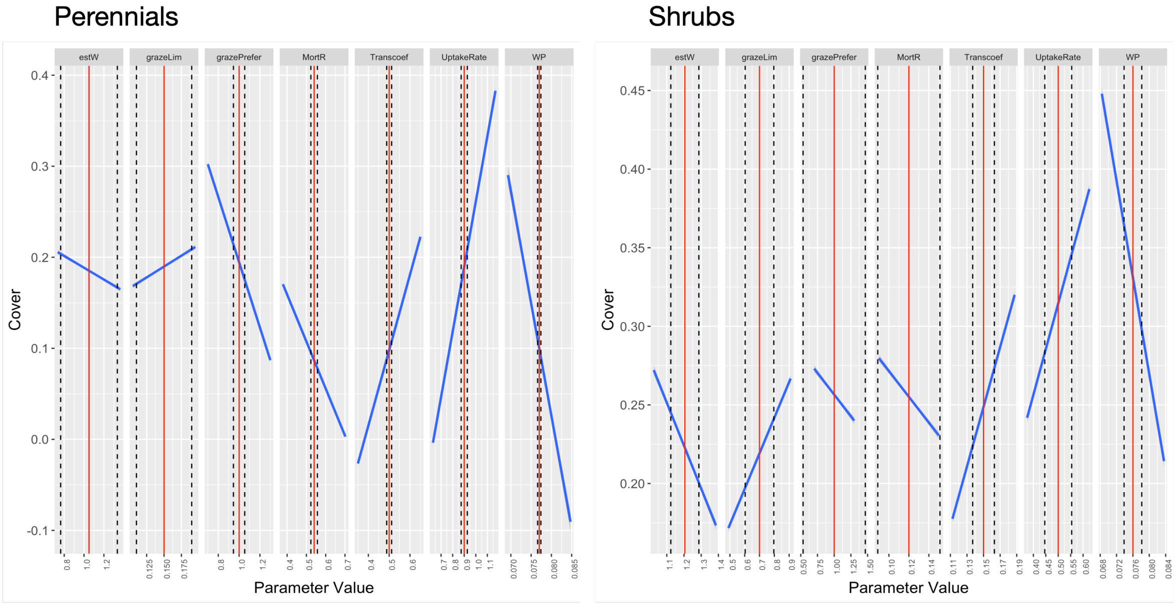

Figure A.1.3: Results of sensitivity analysis for perennial grass (left) and shrub (right) parameters under equal herbivory of grazing and browsing (mixed-feeding).

A.5 Appendix to "Browsing herbivores improve the state and functioning of savannas: A model assessment of alternative land-use strategies"

Supplementary figures

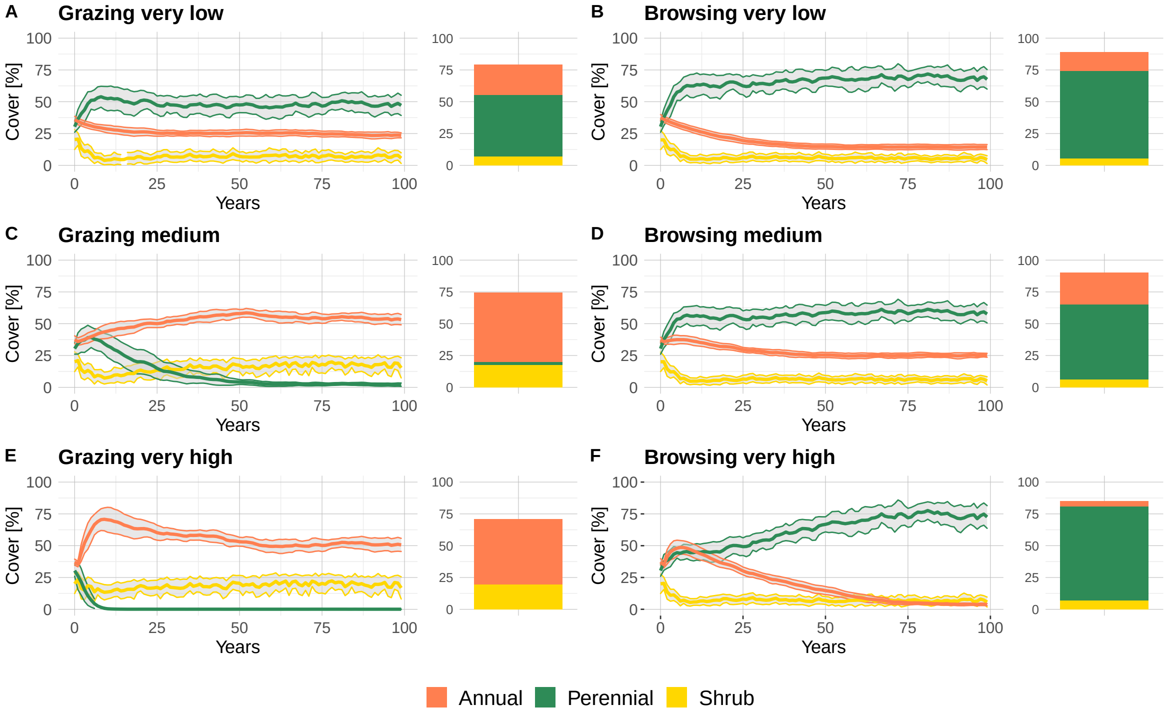

Figure A.1.4: Predicted mean cover ± SD [%] for 30 climate repetitions of the three PFTs for the whole simulation duration (lines) and the last 20 years of simulation (stacked bars) for all land use scenarios. White lines within the stacked bars indicate the occurrence of specific strategy-PFTs.

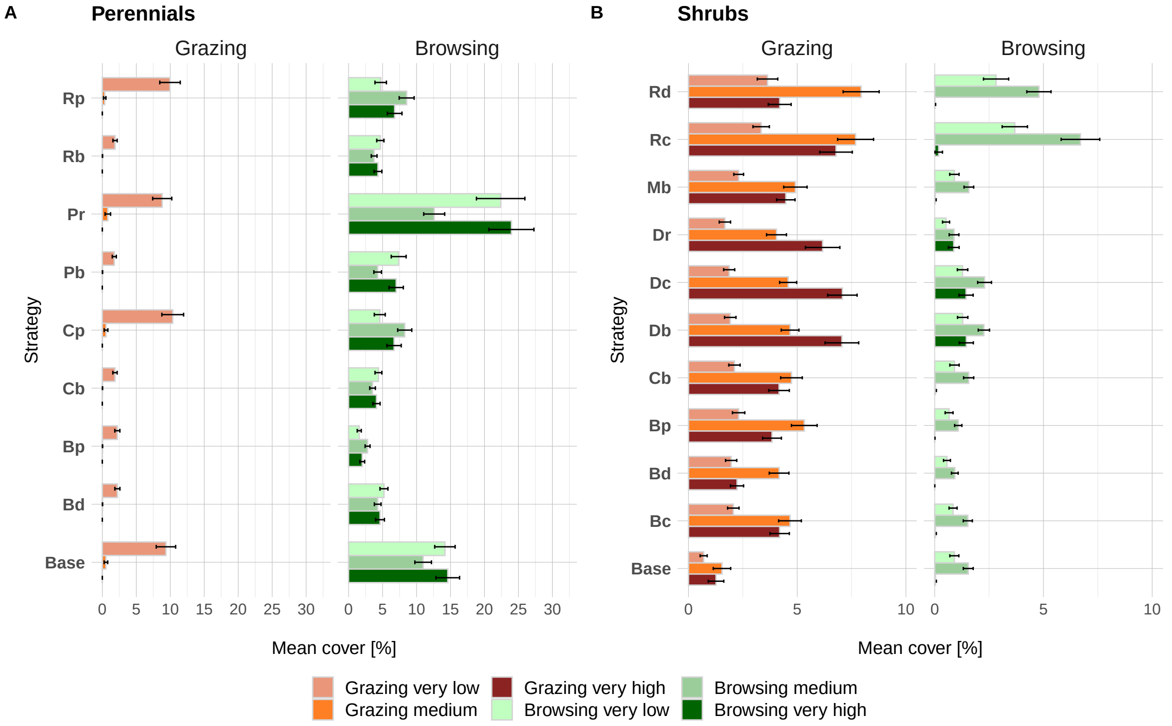

Figure A.1.5: Mean cover ± SD [%] of perennial ($N = 9$) and shrub ($N = 11$) strategy-types in different grazing and browsing scenarios, suggesting which strategy-types dominate in a certain land use scenario. Results represent vegetation cover of the last 20 years of simulation repeated for 30 climate time series. Note that x-axes between perennial grasses and shrubs differ.

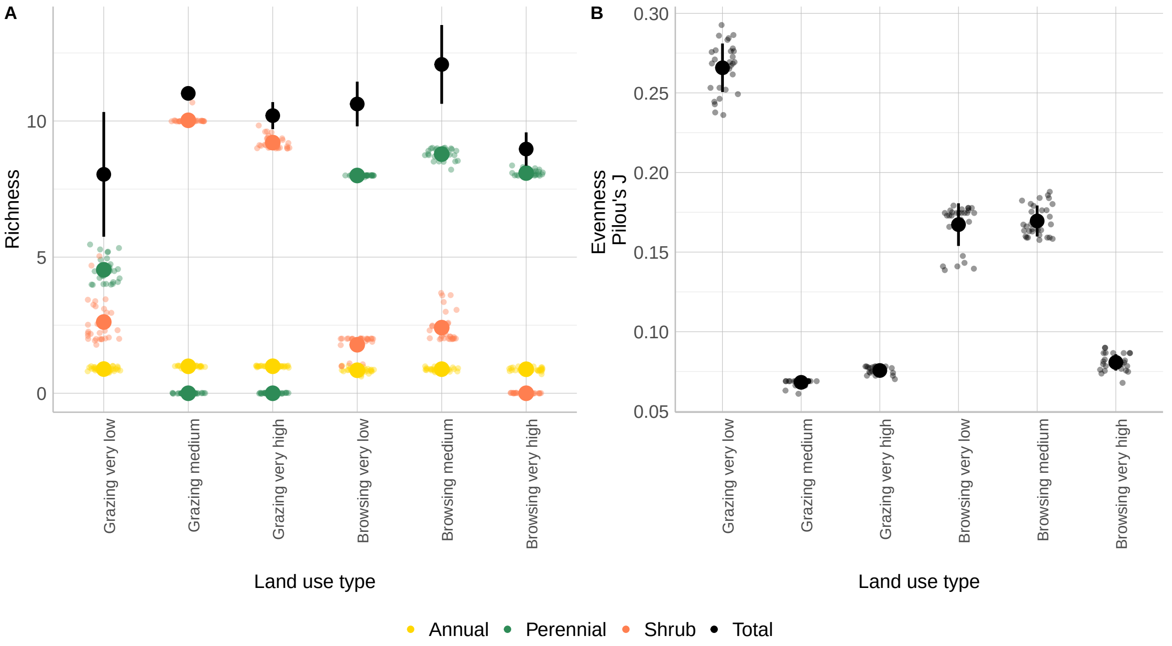

Figure A.1.6: Mean ± SD of species richness (A) and species evenness (B) under all land use scenarios for 30 climate repetitions. Every point represents one climate repetition. The left figure shows the total richness of all PFTs, as well as richness of each meta-PFT for every scenario respectively.

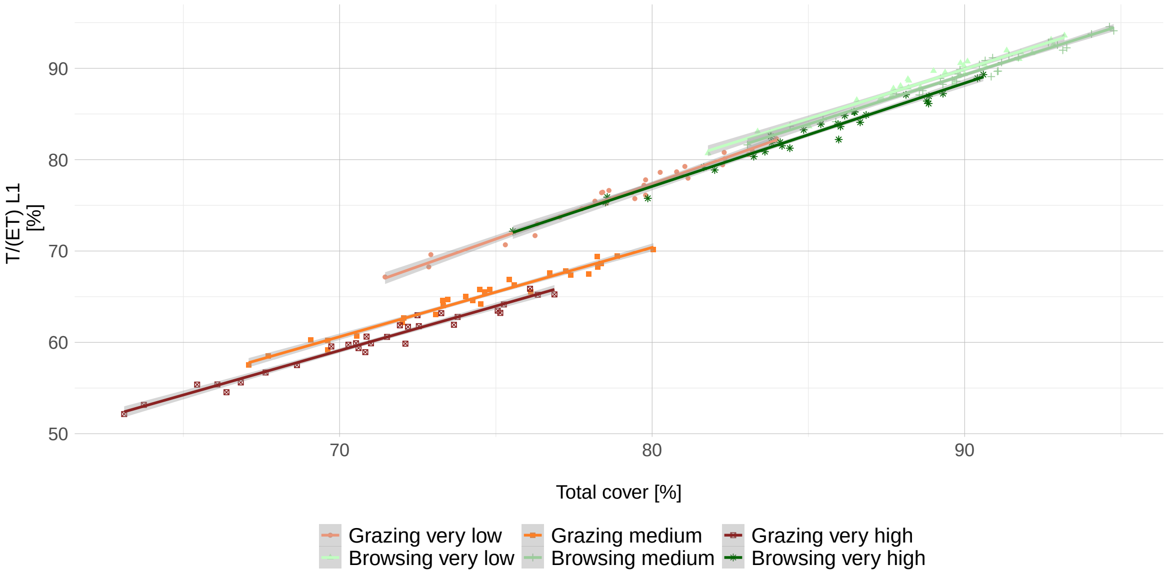

Figure A.1.7: Correlation between the variation in the ratio of transpiration and evapotranspiration (T/ET) [%] as estimator for water use by plants and total plant cover [%], separated for the different scenarios of land use. Results refer to water dynamics in the upper soil layer of the last 20 years of simulation and 30 climate repetitions

A.6 Appendix to "Savanna resilience to droughts increases with the proportion of browsing wild herbivores and plant functional diversity"

Supplementary figures

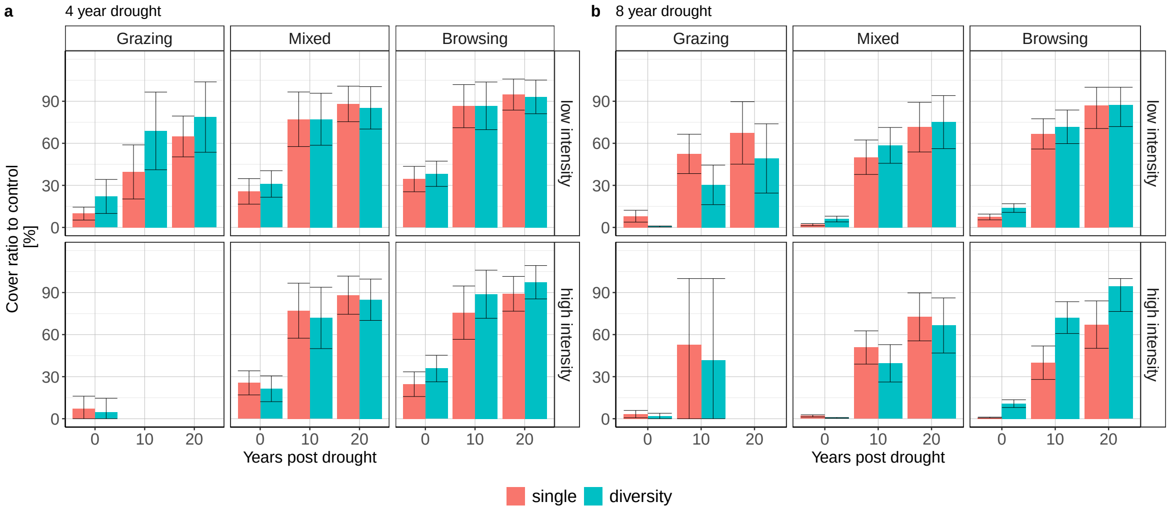

Figure A.1.8: Mean cover percentage ± SD of perennial grass cover to their control cover at different time intervals after the respective drought. Specific colours distinguish the scenario with a single functional plant type (single/red) compared to the scenario with multiple sub-types of the same meta-PFT (diversity/blue).

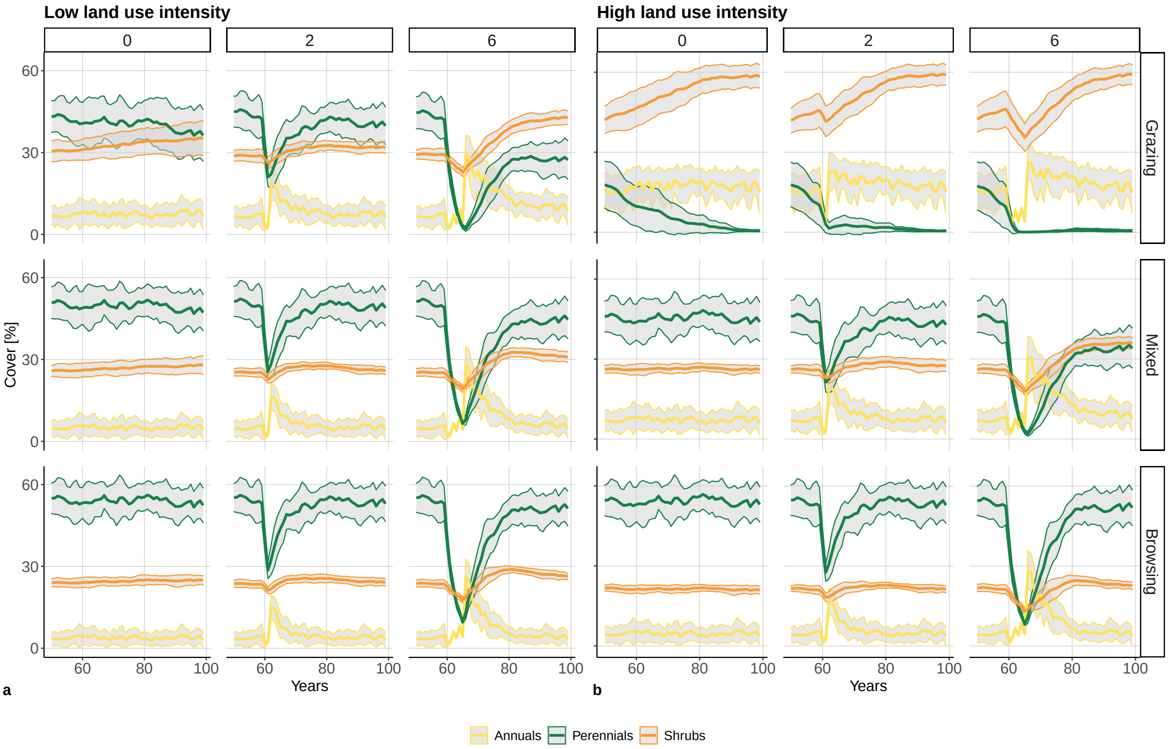

Figure A.1.9: Predicted mean cover ± SD [%] of the three meta-PFTs (lines) under various drought period lengths for all rangeland use scenarios. The numbers (2, 6) at the top correspond to drought duration in years. All droughts began in the year 60. The graphs are shown from year 50. All simulations were repeated for 30 climate repetitions.

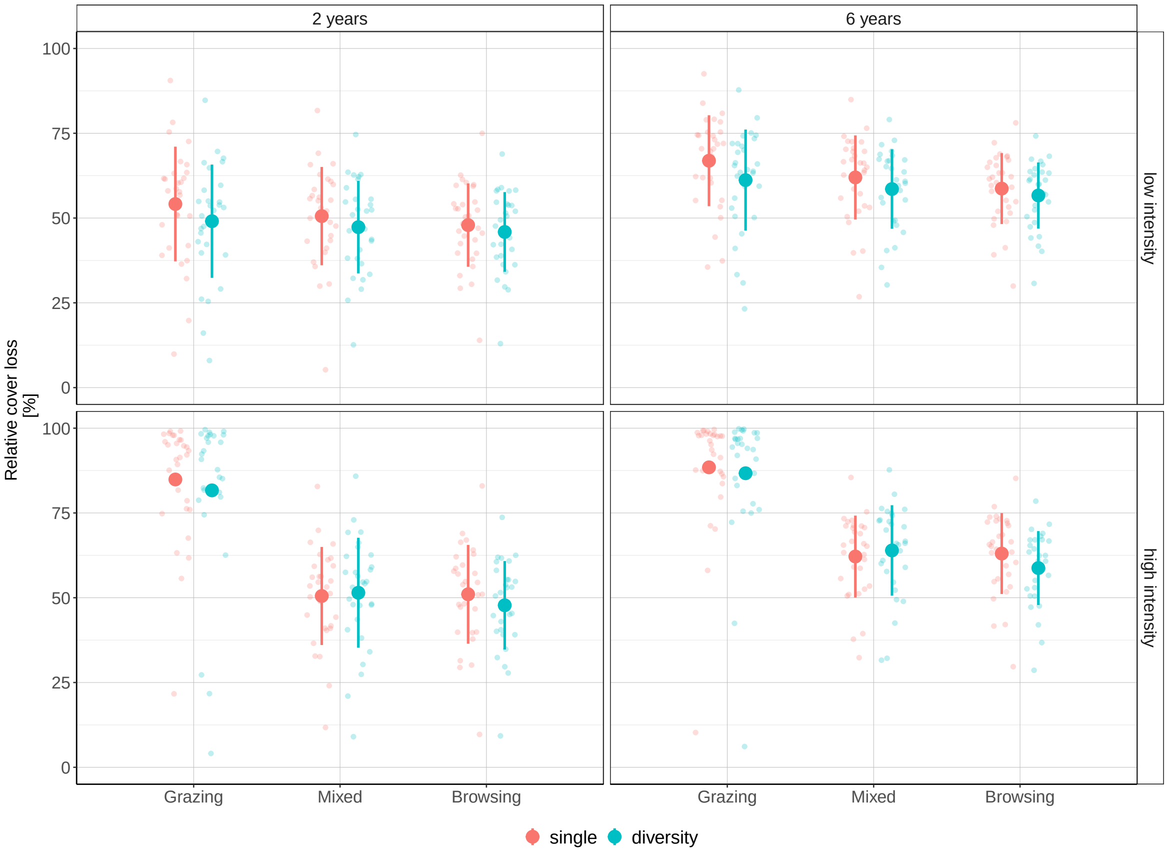

Figure A.1.10: a: Highest mean cover loss ± SD [%] (big points + range) of perennial grasses during the 2 and 6-year long drought periods compared to the cover in the control scenario at the same time for all three rangeland use types. b: Mean time ± standard deviation (in years) until 80% of the control cover was reached after the end of the drought period (big point + range). Specific colours distinguish the scenario with a single functional plant type (single/red) compared to the scenario with multiple sub-types of the same meta-PFT (diversity/blue). Small points in the point cloud indicate the recovery time of each climate repetition, if there are less than 30 points, the cover did not recover back to at least 80% of the control cover. Results are shown for the 30 climate time series.

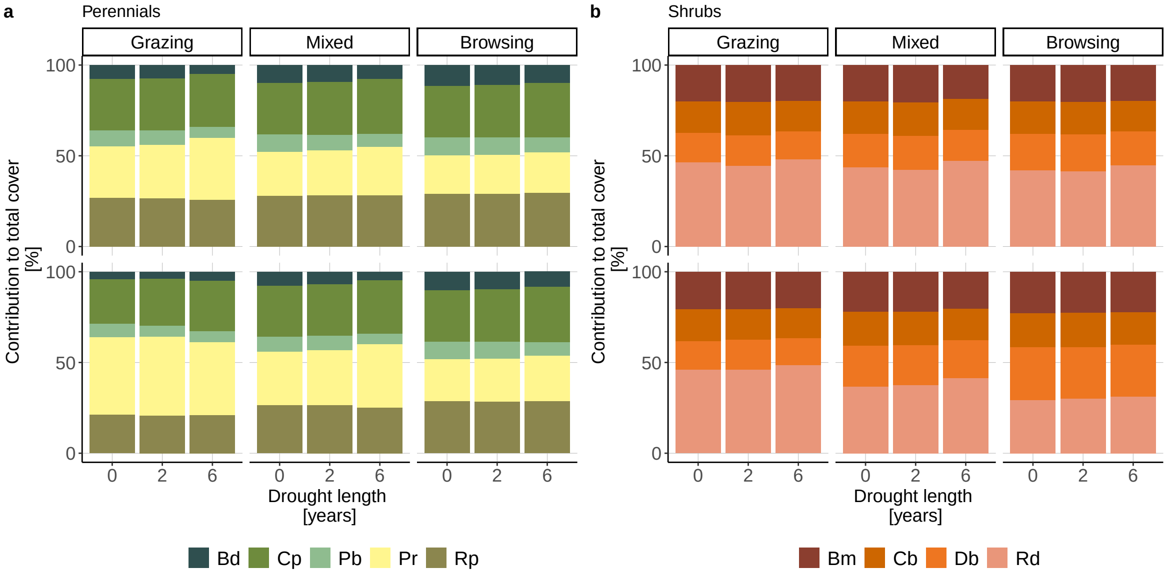

Figure A.1.11: Mean relative cover shift of five perennial and four shrub sub-PFTs in all rangeland use scenarios and under different drought lengths (2 and 6 years) relative to total cover, suggesting how the contribution of sub-PFTs to total cover shift in response to a certain rangeland use scenario and drought. Results represent mean vegetation cover of the first year post drought repeated for 30 climate time series.

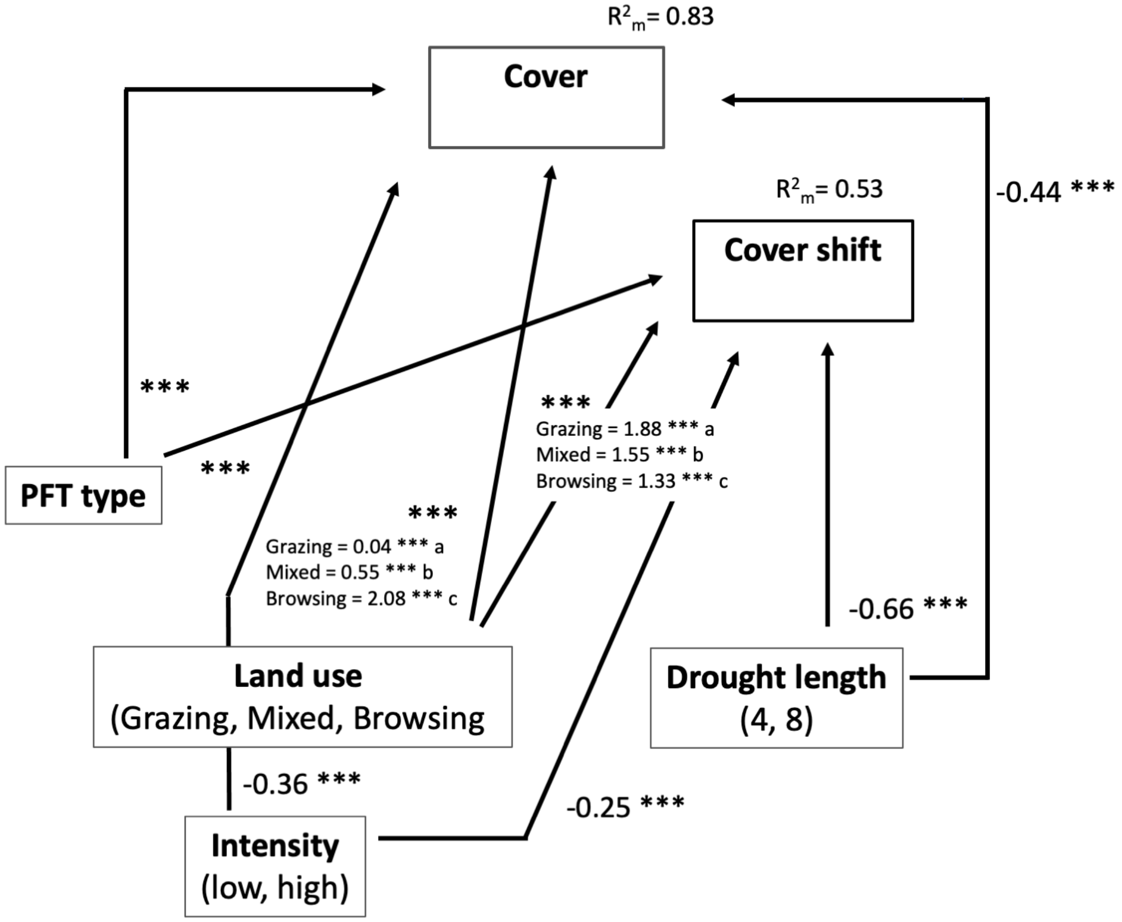

Figure A.1.12: Results of confirmatory path analysis. Coefficients are only computed for direct effects. For the effect of taxa, least-square means are schon for each factor together with a letter indicating significant difference at the 5% level using Tukey's post-hoc test. R^2 shows the explained variance by the fixed effects included in the model.

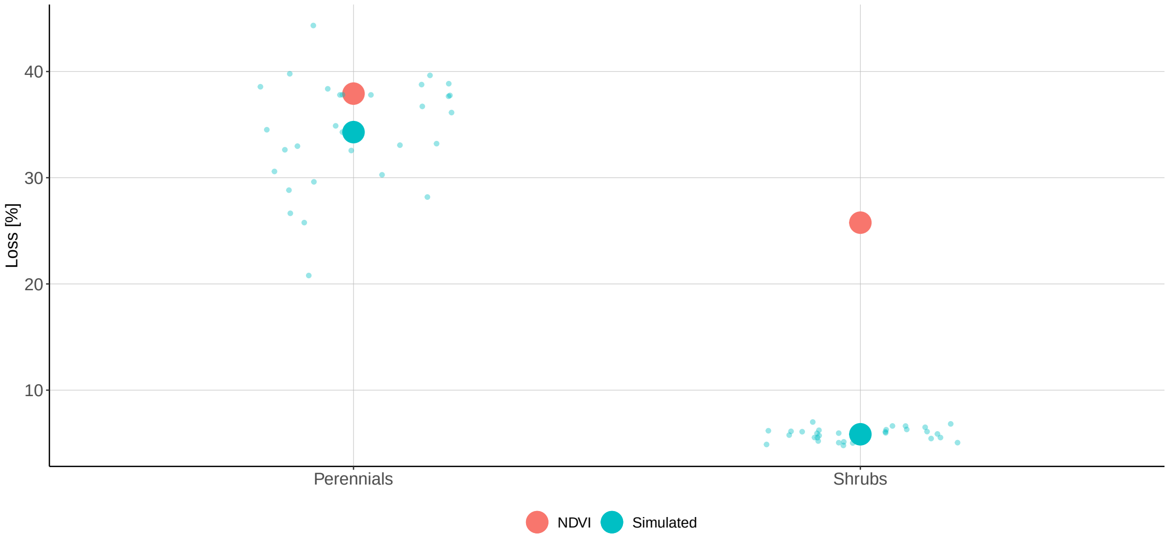

Figure A.1.13: Changes in NDVI for shrubland and open plain compared to simulated perennial grasses and shrub cover after 4 year drought under mixed animal scenario at high animal density. The big point in blue represents the mean of all 30 climate repetitions. Differences in simulated vegetation cover are due to different pre-drought precipitation.

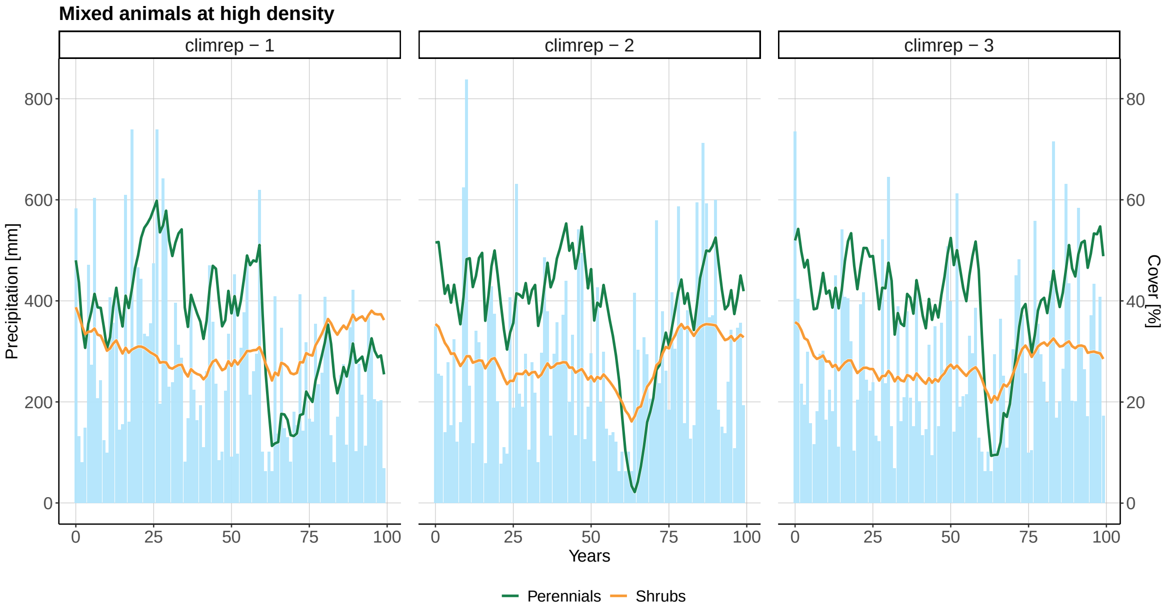

Figure A.1.14: Vegetation cover time series (lines) of three example climate repetitions (panel) for mixed animal at high density in the 4-year drought scenario in response to annual precipitation (blue bars).

Figure A.1.15: Annual precipitation distribution of all climate repetitions for the 8 year drought scenario shown from year 50. The vertical lines show the start of all dry periods (year 60) and the end of the longest drought (year 68).

Statistical output

Table A.1.4: Analysis of Variance of Aligned Rank Transformed Data 10 years post drought. Analysis of Deviance Table (Type III Wald F tests with Kenward-Roger df. Mixed effect linear model (lmer).

Factor	***F***	***Df***	***Df.res***	***P-value***
rangelanduse	1518.63	2	673	<0.001***
intensity	833.411	1	673	<0.001***
droughtlength	826.10	2	673	<0.001***
rangelanduse:intensity	482.07	2	673	<0.001***
rangelanduse:droughtlength	21.15	4	673	<0.001***
intensity:droughtlength	26.54	2	673	<0.001***
rangelanduse:intensity:droughtlength	62.10	4	673	<0.001***

Table A.1.5: Tukey post-hoc test for comparing perennial grass cover differences between rangeland use types 10 years post drought.

Contrast	***Estimate***	***Df***	***t.ratio***	***P-value***
Grazing - Mixed	0.35	1403	23.28	<0.001
Grazing - Browsing	0.55	1403	36.48	<0.001
Mixed - Browsing	0.20	1403	13.20	<0.001

Table A.1.6: Tukey post-hoc test for comparing perennial grass cover differences in the three-way interaction rangeland use and drought length 10 years post drought. Low and high stand for rangeland use intensity, and the numbers behind indicate drought length.

Contrast	***Estimate***	***Df***	***t.ratio***	***P-value***
Browsing, low4 - Grazing, low4	148.87	319	17.43	<0.001***
Browsing, high4 - Grazing, high4	275.70	319	32.27	<0.001***
Browsing, low4 - Mixed, low4	65.50	319	7.67	<0.001***
Browsing, high4 - Mixed, high4	119.33	319	13.98	<0.001***
Grazing, low4 - Mixed, low4	-83.37	319	-9.76	<0.001***
Grazing, high4 - Mixed, high4	-154.37	319	-18.31	<0.001***
Browsing, low8 - Grazing, low8	168.60	319	19.74	<0.001***
Browsing, high8 - Grazing, high8	238.97	319	27.96	<0.001***
Browsing, low8 - Mixed, low8	-79.33	319	9.290	<0.001***
Browsing, high8 - Mixed, high8	152.60	319	17.97	<0.001***

Table A.1.6 continued.

Contrast	***Estimate***	***Df***	***t.ratio***	***P-value***
Grazing, low8 - Mixed, low8	-89.27	319	-10.45	<0.001***
Grazing, high8 - Mixed, high8	-86.37	319	-10.11	<0.001***

Table A.1.7: Effect sizes calculation for 0, 10 and 20 years post drought (YPD). Stars indicate the size of the effect, with one star being a medium, and two stars a large effect.

Factor	***partial η^2***	***0***	***10***	***20 YPD***
rangelanduse		0.75**	0.81**	0.82**
intensity		0.51**	0.55**	0.54**
droughtlength		0.87**	0.71**	0.44**
rangelanduse:intensity		0.49**	0.58**	0.65**
rangelanduse:droughtlength		0.54**	0.11*	0.07*
intensity:droughtlength		0.30**	0.07	0.08*
rangelanduse:intensity:droughtlength		0.46**	0.26**	0.16**

Table A.1.8: Tukey post-hoc test for comparing perennial grass cover differences between diversity scenarios 10 years post drought.

Contrast	***Estimate***	***Df***	***t.ratio***	***P-value***
diversity - single	-61.9	1404	-2.66	< 0.05

Table A.1.9: Generalized linear mixed model output. Resistance to cover loss as response variable. Family = Beta distribution. AIC = -2393.23. Random effects StdDev = 0.32. Phi parameters: 3.26 ± 0.06.

Factor	***Estimate***	***z-value***	***P-value***
Intercept	0.87	11.54	<0.001***
rangelanduseGrazing	1.49	25.72	<0.001***
rangelanduseMixed	0.50	10.48	<0.001***
intensityLow	-0.58	-13.83	<0.001***
length8	1.84	36.38	<0.001***
biodivSingle	0.24	5.78	<0.001***

Table A.1.10: Generalized linear mixed model output. Recovery time of perennial grasses to 80% of control cover as response variable. Family = Poisson distribution. AIC = 24334.9. Random effects 0.05 ± 0.23.

Factor	***Estimate***	***z-value***	***P-value***
Intercept	1.93	42.87	<0.001***
rangelanduseGrazing	0.47	16.79	<0.001***
rangelanduseMixed	0.50	20.17	<0.001***
intensityLow	0.02	0.65	0.52
length8	0.46	18.32	<0.001***
biodivSingle	0.36	14.49	<0.001***

Table A.1.11: : Structural equation model output of perennial grass composition. Standardized and non-standardized path coefficients. Individual R^2 log_cov = 0.83, cover_relative_to_ctrl = 0.54. Note that we can only provide estimates for ordinal coefficients.

Response	***Factor***		***Estimate***	***Df***	***P-value***	***Std. Estimate***
log_cov	drought length		-0.48	1762	0.000	-0.44 ***
	intensity		-0.82	1762	0.000	- ***
	rangeland use		-	2	0.000	- ***
		Grazing		-3.07	0.000	- ***
		Mixed		-0.60	0.000	- ***
		Browsing		0.73	0.000	- ***
	PFT			4	0.000	- ***
		Pr	-1.50	29	0.000	- ***
		Rp	-1.41	29	0.000	- ***
		Cp	-0.68	29	0.000	- ***
		Pb	-0.65	29	0.000	- ***
		Bd	-0.65	29	0.000	- ***
cover_relative_to_ctrl	log_cov		0.021	1761	0.000	- ***

Table A.1.11 continued.

Response	***Factor***		***Estimate***	***Df***	***P-value***	***Std. Estimate***
	drought length		-0.10	1761	0.000	-0.66 ***
	intensity		-0.4	1761	0.000	-0.25 ***
	PFT			4	0.000	- ***
		Bd	0.33	29	0.000	- ***
		Pb	0.33	29	0.000	- ***
		Rp	0.49	29	0.000	- ***
		Cp	0.53	29	0.000	- ***
		Pr	-0.65	29	0.000	- ***
	rangeland use		-	2	0.000	- ***
		Grazing	0.41	29	0.000	- ***
		Mixed	0.43	29	0.000	- ***
		Browsing	0.46	29	0.000	- ***

Table A.1.12: Structural equation model output. Marginal means of rangeland use effects on total perennial grass cover.

Contrast	***Estimate***	***Df***	***t.ratio***	***P-value***
Grazing - Mixed	-2.47	1762	-46.07	<0.001
Grazing - Browsing	-3.8	1762	-70.962	<0.001
Mixed - Browsing	-1.33	1762	-24.89	<0.001

Table A.1.13: Structural equation model output. Pairwise differences of perennial grass cover between rangeland use types.

Contrast	***Estimate***	***Df***	***t.ratio***	***P-value***
Grazing - Mixed	-2.47	1762	-46.07	<0.001
Grazing - Browsing	-3.8	1762	-70.962	<0.001
Mixed - Browsing	-1.33	1762	-24.89	<0.001

Table A.1.14: Structural equation model output. Marginal means of rangeland use effects on deviation of total perennial grass cover from control cover.

Contrast	***Estimate***	***Df***	***t.ratio***	***P-value***
Grazing - Mixed	-2.47	1762	-46.07	<0.001
Grazing - Browsing	-3.8	1762	-70.962	<0.001
Mixed - Browsing	-1.33	1762	-24.89	<0.001

Table A.1.15: Structural equation model output. Pairwise differences of perennial grass cover deviation from its control cover between rangeland use types.

Contrast	***Estimate***	***Df***	***t.ratio***	***P-value***
Grazing - Mixed	-0.07	1762	-5.27	<0.001
Grazing - Browsing	-0.13	1762	-9.45	<0.001
Mixed - Browsing	-0.06	1762	-4.18	0.0001

Table A.1.16: Structural equation model output. Pairwise differences of perennial grass sub-PFT's log-cover using Tukey-post-hoc test.

PFT	***Estimate***	***Df***	***t.ratio***	***P-value***
Bd - Cp	-0.85	1762	-12.297	<0.001
Bd - Pb	-0.09	1762	-1.33	0.67
Bd- Pr	-0.85	1762	-12.369	<0.001
Bd - Rp	-0.82	1762	-11.84	<0.001
Cp - Pb	0.76	1762	10.96	<0.001
Cp - Pr	-0.00	1762	-0.07	1.000
Cp - Rp	0.03	1762	0.45	0.991
Pb - Pr	-0.76	1762	-11.04	<0.001
Pb - Rp	-0.72	1762	-10.51	<0.001
Pr - Rp	0.04	1762	-10.51	0.98

Table A.1.17: : Structural equation model output of shrub cover composition. Standardised and non-standardised path coefficients. Individual R^2 log_cov = 0.78, cover_relative_to_ctrl = 0.59. Note that we can only provide estimates for ordinal coefficients.

Response	***Factor***		***Estimate***	***Df***	***P-value***	***Std. Estimate***
log_cov	drought length		-0.07	1402	0.000	-0.27 ***
	intensity		-0.02	1402	0.01	-0.03 ***
	rangeland use		-	2	0.000	- ***
		Grazing		1.88	0.000	- ***
		Mixed		1.53	0.000	- ***
		Browsing		1.33	0.000	- ***
	PFT			3	0.000	- ***
		Cb	1.30	29	0.000	- ***
		BM	1.41	29	0.000	- ***
		Db	1.41	29	0.000	- ***
		Rd	2.21	29	0.000	- ***
cover_relative_to_ctrl	log_cov		-0.08	1402	0.000	- ***
	drought length		-0.13	1402	0.000	-0.2 ***
	intensity		-0.4	1402	0.000	0.03 ***
	PFT			3	0.000	- ***
		Cb	0.42	29	0.000	- ***
		BM	0.45	29	0.000	- ***
		Db	0.46	29	0.000	- ***
		Rd	0.54	29	0.000	- ***
	rangeland use		-	2	0.000	- ***
		Grazing	0.44	29	0.000	- ***

Table A.1.17 continued.

Response	***Factor***		***Estimate***	***Df***	***P-value***	***Std. Estimate***
		Mixed	0.47	29	0.000	- ***
		Browsing	0.495	29	0.000	- ***

Table A.1.18: Structural equation model output. Pairwise differences of shrub cover between rangeland use types.

Contrast	***Estimate***	***Df***	***t.ratio***	***P-value***
Grazing - Mixed	0.35	1403	23.28	<0.001
Grazing - Browsing	0.55	1403	36.48	<0.001
Mixed - Browsing	0.20	1403	13.20	<0.001

Table A.1.19: Structural equation model output. Pairwise differences of shrub sub-PFT's log-cover using Tukey-post-hoc test.

Contrast	***Estimate***	***Df***	***t.ratio***	***P-value***
Bm - Cb	0.11	1403	6.18	<0.001
Bm - Db	-0.01	1403	-0.40	0.98
Bm - Rd	-0.80	1403	-46.54	<0.001
Cb - Db	-0.11	1403	-6.58	<0.001
Cb - Rd	-0.91	1403	-52.72	<0.001
Db - Rd	-0.80	1403	-46.14	<0.001

Table A.1.20: Recovery times of perennial grasses under different rangeland use types and intensity for a plant community with high functional diversity. Minimum and mean recovery time indicated in years. We left out maximum recovery time as it was in every scenario in year 99, indicating that in every scenario there was one repetition where no recovery to 80% took place. The scenario grazing high is left out as there was no recovery. Note: the mean time here is the overall mean of all 30 climate repetitions, the mean shown in Fig. 3 is the mean of the fastest (min) recovery times across the 30 climate repetitions.

Rangeland use	***Intensity***	***Drought length***	***Min. time***	***Mean time***
Grazing	low	4	1	20.3
		8	13	24.6

Table A.1.20 continued.

Rangeland use	*Intensity*	*Drought length*	*Min. time*	*Mean time*
Mixed	low	4	3	20.88
		8	5	21.55
	high	4	11	22.69
		8	11	24.25
Browsing	low	4	3	20.47
		8	2	19.97
	high	4	4	21.35
		8	4	20.2

A.7 Appendix to "Navigating Uncertainty: Enhancing Climate Change Resilience in Savanna Ecosystems Through Herbivore Communities"

Supplementary figures

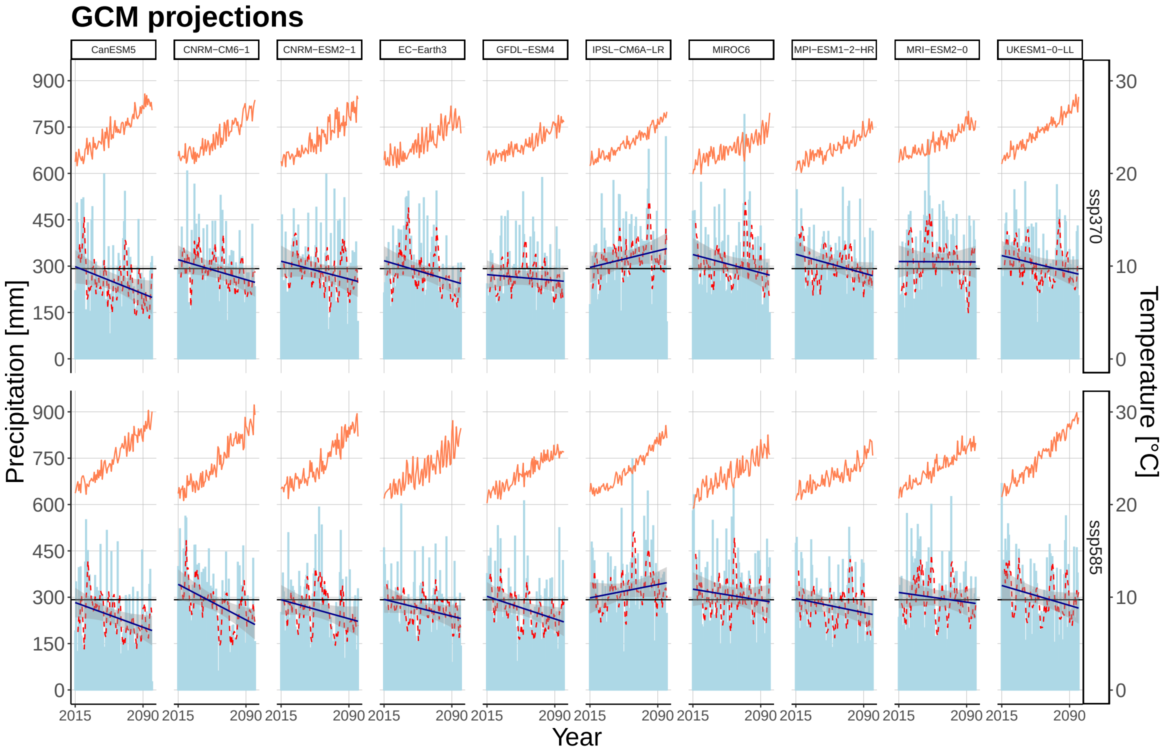

Figure A.1.16: Precipitation and temperature projections from the year 2015 until 2100 predicted by 10 global climate change models under 2 different climate change scenarios (ssp370/585). The blue bars show annual precipitation sums. The red dashed line depicts the moving average over a 4-year window. The straight black line is the current MAP (292 mm). The orange line depicts MAT.

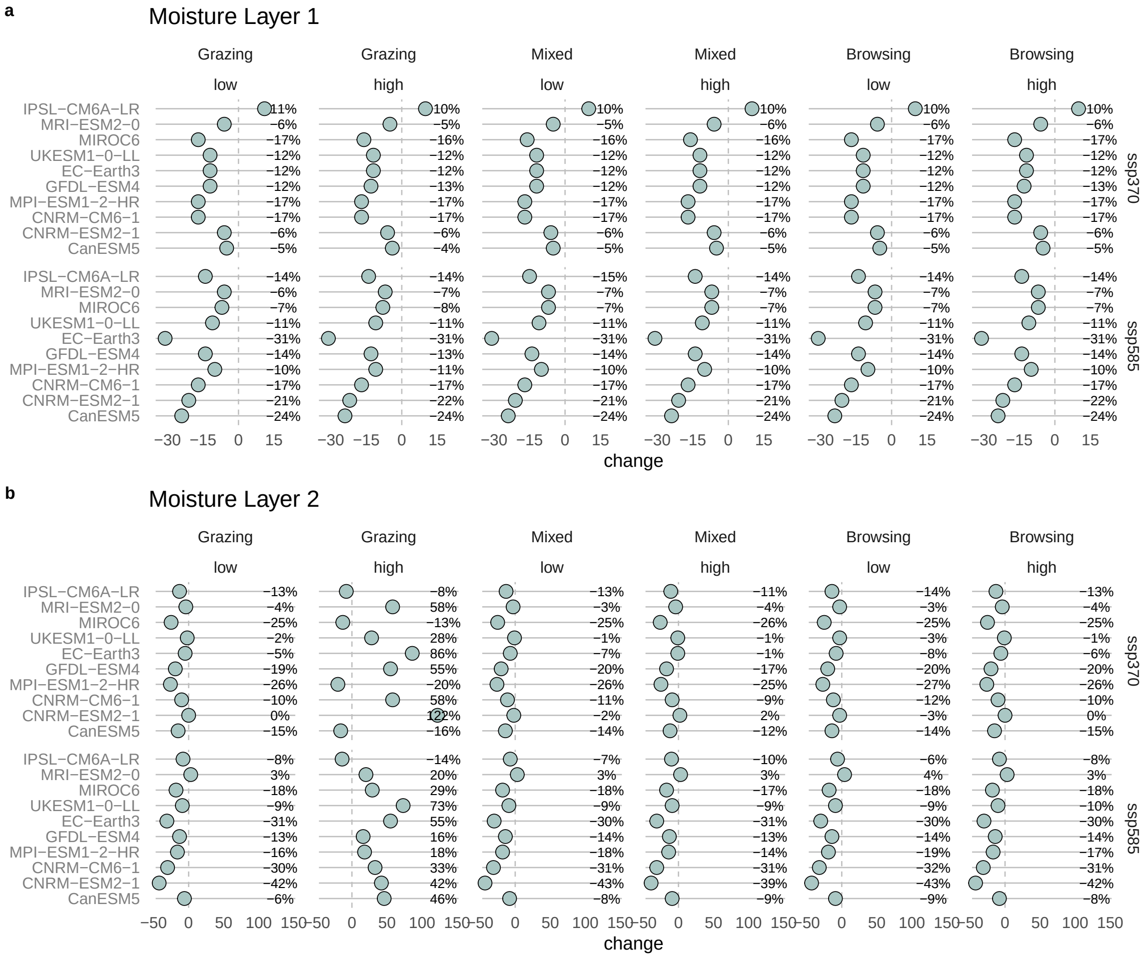

Figure A.1.17: Changes in available water for plant growth in upper (a) and lower (b) soil layer. Average number of days from 2050 to 2060 compared to the average number of days between 2089 to 2099 with moisture above viable threshold. The dashed line at zero depicts the mean number of days in the decade starting 2050. The numbers to the left and right depict by how much this number increased or decreased in 50 years. Output is shown for 10 different GCMs (rows) and 2 climate change scenarios (panels) under 3 land use scenarios (columns).

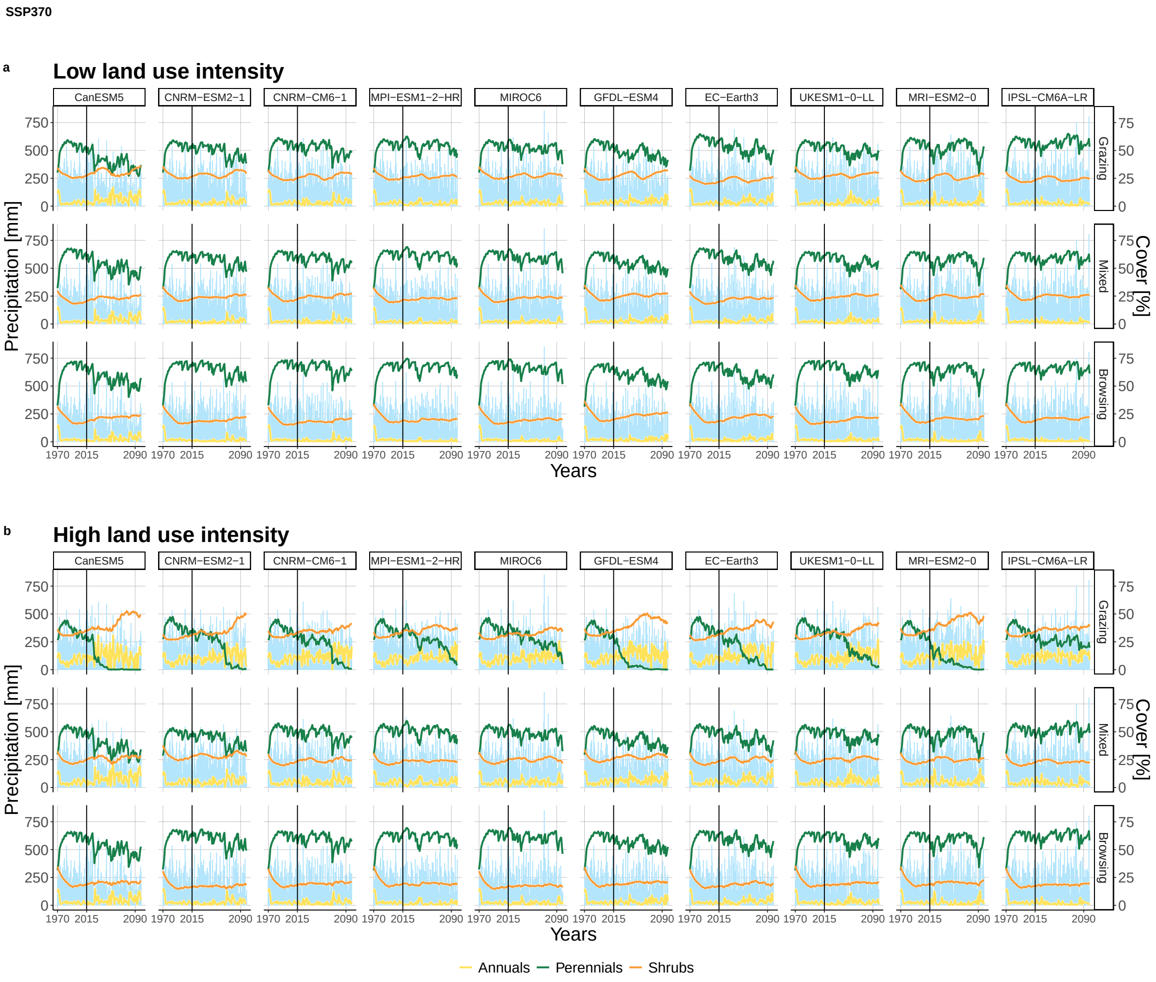

Figure A.1.18: Vegetation cover under different climate change predictions in the SSP370 scenario and three rangeland types at two intensities (a: low, b: high). The simulation starts with historical (partially modelled) data in the year 1970. The horizontal line in the year 2015 depicts the start of the modelled data by the respective GCM. Blue bars in the background denote annual precipitation sums.

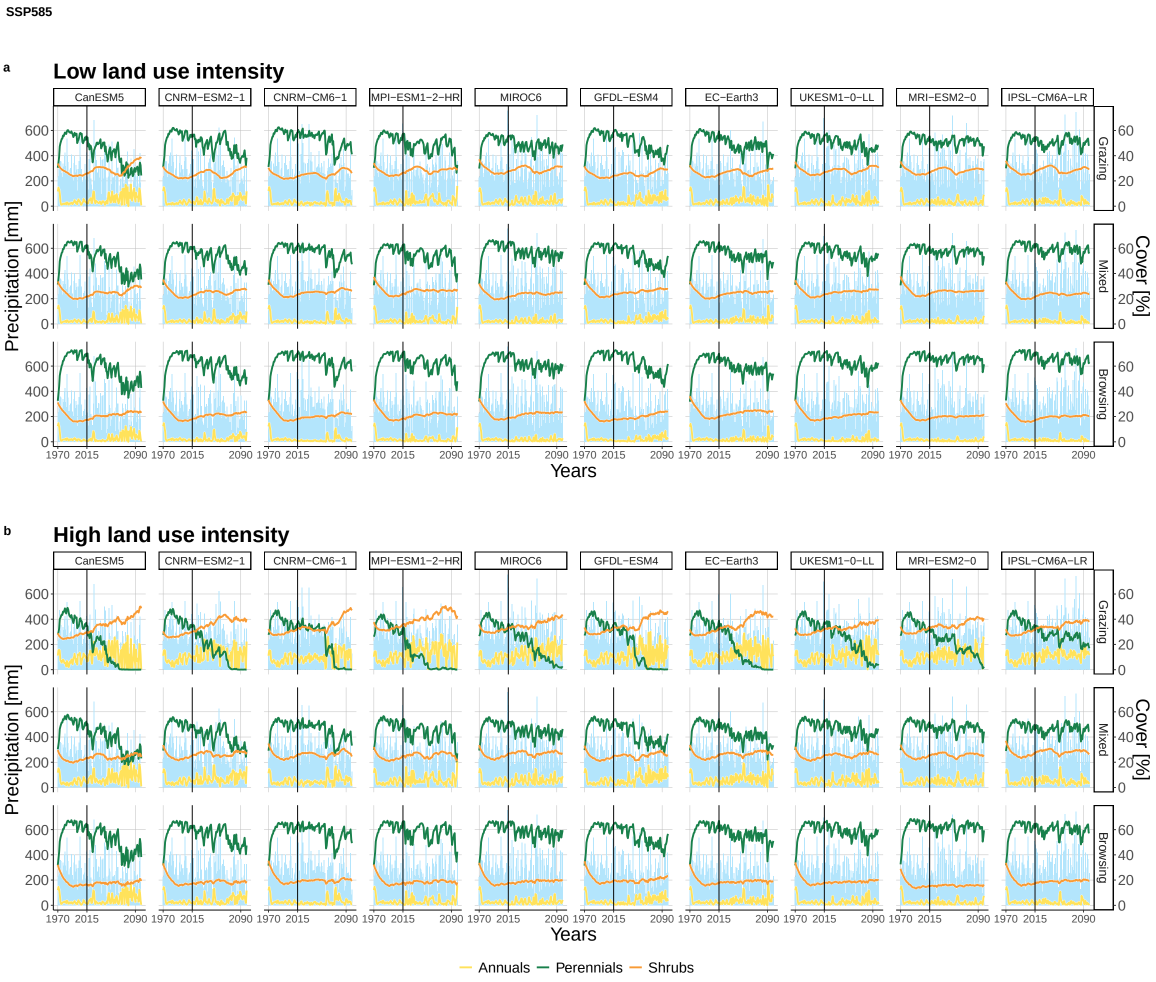

Figure A.1.19: Vegetation cover under different climate change predictions in the ssp585 scenario and three rangeland types at two intensities (a: low, b: high). The simulation starts with historical (partially modelled) data in the year 1970. The horizontal line in the year 2015 depicts the start of the modelled data by the respective GCM. Blue bars in the background denote annual precipitation sums.

Statistical output

Table A.1.21: Mean cover and standard deviation by land use type, intensity and climate change scenario (CCScen) per plant functional type in last 10 years of simulation.

Land use	Intensity	CCScen	Type	mean cover ± SD
Grazing	low	ssp370	Annuals	5.33 ± 1.67
Grazing	low	ssp370	Perennials	44.38 ± 6.09
Grazing	low	ssp370	Shrubs	29.26 ± 2.93
Grazing	low	ssp585	Annuals	5.12 ± 1.73
Grazing	low	ssp585	Perennials	42.4 ± 6.24
Grazing	low	ssp585	Shrubs	30.81 ± 2.54
Grazing	high	ssp370	Annuals	13.9 ± 1.92
Grazing	high	ssp370	Perennials	4.78 ± 7.2
Grazing	high	ssp 370	Shrubs	41.59 ± 4.6
Grazing	high	ssp 585	Annuals	12.57 ± 2.14
Grazing	high	ssp 585	Perennials	3.19 ± 6
Grazing	high	ssp 585	Shrubs	42.57 ± 3.33
Mixed	low	ssp 370	Annuals	3.76 ± 1.33
Mixed	low	ssp 370	Perennials	51.7 ± 4.08
Mixed	low	ssp 370	Shrubs	25.29 ± 1.61
Mixed	low	ssp 585	Annuals	3.77 ± 1.62
Mixed	low	ssp 585	Perennials	49.51 ± 5.92
Mixed	low	ssp585	Shrubs	26.72 ± 1.56
Mixed	high	ssp370	Annuals	7.84 ± 2
Mixed	high	ssp370	Perennials	39.43 ± 6.41
Mixed	high	ssp 370	Shrubs	25.59 ± 2.39
Mixed	high	ssp585	Annuals	7.43 ± 2.13
Mixed	high	ssp585	Perennials	37.64 ± 6.51
Mixed	high	ssp 585	Shrubs	26.81 ± 1.14
Browsing	low	ssp 370	Annuals	2.55 ± 1.2
Browsing	low	ssp370	Perennials	58.07 ± 4.77
Browsing	low	ssp 370	Shrubs	21.95 ± 1.79
Browsing	low	ssp585	Annuals	2.71 ± 1.4
Browsing	low	ssp585	Perennials	56.2 ± 5.9
Browsing	low	ssp 585	Shrubs	22.73 ± 1.17

Table A.1.21 continued.

Land use	**Intensity**	**CCScen**	**Type**	**mean cover ± SD**
Browsing	high	ssp 370	Annuals	4.29 ± 1.58
Browsing	high	ssp370	Perennials	53.31 ± 4.61
Browsing	high	ssp370	Shrubs	19.47 ± 1.2
Browsing	high	ssp585	Annuals	4.18 ± 1.92
Browsing	high	ssp585	Perennials	52.31 ± 6.06
Browsing	high	ssp585	Shrubs	19.3 ± 1.66

Table A.1.22: Mean values of functional diversity indices and standard deviation by land use type, intensity and climate change scenario (CCScen) in last 10 years of simulation.

Land use	**Intensity**	**CCScen**	**mean FEve ± SD**	**mean FDis ± SD**	**mean Rao's Q ± SD**
Grazing	low	ssp 370	0.55 ± 0.03	2.6 ± 0.01	6.83 ± 0.04
Grazing	low	ssp585	0.53 ± 0.04	2.61 ± 0.01	6.87 ± 0.03
Grazing	high	ssp370	0.18 ± 0.06	2.23 ± 0.24	5.85 ± 0.69
Grazing	high	ssp 585	0.17 ± 0.05	2.15 ± 0.19	5.61 ± 0.55
Mixed	low	ssp 370	0.59 ± 0.01	2.59 ± 0	6.8 ± 0.02
Mixed	low	ssp 585	0.58 ± 0.02	2.6 ± 0.01	6.82 ± 0.02
Mixed	high	ssp 370	0.5 ± 0.04	2.58 ± 0.02	6.81 ± 0.06
Mixed	high	ssp 585	0.49 ± 0.04	2.59 ± 0.01	6.83 ± 0.03
Browsing	low	ssp 370	0.6 ± 0.01	2.58 ± 0.01	6.75 ± 0.03
Browsing	low	ssp 585	0.6 ± 0.01	2.59 ± 0.01	6.77 ± 0.03
Browsing	high	ssp 370	0.57 ± 0.01	2.57 ± 0.01	6.75 ± 0.03
Browsing	high	ssp 585	0.57 ± 0.01	2.57 ± 0.01	6.75 ± 0.03

Table A.1.23: Mean values of water use efficiency by land use type, intensity and climate change scenario (CCScen) in last 10 years of simulation. The loss in WUE between high and low land use intensity is also shown.

Land use	**CCScen**	**mean WUE ± SD low**	**mean WUE ± SD high**	**mean WUE loss ± SD**
Grazing	ssp 370	81.09 ± 3.68	66.69 ± 4.69	−17.76 ± 3.92
Grazing	ssp 585	80.86 ± 3.12	65.12 ± 4.85	−19.53 ± 3.94
Mixed	ssp 370	82.38 ± 3.65	76.69 ± 4.2	−6.95 ± 1.47

Table A.1.23 continued.

Land use	CCScen	mean WUE ± SD low	mean WUE ± SD high	mean WUE loss ± SD
Mixed	ssp 585	82.08 ± 3.07	76.26 ± 4.08	−7.11 ± 2.43
Browsing	ssp 370	83.67 ± 3.6	79.96 ± 3.9	−4.45 ± 0.84
Browsing	ssp 585	83.18 ± 3.21	79.23 ± 3.4	−4.76 ± 1.17

Table A.1.24: Time when tipping point, meaning a shift from perennial grass to shrub dominance, was reached for 10 climate models and 2 climate change scenarios. The table only shows the land use scenarios where a vegetation shift occurred. ShrubFrac denotes the proportion of shrubs in total cover and shrubCov the total shrub cover at the end of the simulation.

Land use	Model	CCScen	Year	shrubFrac	shrubCov
Grazing high	CanESM5	ssp 370	2015	99.73	49.01
Grazing high	CanESM5	ssp 585	2017	99.91	48.62
Grazing high	CNRM-CM6-1	ssp 370	2015	95.75	41.54
Grazing high	CNRM-CM6-1	ssp 585	2019	99.82	47.04
Grazing high	CNRM-ESM2-1	ssp 370	2021	99.29	49
Grazing high	CNRM-ESM2-1	ssp 585	2020	99.68	40.22
Grazing high	EC-Earth3	ssp 370	2021	98.64	43.18
Grazing high	EC-Earth3	ssp 585	2016	99.78	42.02
Grazing high	GFDL-ESM4	ssp 370	2015	99.31	42.58
Grazing high	GFDL-ESM4	ssp585	2021	98.64	46.3
Grazing high	IPSL-CM6A-LR	ssp 370	2015	32.7	38.73
Grazing high	IPSL-CM6A-LR	ssp 585	2015	38.23	37.98
Grazing high	MIROC6	ssp 370	2022	74.73	34.18
Grazing high	MIROC6	ssp 585	2019	88.43	43.74
Grazing high	MPI-ESM1-2-HR	ssp 370	2025	75.14	37.73
Grazing high	MPI-ESM1-2-HR	ssp 585	2015	99.69	42.68
Grazing high	MRI-ESM2-0	ssp 370	2015	98.17	47.74
Grazing high	MRI-ESM2-0	ssp585	2016	89.09	40.69
Grazing high	UKESM1-0-LL	ssp370	2017	91.19	40.93
Grazing high	UKESM1-0-LL	ssp585	2025	83.89	38.85
Grazing low	CanESM5	ssp 370	2053	-1	36.22
Grazing low	CanESM5	ssp585	2073	21.8	37.84

Table A.1.24 continued.

Land use	**Model**	**CCScen**	**Year**	**shrubFrac**	**shrubCov**
Grazing low	MPI-ESM1-2-HR	ssp585	2098	-4.28	30.04
Mixed high	CanESM5	ssp 370	2080	-9.13	28.42
Mixed high	CanESM5	ssp 585	2069	2.38	24.17
Mixed high	CNRM-CM6-1	ssp585	2072	-14.95	24.57
Mixed high	CNRM-ESM2-1	ssp 370	2076	-7.53	27.76
Mixed high	CNRM-ESM2-1	ssp 585	2089	-3.22	28.1
Mixed high	EC-Earth3	ssp 585	2090	-12.83	25.89
Mixed high	MPI-ESM1-2-HR	ssp585	2098	-8.74	22.71
Mixed high	MRI-ESM2-0	ssp 370	2091	-30.74	25.99

Additional tables

Table A.1.25: Perennial grass and shrub plant life strategies in a semi-arid savanna. The letter code refers to the strategy name. The name of the sub-type always consists of capital and lowercase letters, corresponding to the characteristics listed above. The capitalised letters refer to the specialisation in a specific property, that is, the trait the plant benefits from by increasing its cover by 10%. The lowercase letters represent its trade-offs that lead to a 10% cover decrease.

Perennials	**Example species**	**Shrubs**	**Example species**
BCMRde	*Stipagrostis uniplumis*	BCDMRep	*Colophospermum mopane*
BEmpr	*Fingerhuthia africana*	BPRd	*Grewia olukondae*
BMPcde	*Chloris virgata*	CBRedp	*Boscia albitrunca*
CMde	*Eragrostis echinochloidea*	CDEMRp	*Acacia reficiencs*
CMPRbde	*Eragrostis nindensis*	CMRp	*Catophractes alexandri*
DEMpr	*Bothriochloa radicans*	Dmp	*Dichrostachys cinerea*
EMPdcr	*Brachiaria marlothii*	DMRep	*Acacia mellifera*