# The role of diversity in savannas: modelling plant functional diversity and its effects on ecosystem functioning

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by

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# Foreword

This dissertation is a cumulative work of manuscripts from my publication list, either published or submitted or finished. This thesis is based on the following papers:

1. **Guo, T.**, Lohmann, D., Ratzmann, G., Tietjen, B., 2016. Response of semi-arid savanna vegetation composition towards grazing along a precipitation gradient – the effect of including plant heterogeneity into an ecohydrological savanna model. *Ecol model* 325, 47-56. doi: 10.1016/j.ecolmodel.2016.01.004

2. Lohmann, D., **Guo, T.**, Tietjen, B.. Zooming in on coarse plant functional types – simulated response of functional savanna vegetation composition in response to aridity and grazing. *Submitted to Theoretical Ecology on 23$^{rd}$ of February 2017*.

3. **Guo, T.**, Weise, H., Fiedler, S., Lohmann, D., Tietjen, B.. The role of landscape heterogeneity in regulating plant functional diversity under different precipitation and grazing regimes in semi-arid savannas. *To be submitted soon.*

# Contents

# Chapter 0

# General introduction

## 0.1 Motivation

Savannas approximately cover 20% of the global land surface and account for 30% of the terrestrial net primary production (Sankaran et al., 2005; Grace et al., 2006). Moreover, they form integral parts of the global carbon and water cycles (Donohue et al., 2013; Poulter et al., 2014). The savanna biomes are located in Africa, South America, Australia and India (Fig. 0.1) (Mistry, 2000). Ecosystem services in savannas sustain an estimated one-fifth of the human world population (Lehmann et al., 2014). Savannas in general can be roughly grouped into arid, semi-arid and humid savannas. Humid savannas are found in regions experiencing more than around 800 mm mean annual precipitation (MAP) (Baudena et al., 2015) whereas arid savannas are located in the dry edge characterized by typically less than 300mm MAP (Falkenmark and Rockström, 2004). Semi-arid savannas are found in regions with MAP ranging between 300 mm to 800 mm (Whitford, 2002) and are generally characterized by a plant matrix of predominant perennial grasses and a discontinued cover of woody plants (Walker et al., 1981). As this sub-biome is found in regions with limited amounts of rainfall input, it is strongly water controlled which is further underlined by a typically low ratio of precipitation to potential evapotranspiration (Wang et al., 2012). The highly variable annual rainfall, jointly with human land use, dominantly control ecosystem processes and vegetation dynamics (Holmgren et al., 2006). Despite their importance for human well-being and global carbon and water cycles, savannas face increasing levels of degradation globally (Zika and Erb, 2009).
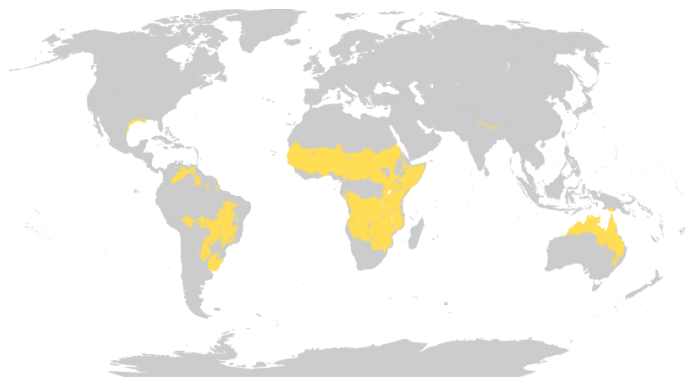


Figure 0.1 Global distribution of savanna biome. Picture source: ASU school of life science. This

picture is used by permission. URL: https://askabiologist.asu.edu/explore/savanna

An example of land degradation affecting many semi-arid savanna ecosystems is the so called shrub encroachment (Roques et al., 2001). Shrub encroachment refers to a shift from a grass-dominated state of the ecosystem to a state which is mainly dominated by woody plants. Degradation in general can be defined as changes in ecosystem functioning (Eldridge et al., 2011), ultimately leading to a loss of ecosystem services (Chapin et al., 2002). In savanna ecosystems, this typically manifests in a change of primary production, the rate of water fluxes and the stability of plant communities leading to a loss of forage provision to grazers, habitat fitness and maintenance of plant biodiversity.

As highlighted by the example of shrub encroachment, savanna plant community structure as well as functional diversity are key attributes for ecosystem functioning (Solbrig et al., 1996). However, this vegetation diversity in semi-arid regions is highly sensitive to changes in land use and climatic conditions (Cowling et al., 1994; Rutherford and Powrie, 2011), which will even gain importance in the coming decades given projected changes in land use and climate (IPCC 1996 a, b). For example, heavy land use often leads to a decreased plant species diversity (Rutherford and Powrie, 2011) which can be aggravated by drought events (Palmquist et al., 2014). Besides those environmental effects, the diversity of savanna vegetation is also affected by edaphic conditions (Williams et al., 1996; San Jose et al., 1998). Locally heterogeneous soil conditions can accommodate a wealth of small-scale habitats and consequently promote vegetation diversity. Thus, a deeper understanding is required how environmental conditions affect vegetation biodiversity and ecosystem processes in savanna ecosystems, as well as the provision of feasible schemes for predicting vegetation dynamics in the future environment. However, large-scale vegetation field studies and surveys under different environmental conditions are typically time consuming and costly. Simulation models are a useful tool to overcome this caveat by describing all relevant components of ecosystems and the associated driving forces (Jørgensen, 2012). They are able to disclose the effects of environmental drivers (such as aridity, land use and landscape heterogeneity) on vegetation dynamics at a long temporal and at a large spatial scale, as well as the underlying mechanisms of vegetation diversity. The present thesis aims at furthering our understanding of semi-arid savanna ecosystem functioning with a particular focus on vegetation functional diversity in semi-arid savannas using a process-based simulation model.

### 0.1.1 Savanna vegetation in different environmental conditions

Semi-arid savanna ecosystems are in their functioning and vegetation composition direct outcomes of long-term environmental framing conditions. A main factor determining the fate of those savannas is rainfall. Besides setting the overall boundaries for semi-arid savannas (see chapter 0.1), the overall effects of MAP are, however, modulated by a generally high variability of interannual precipitation (D'Odorico and Bhattachan, 2012). The intra-annual rainfall distribution is characterized by a strong seasonality with virtually the entire precipitation of one year falling within the wet period covering three to six months (Schultz, 2002). How a given rainfall event affects ecosystem functioning and processes depends on local conditions, such as soil texture, as well as on feedbacks between the vegetation and the soil. Rainfall input to the soil positively affects the local soil water balance and provides plant available water through increased soil moisture. Plants in turn take advantage of this soil water to produce new biomass which on the one hand decreases soil moisture through transpiration but also decreases the evaporative demand by increased soil shading. Those local processes then lead to typical local ecosystem structures and compositions which, as emerging properties, form large scale patterns along climatic gradients, such as MAP. For example, MAP has been shown to control the relative share of trees in total vegetation cover as well as their maximum attainable cover (Sankaran et al., 2005). The mechanism by which higher MAP allows for a higher woody cover is mainly found in a higher infiltration into deep soil layers, which promotes the growth of deep-rooted plants such as most woody species. The importance of single rainfall events, however, differs between individual plant in semi-arid ecosystems. This is due to different strategies of plants to take advantage of available soil water such as wilting points and water use efficiencies (Ogle and Reynolds, 2004).

Besides precipitation, grazing is a strong factor for shaping semi-arid savanna ecosystem functioning and vegetation composition (O'Connor, 1991; Eldridge et al., 2013). In their pristine form, savannas are a habitat for a multitude of grazers, such as wildebeest (*Connochaetes gnou*) or zebra (*Equus quagga*) in African savannas (Archibald and Bond, 2004; Codron and Brink, 2007). Those large herbivores have to date been vastly replaced by human livestock such as cattle or goats (Wigley et al., 2010). Such grazers can have different effects on ecosystems. Through trampling they may decrease soil porosity and thus affect the infiltration or percolation of soil water. Further, grazer feces can alter nutrient availability and soil carbon and nitrogen storage (Metzger et al., 2005). The direct effects of grazing on the vegetation mainly manifest in a loss of photosynthetic leaf area and reduction in apical meristems (Ash and McIvor, 1998). On the long term, continuously high stocking rates and

thus grazing pressure can lead to a permanent decline of the abundance and cover of perennial grasses which often lead to an increment of woody cover (Brown and Archer, 1999). This shrub encroachment is an irreversible process. Once established, shrubs and trees form dominant parts of the ecosystem and outcompete grass seedlings in both light and water acquisition. In general, however, the actual effect a grazer has through trampling or biomass removal may largely depend on the local soil conditions as well as on the local vegetation composition (Fuhlendorf and Smeins, 1998).

A third important factor for plant productivity and vegetation composition in semi-arid savannas are local soil conditions (Fernandez-Illescas et al., 2001). Patchy or clustered distributions of vegetation are characteristic for savanna landscapes (Aguiar and Sala, 1999; Augustine, 2003). The emergence of spatial vegetation mosaics is often linked to local differences of topography and edaphic variables such as soil texture and soil depth (Williams et al., 1996; Fuhlendorf and Smeins, 1998; Bestelmeyer et al., 2006). Soil texture, which describes the soil composition with respect to grain sizes, is a first order determinant for the potential of soils to take up water (infiltration) as well as to hold plant available water (Fernandez-Illescas et al., 2001). For example, local patches of coarse textured soil allow more water to infiltrate into deeper soil layers, which favors the growth of deep-rooted plants. Another key variable for plants is soil depth (Rodriguez-Iturbe and Porporato, 2004), which describes the available space for plants to develop roots. Deep rooted shrubs, for example, are more susceptible to drought on shallow soils compared to deep soils (Munson, 2013). Further, topography can have a large effect on local above-ground water redistribution (Bergkamp, 1998). These edaphic and topographic variables often co-vary spatially which can create heterogeneous landscapes and thus different microhabitats on a relatively small scale.

## 0.1.2 Functional diversity of savanna vegetation

Plant communities in semi-arid savannas are characterized by a high functional diversity (Cowling et al., 1994). A compelling example for this is the co-occurrence of different growth forms, such as grasses, shrubs and trees (Jeltsch et al., 1996). More generally, single plant species can be assigned to different functional types based on morphological, physiological and phenological differences (Tilman et al., 1997). Those different functional types may occupy various ecological niches in space and time. In semi-arid regions plants are typically broadly grouped based on their growth form into woody and herbaceous plants (Scholes and

Archer, 1997). Besides growth form, those groups also differ in, e.g., resource utilization and grazing resistance. Woody plants can often utilize water from deeper soil regions because of their typically deeper root system. This plant strategy can allow them to use soil water even during drought periods when top soil water reservoirs are depleted (Eagleson and Segarra, 1985). Contrastingly, grasses tend to use water from the top soil where soil moisture is comparatively high during rainfall periods (Walter, 1954). Those complementary water use strategies of woody plants and grasses can allow for their coexistence (Jeltsch et al., 1996). Besides this vertical root niche separation, differences between the two growth forms in their functional strategies of resource use efficiency and of coping with disturbance exist. Grasses tend to use available soil water more efficiently than woody plants (Scholes and Archer, 1997). At the same time, they are usually more negatively affected by drought periods leading to relatively higher drought-induced biomass losses (Milton and Dean, 2000). Moreover, they tend to be more attractive to herbivores than woody plants due to higher leaf protein contents (Olff et al., 1999). Woody types have often additionally evolved defense mechanisms such as thorns to prevent them from herbivory. This difference of plant strategies can also have positive effects on the maintenance of community level diversity. However, numerous studies show that within a broad functional type, such as woody and herbaceous plants, functional variability can be considerable in arid and semi-arid regions (Busso et al., 2001; Kos and Poschlod, 2010; Batalha et al., 2011; Kattge et al., 2011). This functional variability is usually described quantitatively using functional traits. Those traits are assumed to represent vegetation function and particular combinations of trait values may be used to describe strategies of plants to cope with environmental conditions and disturbance. Key functions of single plant types as well as of communities such as water or nutrient utilization and grazing resistance may be thus described through quantifying a given trait distribution (Diaz and Cabido, 2001). More generally, plant trait distributions in a community can also be a useful tool to predict changes in vegetation functional diversity (Lavorel and Garnier, 2002; Laliberte and Legendre, 2010). Thus, using community weighted mean trait values to describe broad functional strategies such as woody and herbaceous types often does not reflect the functional variance within those types and may lead to an erroneous quantifications of ecosystem functioning.

The effect a set of traits has on the performance and the fate of a given plant type depends on the environmental conditions the plant is growing in. Plants with their particular strategies being made up by a suit of traits are usually assumed to be adapted to their native

environment (Diaz et al., 1998). This is a direct outcome of evolutionary mechanisms by which the environment acts as a filter removing plant types with poorly performing strategies (or suits of traits). Thus, the vegetation functional diversity in a community is the direct outcome of environmental filtering. For example, seed mass and leaf area follow distinct patterns along a gradient of MAP in semi-arid regions. Seed mass increases linearly with MAP (Sandel et al., 2010), while leaf area has a unimodal response along MAP (Gross et al., 2013). Besides the selective force of precipitation, community functional trait compositions are also determined by the local grazing regime (Díaz et al., 2007). For example, Diaz et al. (2007) found that high grazing pressure leads to a community characterized by plants with an annual life history, lower height, and prostrate or stoloniferous architecture. In addition, grazers often select palatable species which then leads to a community mainly comprising poorly palatable species (Westoby et al., 1989). Grazing can also interact with precipitation in its effect on functional composition and diversity. Under high annual precipitation, grazing may increase plant functional diversity. In contrast, grazing tends to have negative effects on the diversity under low annual rainfall (May et al., 2009), since the convergent effects of aridity and grazing may lead to a selection of specific traits and thus of plant types (Quiroga et al., 2010). Besides precipitation and grazing, soil condition are strong determinants of the performance of functional strategies and the functional diversity of a plant community. Single edaphic or topographic variables have been shown to have similar filtering effects as rainfall and grazing. For example, deeper soils and gentle slopes favor grass species with a higher plant height and a larger leaf area index (Harzé et al., 2016). Plants often have a deeper root system in coarser textured soils because such soil properties typically have a low water retention capacity which leads to a stronger infiltration into deeper soil regions (Schenk and Jackson, 2002). Generally, locally heterogeneous soil conditions can provide diverse microhabitats and thus increase the available niche space for different functional strategies in a community (Stein et al., 2014). In summary, environmental conditions can determine the trait performance and thus strongly affect vegetation functional diversity in semi-arid savannas.

From an ecosystem perspective, functional diversity of plant communities is a key attribute for whole ecosystem functioning (Diaz and Cabido, 2001; Maestre et al., 2012; Valencia et al., 2015). Ecosystem functioning may be defined as the magnitude and the dynamics of ecosystem processes which determine plant productivity and resource cycling. The relative contribution of individual plant types to whole ecosystem functioning may thereby vary with

their abundance and singular effect (Naeem et al., 1999). Changes of vegetation functional diversity can therefore largely alter the manners in which ecosystems work, like handling short term water resource fluctuations and maintaining long term plant community stability, as the changes of diversity may lead to occurrence or loss of some key plant types. The associated mechanisms of the relationship between vegetation functional diversity and ecosystem functioning have been extensively studied (Tilman et al., 1997; Loreau et al., 2001; Hooper et al., 2005). So-called key species play a pivotal role in linking functional composition and ecosystem functioning. Key species are typically the most abundant species which in their functioning are characteristic for a given ecosystem (Grime, 1998). For example, communities mainly composed of fast-growing plant types may rapidly recover above ground productivity after water stress-induced mortality, which may lead to a relative maintenance of ecosystem functioning under drought conditions (Galmés et al., 2005). Considering the effects of grazing, plant communities dominated by types which are attractive to herbivores tend to become unstable under high grazing pressure (Walker et al., 1981). Another important effect of functional composition has on ecosystem functioning is that functional diversity can stabilize ecosystem functioning through mechanisms such as complementation of different plant types. Complementation generally refers to community resource use optimization through the exploitation of different niches. In addition, facilitation between plants may also play an important role for ecosystem functioning. For example, trees might increase the productivity of grasses growing under their canopy by shading-induced reductions of top soil evaporation (Synodinos et al., 2015). On the other hand, environmental perturbations can alter ecosystem functioning through their effect on vegetation functional diversity (De Laender et al., 2016). Intermediate levels of disturbance were found to maximize vegetation diversity which in turn led to an increase of community productivity (Kondoh, 2001). Vegetation functional diversity may in turn respond to environmental conditions, which may maintain ecosystem functioning by buffering against external disturbances such as intensification of land use and drought through its response diversity to environmental fluctuations (Loreau et al., 2003; Randall, 2015). These manifold interactions between vegetation diversity, ecosystem functioning and environmental conditions are shown in Fig. 0.2.
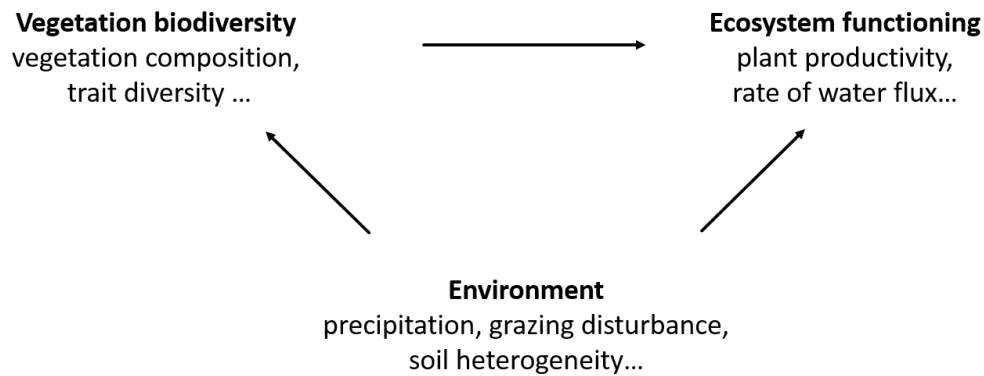
**Vegetation biodiversity**
vegetation composition,
trait diversity …

**Ecosystem functioning**
plant productivity,
rate of water flux…

**Environment**
precipitation, grazing disturbance,
soil heterogeneity…

Figure 0.2 Interactions between vegetation biodiversity, ecosystem functioning and the environment. Modified after Loreau (2010).

### 0.1.3 Modelling savanna vegetation

Simulation models are ideal instruments for understanding the complex interactions between vegetation processes and diversity in savanna ecosystems. Typically, process-based modelling describes vegetation and water processes by an adequate level of simplification, such as characterizing key system aspects like grouping species into plant functional types (PFTs). Those PFTs thereby represent distinct strategies to use available soil water or to cope with disturbances such as grazing. In contrast to simulating single species, simulating PFTs explicitly describes vegetation functional diversity and its response to environmental variables (Pillar, 1999). More specifically, the effect of each functional type and thus of functional diversity on whole ecosystem functioning can be quantified.

Modeling vegetation dynamics usually starts with an identification of plant traits, e.g., growth rate, mortality rate or seed dispersal, which are key to describe vegetation functions. One PFT is then represented by a combination of distinct trait values making up a given functional strategy. Those functionally different plant types can thus be expected to distinctively respond to external factors like resource input (precipitation) and disturbance (grazing). The traits identified to describe PFTs are then used as parameters for the modelling process. A growing archive of field studies provides a wealth of field data on morphological and phenotypic traits in savannas, such as relative growth rate, plant height, leaf area index or root length, which can serve as a valuable reference for functional trait parameterization. In semi-arid savannas, the simulated plant community is typically described by woody plants, perennial grass and sometimes annual grass (Jeltsch et al., 1998; Weber et al., 2000; Williams and Albertson, 2005; Wiegand et al., 2006). These broad PFTs (hereafter called meta-PFT) are typically

assumed to possess fixed trait combinations (or mean trait values) for a simulated meta-PFT. Yet, as highlighted in chapter 0.1.2, the functional variability within each meta-PFT can be considerable. Thus, ignoring this functional diversity in simulations might lead to a false quantification of ecosystem functioning. Simulating trait variability within a meta-PFT may guide the way to simulate functional diversity and consequently ecosystem response diversity to environmental factors in savannas. Trait variability thereby cannot be assumed to be random. That is, traits are typically not independent but suits of traits tend to scale along a common axis. End points of such axis are widely used for plant strategy classification (Grime, 2001; Wright et al., 2004; Reich, 2014). From an evolutionary perspective, each axis consisting of several traits forms a necessary trade-off (Diaz et al., 2016). For example, plants which possess a relatively high growth rate trade this for a relatively short tissue longevity (and thus biomass turnover) (Reich, 2014). Another example from semi-arid savannas is that plants which are comparatively attractive to grazers and highly palatable have developed rapid regrowth mechanisms in order to compensate for the frequent removal of leaf biomass (DuToit et al., 1990). Those trade-offs are thus key elements for simulating a functionally diverse community.

## 0.2 Objectives of the thesis

The overall objective of this thesis is to better understand vegetation functional diversity and its relationship with ecosystem functioning in semi-arid savannas, as well as to assess shifts in vegetation composition at the trait and the community level under different environmental conditions.

Despite its proven importance for vegetation communities, trait variability within the meta-PFT level is vastly ignored in to-date savanna ecosystem models. In the present study I provide a concept of integrating trait variability into an existing savanna ecosystem model. In so doing, I aim at furthering the understanding of how the composition within one meta-PFT responds to altered mean annual precipitation and grazing intensity. Moreover, I assess how ecosystem functioning is affected by the diversification within one PFT.

Taking this concept of explicitly modelled functional diversity as a starting point, I investigate how a suite of traits affects the fate of a given meta-PFT in different environments. Traits are thereby chosen in a manner which accounts for necessary trade-offs between life history characteristics, such as growth rate, mortality, dispersal capacity and grazing defense. I

moreover address the question which traits are important under a given set of environmental conditions to grant competitiveness for the analyzed functional types.

Besides the effects of precipitation and grazing intensity, landscape heterogeneity with respect to edaphic conditions affects vegetation functional diversity as well. To better understand those effects I simulate a set of heterogeneous landscapes. I further ask whether ecosystem functioning is significantly affected by increasing landscape heterogeneity through its effects on functional diversity, and whether precipitation and land use modulate the impact of landscape heterogeneity on ecosystem functioning.

## 0.3 Structure of the thesis

To achieve the objectives of the thesis I extended the spatially explicit ecohydrological savanna model EcoHyD (Tietjen et al., 2009; Tietjen et al., 2010; Lohmann et al., 2012). I choose this model as a basis for my study since it has been proven to successfully simulate the dynamics of three meta-PFTs, namely perennial grasses, shrubs and annual grasses. In this model, key hydrological and vegetation processes are represented at a moderate level of complexity.

In chapter 1, I simulate trait variability within one meta-PFT (perennial grass). The model EcoHyD is technically updated with respect to ecological and hydrological processes, and most importantly trait diversity within the meta-PFT perennial grass is included. The diversification within perennial grass PFT is realized by trade-offs between traits (i) growth rate and longevity and (ii) resistance to grazing and regrowth, which both represent different axes of strategies to cope with a given environment. In a first step the functional composition of perennial grasses is analyzed along gradients of annual precipitation and grazing intensity. The extended model is further used to assess the relationship between functional diversity and ecosystem functioning in different environmental scenarios.

In chapter 2, I investigate the response of savanna vegetation at the trait and the community level to different environmental conditions. Moreover, I assess which traits are important for the fate of dominant meta-PFTs. New sub-PFTs are constructed based on relatively balanced trade-offs between suits of functional traits. Besides simulating different perennial grass sub-types, I also quantify the effects of trait diversity of shrub and annual grass meta-PFTs.

In chapter 3, I ask how landscape heterogeneity with respect to physical soil properties affects vegetation functional diversity. This spatial heterogeneity of soil properties is based on a relatively small-scale high variance of soil conditions. The simulated plant assembly is assumed to be an outcome of the filtering effects of different soil conditions. The relationship between landscape heterogeneity and functional diversity is assessed across different spatial scales and scenarios of mean annual precipitation and grazing intensity. I also assess the interactive role played by landscape heterogeneity with precipitation and grazing for ecosystem functioning.

In the general discussion (chapter 4), I discuss variations of functional trait composition under different environmental conditions and the role of vegetation functional diversity for ecosystem functioning on the background of results presented in chapters 1-3. Further, the effects of vegetation functional diversity on ecosystem functioning and the underlying mechanisms are discussed. I moreover analyze possible limitations of modelling trait variability in savanna vegetation models. This is followed by an outlook of potential future simulation studies on trait diversity and related questions. I finish with a general conclusion based on the main results of this thesis.

# Chapter 1

# Response of semi-arid savanna vegetation composition towards grazing along a precipitation gradient – the effect of including plant heterogeneity into an ecohydrological savanna model

# Link to Chapter 2

In chapter 1 I described an extended version of the ecohydrological savanna model EcoHyD. I parameterized and validated the model based on vegetation dynamics of earlier versions tested by empirical data of savannas. The module describing hydrological processes was updated (separation of actual evaportranspiration into evaporation and transpiration) as well as the module describing ecological processes (relate plant growth to transpiration). Most importantly, I incorporated trait diversity within the meta-PFT level into the model. This was done as a first step for the meta-PFT perennial grass. My simulation results showed that increasing grazing intensity leads to a dominance of the fast-growing and short lived perennial grass type as well as a dominance of the poorly palatable perennial grass type. Increasing precipitation reduces the magnitude of grazing-induced shifts in perennial grass types. Further, the total vegetation cover and water use efficiency of plant community generally increase with a diversification of perennial grass PFT. That is, the ecosystem functioning is strengthened in a diverse plant community in semi-arid savannas.

The results of chapter 1 emphasize effects of trait variability on the vegetation composition and ecosystem functioning, especially in face of complex environmental conditions in savanna ecosystems. In addition, the study presented in chapter 1 proves the theoretical feasibility of simulating trait variability by means of necessary life-history trade-offs.

Following the work for chapter 1, I diversified shrub, perennial and annual grass meta-PFTs based on trait trade-offs. Traits are useful measures for ecosystem functioning due to their direct link to different functional ecosystem processes. One example is, that growth rate is typically directly linked to primary production. In addition, the effects of traits on a given plant type are dependent on environmental conditions, which can filter out poorly performing plant types. However, the response of community composition to changes in environmental conditions at the trait level is relatively understudied. These are the framing conditions which motivated the work in chapter 2, namely, how savanna vegetation adapts to environmental conditions at different ecological levels.

To this end, in chapter 2, I used the abovementioned extended model to assess the response of different traits to changes in mean annual precipitation and grazing intensity for all meta-PFTs. Further, I quantified the effect of both rainfall and grazing intensity on the functional trait composition and community level composition.

# Chapter 2

# Zooming in on coarse plant functional types – simulated response of functional savanna vegetation composition in response to aridity and grazing

**Summary**

- Precipitation and land use in terms of livestock grazing have been identified as two of the most important drivers structuring the vegetation composition of semi-arid and arid savannas. Savanna research on the impact of these drivers has widely applied the so-called plant functional type (PFT) approach, grouping the vegetation into two or three broad types (here called meta-PFTs): woody plants and grasses, which are sometimes divided into perennial and annual grasses. However, little is known about the response of functional traits within these coarse types towards water availability or livestock grazing. In this study, we extended an existing eco-hydrological savanna vegetation model to capture trait diversity within the three broad meta-PFTs to assess the effects of both grazing and mean annual precipitation (MAP) on trait composition along a gradient of both drivers.

- Our results show a complex pattern of trait responses to grazing and aridity. The response differs for the three meta-PFTs. From our findings, we derive that trait responses to grazing and aridity for perennial grasses are similar, as suggested by the convergence model for grazing and aridity. However, we also see that this only holds for simulations below a MAP of 500 mm. This combined with the finding that trait response differs between the three meta-PFTs leads to the conclusion that there is no single, universal trait or set of traits determining the response to grazing and aridity.

- We finally discuss how simulation-models including trait variability within meta-PFTs are necessary to understand ecosystem responses to environmental drivers, both locally and globally and how this perspective will help to extend conceptual frameworks of other ecosystems to savanna research.

## 2.1 Introduction

Semi-arid and arid savanna vegetation composition is shaped by dry and highly variable rainfall conditions and the impact of large ungulate herbivores (Lauenroth and Sala, 1992; Rutherford and Powrie, 2013; Ratzmann et al., 2016). Anthropogenic impacts on herbivore herd composition and densities have been found to alter the vegetation composition resulting in mainly two alternative degradation patterns: Either, an overall loss of vegetation alongside with an increase in bare soil (Westoby et al., 1989; Jeltsch et al., 1997; D'Odorico et al., 2013) or alternatively an increase of woody vegetation at the cost of perennial grasses, also called shrub encroachment (Westoby et al., 1989; Wiegand et al., 2006; Graz, 2008; Eldridge et al., 2011). Such changes in the composition of the plant community will have major consequences for ecosystem functioning and resilience and subsequently for the provision of important ecosystem services, such as biomass production and protection from soil erosion, that support millions of human livelihoods in drylands all over the world (Reynolds et al., 2007b; Eldridge et al., 2012; Soliveres and Eldridge, 2014; Eldridge et al., 2016).

Not surprisingly, such degradation patterns and the vegetation dynamics of savannas in general have been subject to a vast body of research for the last decades. Here, especially the "savanna question" of why and under what circumstances woody plants and grasses can coexist in savannas has been in the spotlight of numerous studies (Scholes and Archer, 1997; Jeltsch et al., 2000; Sankaran et al., 2004; Scheiter and Higgins, 2007; Bond and Midgley, 2012; Synodinos et al., 2015). As a consequence of this focus on woody plants versus grasses, savanna ecologists have often focussed on the relative abundance of broad plant functional types (PFTs), e.g. woody plants vs. perennial and annual grasses, rather than on species (McIntyre and Lavorel, 2001; Linstädter et al., 2014; Lohmann et al., 2014; Moncrieff et al., 2015). The use of such broad PFTs started with Walter's two-layer hypothesis (Walter, 1954) on differing access of PFTs to water. Generalizing approaches like the state and transition concept of Westoby et al. (1989) describing transitions between principle states of savannas, and simulation-based approaches (e.g. Ludwig et al., 2001; Boer and Stafford Smith, 2003; Liedloff and Cook, 2007; Jeltsch et al., 2008; Higgins et al., 2010; Synodinos et al., 2015) picked up the concept of PFTs. Herein, the grouping into PFTs was successfully applied to analyse general principles driving dynamics of savanna vegetation, or theories on mechanisms leading to coexistence or resilience of vegetation. In addition, PFTs have proven to be useful to compare observations or simulation results with data from remote sensing approaches (Archibald and Scholes, 2007; Ustin and Gamon, 2010; Snell et al., 2013).

The distinction into broad PFTs is clearly highly useful for understanding principle processes of savanna dynamics. However, it might be too simplified, when assessing the impacts of the two most important drivers of vegetation and degradation dynamics, namely livestock grazing and water availability. Empirical studies, which regularly consider the species level, have shown that there can be strong shifts in community composition as a whole but also in the plant species diversity within one plant functional type as a result of grazing and aridity (Orr and O'Reagain, 2011; Wesuls et al., 2013; Hanke et al., 2014) . The response of certain plant species might indicate whether livestock production is sustainable or whether ecosystem functioning of the savanna system might be disturbed (Wesuls et al., 2013; Soliveres and Eldridge, 2014). It was shown for drylands in general (including but not explicitly addressing savanna vegetation in particular) that a change in the composition of a plant community, especially in the functional composition within the woody plant community (Soliveres and Eldridge, 2014), will also alter the functions and services provided by the ecosystem (Maestre et al., 2012; Soliveres et al., 2014). However, empirical studies of savanna vegetation on the species level, did so far pay little attention to the trait composition of the species assemblages (see e.g. Rutherford and Powrie, 2013), and very little empirical work done in savanna systems explicitly addresses the community trait response of the ecosystem to grazing and aridity (but see e.g. McIntyre & Lavorel 2001 for an assessment of grazing effects on PFTs in open woodlands of Australia).

The few existing studies addressing the response of dry grasslands' (but not savannas' in particular) trait composition to grazing and aridity suggest that the short-term response of trait composition depends on the long-term evolutionary history of grazing and on resource limitation (here aridity) of the system (Adler et al., 2004; Adler et al., 2005; Evans et al., 2011). Those studies predict lower compositional changes in response to grazing for arid conditions than for more mesic ones, as well as for systems with a long evolutionary history of grazing compared to those with a shorter evolutionary history. The underlying convergence model of grazing and drought suggests that both drivers select for the same traits and will hence lead to systems that are similarly adapted to grazing and drought (Milchunas et al., 1988). Consequently, it might be difficult to explicitly disentangle compositional and thus functional responses to grazing and drought in many dryland systems especially when they exhibit a long history of grazing like most African drylands (Linstädter et al., 2014).

However, empirical studies have shown that environmental filters, especially soils and precipitation are relevant for species composition of dryland vegetation (Williams et al., 1996; Bestelmeyer et al., 2006) but for a given set of environmental conditions, grazing has a significant impact on community composition (Wesuls et al., 2012).

The insight that trait-based modelling approaches, including the dimension of trait variability within broader functional groups, can help to understand plant community dynamics and their response to grazing or environmental changes is not new and is underpinned by recent studies from other tropical ecosystems (Sakschewski et al., 2016) or temperate grasslands (Weiss and Jeltsch, 2015) and from cross-ecosystem studies by global vegetation models (Scheiter et al., 2013). Since ecosystem functioning and services are closely linked to plant traits (Mayfield et al., 2010), a higher-resolved representation of trait composition in savanna vegetation models will help to predict those services more accurately (Scheiter et al., 2013).

In this study, we specifically look into the response of the simulated vegetation composition of semi-arid savannas beyond the coarse definition of "classical" PFTs to understand the role of trait variability within these broad PFTs on the response of savanna vegetation to water availability and livestock grazing. For this, we extended the eco-hydrological dryland model EcoHyD (Tietjen et al., 2009; Tietjen et al., 2010) by the concept of sub-PFTs. For this, we allowed for trait variability within the three broad meta-PFTs (perennial grasses, shrubs and annual grasses) leading to numerous sub-PFTs reflecting diversity within PFTs. We used the model to assess the dominance of specific traits along environmental gradients of rainfall and livestock grazing, and to evaluate if meta-PFTs respond differently in their adaptation to environmental conditions.

## 2.2 Methods

### 2.2.1 The model EcoHyD

This study extends the eco-hydrological, grid-based vegetation model EcoHyD (Guo et al., 2016) with a spatial resolution of 5 m by 5 m. EcoHyD consists of two sub-models that are dynamically linked (Fig. 1): one hydrological model (Tietjen et al., 2009) simulating soil moisture dynamics in two soil-layers and surface water fluxes and one vegetation sub-model (based on Tietjen et al. 2010 and Lohmann et al. 2012) simulating the vegetation dynamics of three broad plant functional types (PFTs).

The hydrological processes explicitly accounted for in the model are: Infiltration, evaporation, transpiration, diffusion between soil layers and run-off. These processes are influenced by the current vegetation. The vegetation model simulates growth, mortality, dispersal and establishment, grazing and browsing effects, as well as competition for space and for water in two soil layers. All processes are influenced by the availability of soil moisture as calculated by the hydrological model. A more detailed model description and related model parameters is given in the supplementary information (see the Appendix 2.A).
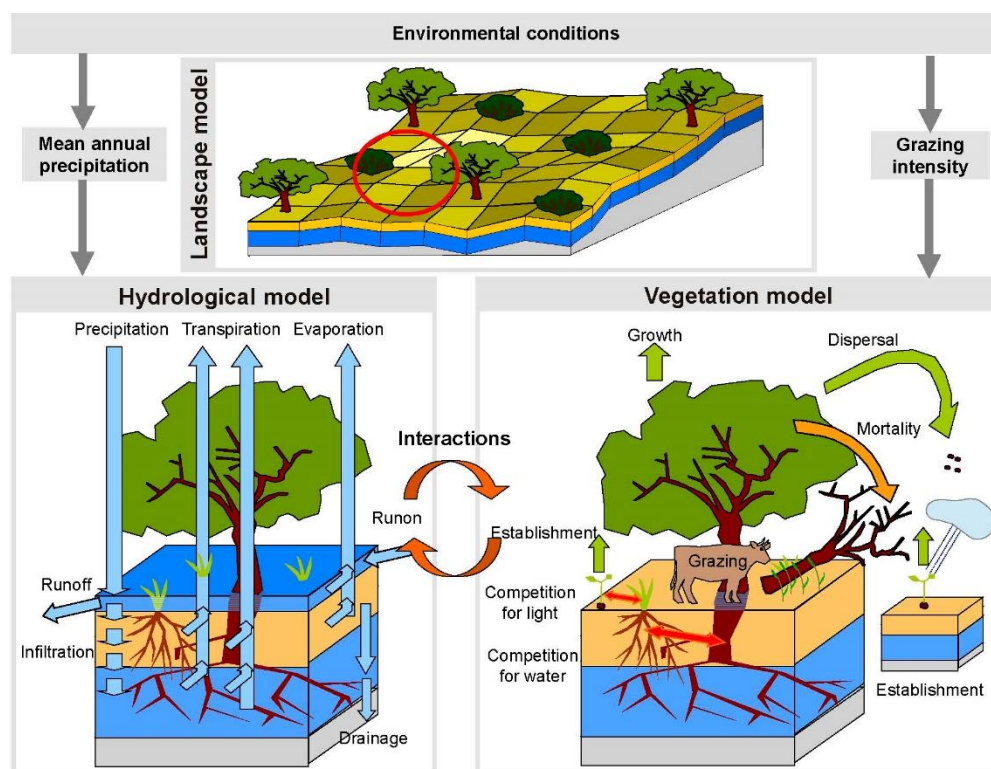
Fig 1 Simulated processes in one (5 x 5 m$^2$) grid cell of EcoHyD, adapted from Tietjen (2016); left panel: hydrological processes, right panel: ecological processes. Models exchange data on soil moisture and vegetation cover every 14 days. Temporal resolution of the process simulations depends on the respective process and ranges from hourly to annual.

### 2.2.2 Representation of vegetation in EcoHyD

Vegetation is represented by plant functional types (PFTs). These types are distinguished on two levels. First, we defined three typical major functional types relating to the main functional groups in the savanna ecosystem, namely perennial grasses, annual grasses and woody vegetation (meta-PFTs). These meta-PFTs are determined by differences in their live-cycle (annual vs. perennial) and by their growth form (woody vs. non-woody), and are characterised by different processes and parameters describing their traits. Second, the model allows for a sub-classification into any number of sub-PFTs within the meta-PFT definition. These sub-PFTs can differ in their traits, but they feature the same processes as defined by their respective meta-PFT.

### 2.2.3 Simulation design

We simulated vegetation dynamics for 100 years on a 150 m by 150 m grid (30 by 30 grid cells) along a rainfall gradient (mean annual precipitation: 300 mm, 400 mm, 500 mm, 600 mm, 700

mm, 800 mm) and for different livestock grazing intensities (very low: 2 LSU/100 ha; low: 5 LSU/100 ha; high: 8.33 LSU/100 ha, with a large stock unit (LSU) relating to a 450 kg live weight cattle) in a full factorial design, resulting in 18 scenarios. Each combination was replicated five times with individual, stochastic precipitation time series (see Lohmann et al. 2012 for a description on the generation of precipitation data).

To assess the effects of precipitation and livestock density on the functional composition of the plant community, we defined several sub-PFTs for each meta-PFT (Table 1 gives the standard parameters of the meta-PFTs as provided by Lohmann et al. 2012 and Guo et al. 2016). For each of the 18 scenarios we considered 50 independent simulations, each with unique and randomly assembled sub-PFTs. This led to an overall number of 4500 simulations (6 MAP x 3 grazing scenarios x 50 sub-PFT communities x 5 rainfall replications). For each simulation, we recorded the trait parameters of the two most successful (in terms of cover) sub-PFTs of each meta-PFT after 100 years.

### 2.2.4 Trait variation within sub-PFTs

To assemble the sub-PFTs, we first chose seven PFT parameters (annual grasses: five parameters), relating to plant traits. For this selection, we excluded those parameters that showed very high sensitivity in a comprehensive sensitivity analyses (see the Appendix 2.A), since their impact would superimpose the response to variations in other, less sensitive parameters. Consequently, we included the following seven parameters for woody plants and perennial grasses: growth rate (r), mortality rate (mrd), grazing preference (GP), non-edible biomass fraction (glim), water uptake rate per biomass (Θ), dispersal fraction (e) and root distribution (root). For annual grasses, two of these parameters are not defined: 1) root distribution, as we assume them to exclusively root in the upper soil layer; 2) dispersal fraction, as by definition annual seeds are assumed omnipresent within the simulated landscape.

For each single simulation, we assembled a community of 25 sub-PFTs (10 woody plants, 10 perennial grasses, 5 annual grasses), which we gathered as follows: To allow for a systematic assessment on trait variation, we defined a standard parameter set for each meta-PFT (see table 1 for varied parameters and the Appendix 2.A for comprehensive parameter table). Each parameter of each individual sub-PFT could deviate by -10%, 0% or +10% from this standard value (table 1). To avoid the creation of "super types", i.e. sub-PFTs that have a favourable variation in many or all parameters at the same time (e.g. a sub-PFT that is likewise fast growing, long-lived, grazing resistant and competitive), we assigned an index to the variation of each parameter: Using the results of the sensitivity analysis (see the Appendix 2.A), we first

determined whether an increase in a parameter was beneficial or detrimental for the resulting cover of this PFT (under low grazing and a MAP of 500 mm). If the change was beneficial, we attributed this change an index value of +1, otherwise -1. We restricted our analysis to those sub-PFTs with a total index sum of 0 (sum of all index values) to artificially enforce trade-offs between parameter values without pre-defining the nature of the trade-off. This resulted in a sub-PFT pool of 353 woody sub-PFTs, 353 perennial grass sub-PFTs and 51 annual sub-PFTs, from which we assembled the simulated community by randomly drawing 10 woody, 10 perennial grass and 5 annual grass sub-PFTs.

In order to assess which trait combinations were successful in our aridity and grazing scenarios, we calculated the mean trait index of the two most dominant sub-PFTs for each simulation and for each trait of each meta-PFT.

Table 1 Standard values and the index +1, index -1 values of the 7 varied trait parameters

| Parameter / Trait | Description | perennial grass | | | shrub | | | annual grass | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | -1 | standard | +1 | -1 | standard | +1 | -1 | standard | +1 |
| r | potential growth rate [mm$^{-1}$ * yr$^{-1}$] | 0.45 | 0.5 | 0.55 | 0.135 | 0.15 | 0.165 | 1.35 | 1.5 | 1.65 |
| mrd | Mortality rate dependent on soil moisture [mm$^{-1}$ * yr$^{-1}$] | 0.594 | 0.54 | 0.486 | 0.132 | 0.12 | 0.108 | 0.88 | 0.8 | 0.72 |
| root | fraction of roots in the upper soil layer [-] | 0.567 | 0.63 | 0.693 | 0.324 | 0.36 | 0.396 | - | 1 | - |
| $\Theta$ | relative uptake rate per biomass [mm * (yr * g)$^{-1}$] | 0.81 | 0.9 | 0.99 | 0.45 | 0.5 | 0.55 | 0.18 | 0.2 | 0.22 |
| e | rate of successful establishment [yr$^{-1}$] | 0.045 | 0.05 | 0.055 | 0.0045 | 0.005 | 0.0055 | - | - | - |
| GP | grazing preference [-] | 1.1 | 1 | 0.9 | 0.33 | 0.3 | 0.27 | 0.66 | 0.6 | 0.54 |
| gLim | non-edible biomass fraction [-] | 0.135 | 0.15 | 0.165 | 0.81 | 0.9 | 0.99 | 0.045 | 0.05 | 0.055 |

In our analyses, we first systematically evaluated resulting trait indices for a scenario of low grazing (5 LSU/100 ha) and a MAP of 500 mm. In a second step, we analysed the responses of trait values within meta-PFTs and the abundance of meta-PFTs along the grazing and the aridity gradients.

## 2.3 Results

### 2.3.1 Trait composition of most dominant sub-PFTs

The results show clear patterns, indicating which traits are especially important for performing well in an environment of 500 mm rainfall and low grazing intensity (Fig. 2). Here, we interpret

those traits as being important for dominating the respective meta-PFT community that show a positive index value, and those as less important (i.e. tradeable) that show a negative index value. Some of the traits show a similar level of importance for all meta-PFTs (e.g. the mortality rate or the fraction of non-edible biomass), but the importance of other traits differs between the three meta-PFTs (e.g. growth rate of very high importance for annuals, but only of high importance for the perennial types).

Most abundant annual plant types are clearly those that strengthen their opportunistic life history strategy. The results show that annual plants with a high growth rate (r) at the cost of the grazing related traits, non-edible biomass fraction (gLim) and palatability for animals (GP) perform best. The most successful shrub sub-PFTs are those that do not invest in the grazing resistance parameters but improve their competitive strength for water uptake (Ө). Both, successful perennial grasses and successful shrubs invest in a dense rooting system in the upper soil layer for harvesting water directly after a rainfall event. For perennial grasses, also a high growth rate is of importance and is traded against grazing resistance in terms of non-edible biomass fraction (gLim). Further, those perennial grass types with a high competitive strength (Ө) for water are among the dominant ones, while the establishment rate (e) plays a minor role.
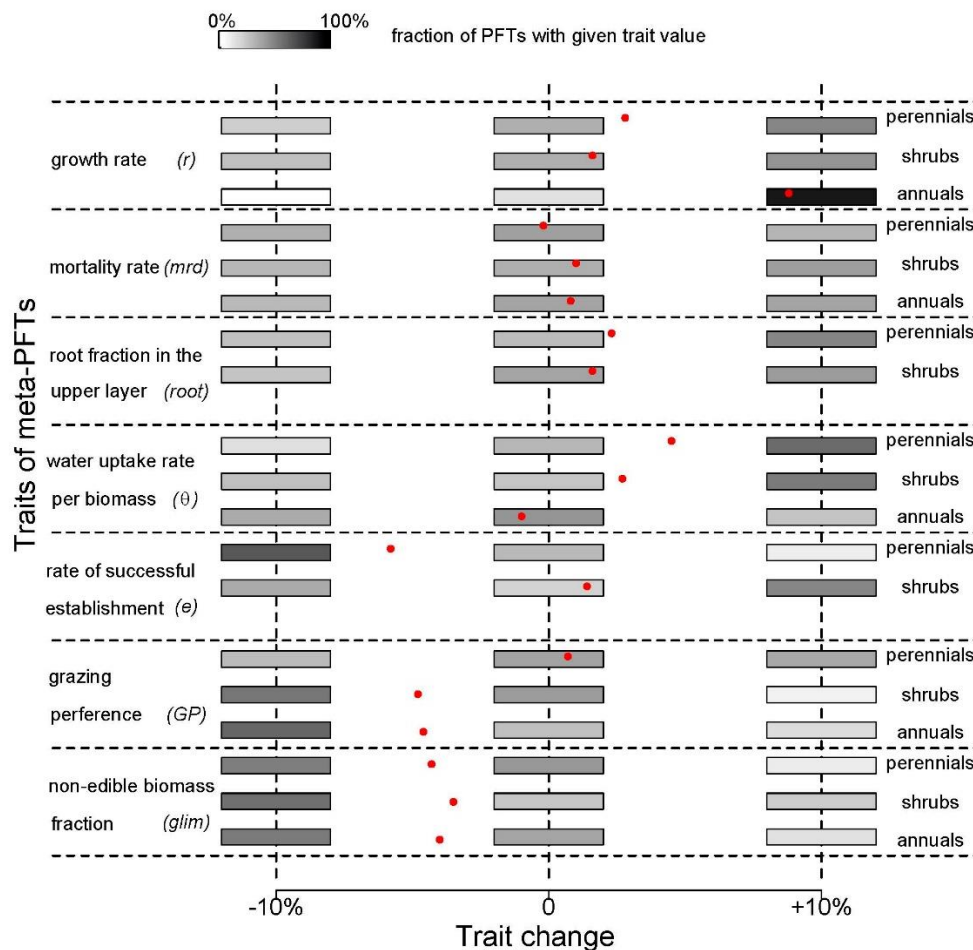
Fig 2 Resulting trait index of the two most dominant sub-PFTs of each meta-PFT after 100 years for a moderate MAP (500 mm) and grazing intensity (5 LSU/100 ha). Circles represent the mean trait index of repeated simulations as described in the methods and shading indicates the percentage of dominant sub-PFTs having a certain index. Note: every trait index can only be -1, 0 or +1 and has to sum to 0 for a given sub-PFT.

### 2.3.2 Trait responses along the aridity and grazing gradient

The previous section reflects the distribution of plant traits of the successful sub-PFTs under moderate aridity and grazing conditions. In this analysis, we evaluate which traits are successful under different scenarios of grazing intensity and mean annual precipitation. The results clearly indicate that meta-PFTs differ in their response to environmental conditions (Fig. 3). Annual plants are generally less responsive to environmental conditions, and dominant annual sub-PFTs are characterized by similar trait combinations under most environmental settings. In contrast, optimal trait combinations of perennial grasses and shrubs are highly dependent on rainfall, but also on grazing, especially under very arid conditions.

The results along the two gradients confirm the findings for the moderate scenario analysed in the previous section: One of the most important parameters determining success of all meta-PFTs is a high growth rate (r). This result is very pronounced for annual grasses, but also evident for the other meta-PFTs. For perennial grasses, a high growth rate becomes especially important under very stressful conditions with low rainfall and high grazing intensity. This goes along with a lower priority to reduce mortality (mrd), which is consistent for both perennial grasses and shrubs.

The vertical root distribution (root) of perennial grasses and shrubs exhibits a unimodal response along the precipitation gradient: while plants with a shallow rooting system are more successful between 400 and 600 mm MAP, the optimal rooting depth shifts towards the deeper soil layer for very arid or for moister conditions. The same pattern appears for the competitive strength for water uptake ($\Theta$) of shrubs, where under moderate MAP conditions, those sub-PFTs are dominant that invest into their competitive strength, while this seems to be less important under more stressful as well as relatively relaxed conditions regarding water availability. In contrast, most abundant annual grass types show low competition strength along both environmental gradients, while this trait seems to be essential for perennial grasses under all environmental conditions.

Under high rainfall conditions with strong competition for space, those woody sub-PFTs with a high establishment rate (e) are among the successful ones, while the establishment rate is less important under conditions that are more arid. For perennial grasses, which are defined to be less establishment limited as woody savanna plants with their well-known establishment bottleneck, this parameter does not impact their success.

The response of the grazing preference trait (GP), which aggregates tastiness and defence mechanisms and thus the preference of livestock for this PFT, is little impacted by either of the simulated gradients. Dominant perennial grass sub-PFTs show a slightly positive trait index that increases with grazing pressure, indicating that those with a lower tastiness perform better under high grazing pressure. In contrast, this trait is not important for annual or woody PFTs, which are generally assumed to be less tasty and show a lower sensitivity to a 10% change in their standard value.

The amount of biomass of a plant that is not available for grazing (gLim, e.g. woody or very spiky parts, parts aggregated in the centre of dens tussocks or other non-edible plant material) does not seem to be important for perennial and annual grasses. In contrast, for woody sub-PFTs it seems to be essential to exhibit non-edible parts under very stressful conditions.
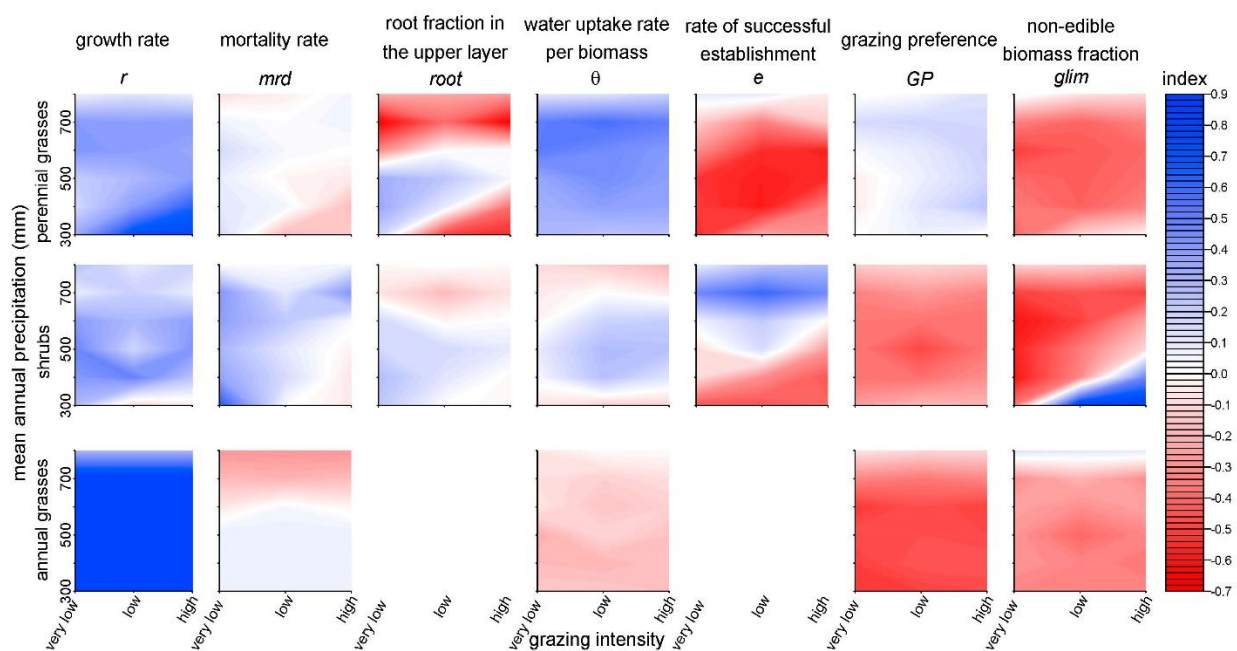


Fig 3 Trait parameter response towards precipitation and grazing. The trait response of the two most dominant sub-PFTs of each meta-PFT: perennial grasses (upper row), shrubs (middle row) and annual grasses (lower row). Red colours indicate a negative mean index value, and blue colours a positive index value. Results are based on 50 repeated simulations of 100 years with 25 sub-PFTs, each repeated for 5 precipitation scenarios.

## 2.3.3 Response of the meta-PFT abundance along simulated gradients

In addition to a shift in trait parameter composition within meta-PFTs, we evaluated the response of the overall vegetation structure, which we define as the plant cover of meta-PFTs, along both simulated gradients (Fig. 4). For each of the meta-PFTs, a clear impact of grazing and precipitation is observable: perennial grasses have highest cover under very low grazing and high rainfall, shrubs perform best under high rainfall and high grazing, and annual grasses can benefit from low competition under high grazing and low rainfall. This leads to the following structure of the plant community: under low rainfall and low grazing perennial grasses dominate the system with very low shrub and annual plant cover. Under increased rainfall annual grasses are to some extent substituted the by shrubs with both types being on a very low level still, while perennial grass cover increases strongly. Under high precipitation, increased grazing will benefit shrubs at the cost of perennial grass cover leading to a shrub encroached ecosystem. In contrast, high grazing intensity under low mean annual rainfall leads to the dominance of annuals with some sparse shrubs and almost no perennial grasses left in the system.

A particular result is worth mentioning: when evaluating the impact of the two gradients on trait composition of the sub-PFTs, shifts in trait composition are mostly related to water availability along the precipitation gradient (Fig. 3). However, the community composition pattern of the meta-PFTs is additionally clearly affected by the grazing gradient.
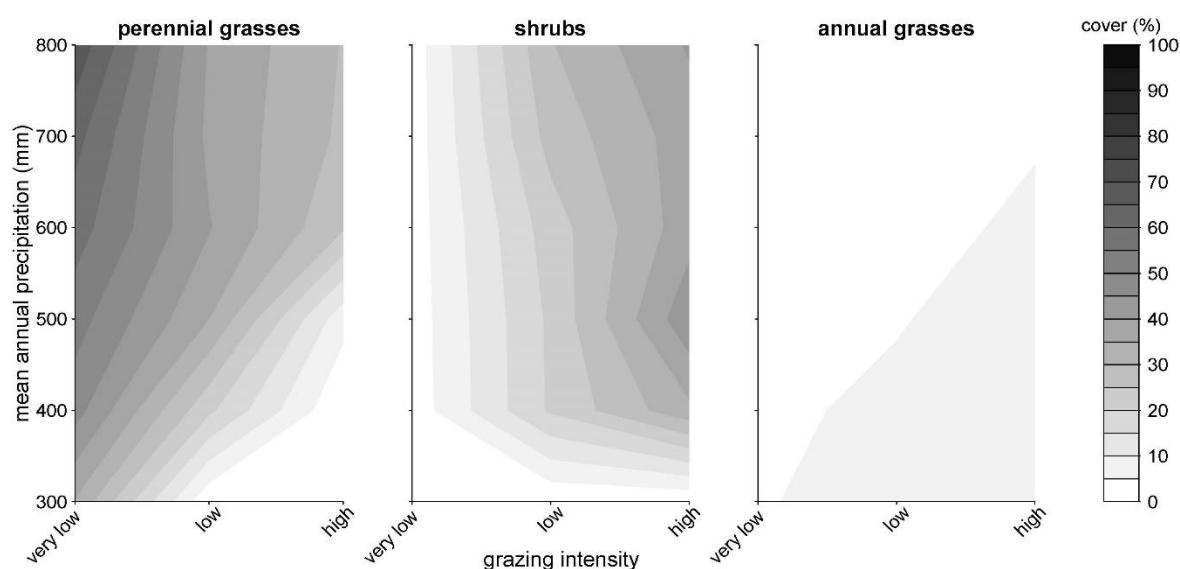


Fig 4 Vegetation cover of the three meta-PFTs dependent on grazing intensity and precipitation. Results of 50 repeated simulations with 25 sub-PFTs, each repeated for 5 precipitation scenarios. Cover values represent mean cover of years 80 to 100.

## 2.4 Discussion

In this study, we analysed the response of savanna vegetation to two of the most important drivers of dryland systems: mean annual precipitation (MAP) and grazing intensity (Reynolds et al., 2007b). Our modelling approach is one of the first savanna vegetation models that gives insights into the response of plant communities with a resolution of functional composition beyond the coarse distinction of functional groups (but see Scheiter et al. 2013 for a further example and Guo et al. 2016 for an earlier but simpler version of this model). By allowing for trait variations, we distinguish between several sub-PFTs within each of the three meta-PFTs. As a result, we get a differentiated picture of the functional response to grazing and aridity.

### 2.4.1 Response of the meta-PFTs

The simulated response of the total cover of the three meta-PFTs in savanna ecosystems is well in line with the vast majority of savanna literature: under lowest rainfall conditions, high grazing pressure leads to a decrease in overall vegetation cover and thus to an increase in the fraction of bare soil (Westoby et al., 1989; Jeltsch et al., 1997; Porensky et al., 2013). In contrast, under higher rainfall conditions, high grazing pressure leads to an increase in woody cover, usually referred to as shrub (or bush) encroachment (Van Auken, 2000; Roques et al., 2001; Fensham et al., 2005; Graz, 2008; Stevens et al., 2016). The reasons for these responses have been discussed elsewhere (e.g. see an overview in Lohmann et al. 2012): the establishment of shrubs is generally limited by low water availability under arid conditions (so called demographic bottleneck of establishment, see Joubert et al., 2008). Under higher rainfall conditions, competition with grasses limits seedling growth once the bottleneck has been passed (Wiegand et al., 2006; Buitenwerf et al., 2011). Hence, if livestock grazing reduces the grass matrix, shrubs are released from competition under higher rainfall conditions and can thus establish and encroach into the ecosystem.

### 2.4.2 Response of traits within functional groups

It has been shown before, that responses within meta-PFTs are relevant to understand the response of the plant community to grazing intensity and aridity (McIntyre and Lavorel, 2001; Linstädter et al., 2014). While the composition of the meta-PFTs in our study is highly responsive to both, grazing intensity and altered water availability along the precipitation gradient, the composition of the sub-PFTs within the meta-PFTs responds mainly to precipitation. In the following, we discuss why we see such responses on the sub-PFT level.

*Perennial grasses*

The response of perennial grass types relates in many ways to the predictions of the so-called convergence model of grazing and aridity formulated by Milchunas et al. (1988) and Milchunas & Lauenroth (1993). This theoretical framework predicts a similar response of the functional composition in grassland systems to grazing and to aridity, since both drivers select for similar plant traits (De Bello et al., 2005; Quiroga et al., 2010). Our results for perennial grasses indeed show a similar response of the trait composition to grazing and aridity for mean annual rainfall of 500 mm and below. However, for settings with a MAP above 500 mm, trait composition within the perennial grass type is mainly determined by rainfall, while the overall meta-PFT abundance depends stronger on grazing.

Under both, severe aridity and high grazing pressure, grasses in our simulations do not focus on harvesting rainfall immediately in the topsoil but invest more into deeper roots reaching the subsoil (root trait response), in which more water can be found. This trait change relates well to the convergence model: Both grazing and aridity (at the extreme end of the gradient) lead to an overall decline in vegetation cover. Hence, infiltration decreases, evaporation increases, and water availability in the upper soil layer is on average very low (Tietjen et al., 2009; Lohmann et al., 2012; Metzger et al., 2014; Eldridge et al., 2015). Therefore, plants have to develop a deeper rooting system to have access to a more reliable water source. This is also supported by the result that woody plants with their deeper rooting system (per definition of the meta-PFT) show a less pronounced response of this parameter. Our results reflect the strategies described in Walter's Two-Layer hypothesis (Walter, 1954), where grasses are assumed to be stronger competitors in the upper soil layer, while shrubs dominate the lower soil layer.

Furthermore, and also in accordance with the convergence model of Milchunas et al. (1988), our results show a change of the perennial grasses towards a faster growing, more short lived type (manifested in lower mortality and higher growth rates) in response to both, severe grazing and aridity. While this adaptation has been found and stated in several studies on the effects of grazing (Vesk et al., 2004; Klumpp et al., 2009), this response was hardly ever described in terms of an adaptation to aridity. However, Quiroga et al. (2010) found that in Argentina both, aridity and grazing lead to e.g. increased grazing tolerance (in terms of faster leave elongation) of the C4 perennial bunchgrass Trichloris crinita in a transplant experiment along a precipitation gradient.

One additional explanation for the simultaneous responses of several traits to aridity and grazing in our simulations might be found in the intensity of grazing stress from an individual plant's perspective. Under very arid conditions vegetation cover is low. Since grazing intensity is,

however, simulated as density of grazing ungulates per area, individual plants face a higher rate of defoliation if biomass production is low due to drought. Therefore, in our simulation design, aridity and grazing intensity are not completely independent. This is, however, also the case in managed rangelands, where herd sizes are often disconnected from climatic and environmental conditions and changes therein, and rather depend on management concepts relying on more or less fixed carrying capacities that might even be biased by economic and other aspects (Higgins et al., 2007; Quaas et al., 2007; Lohmann et al., 2014).

Until now, the literature does not define the range of MAP and grazing intensity for which the convergence model is a valid assumption. An important message of our study is that the convergence model cannot not necessarily be applied along the whole gradient of MAP and grazing. Therefore, we call for studies that explicitly address this issue in the future.

*Shrubs*

Woody plants show a strong response of the grazing resistance trait for very arid and intense grazing conditions. Our simulations show that in cases with low vegetation cover, cattle cannot graze selectively anymore, and animals will browse woody plants to some extent (Tainton, 1999; see Lohmann et al 2012 for details on how browsing under such conditions is implemented in EcoHyD). Since investing into one plant trait comes with costs in our simulation setup, successful shrub sub-PFTs with high grazing resistance had to trade this for increased mortality rates.

Under less extreme aridity the establishment rate, which assists woody plants to overcome their recruitment bottleneck (Joubert et al., 2008; Lohmann et al., 2012), becomes very important. In contrast, under rather arid conditions, the recruitment success will depend much more on physiological traits like the wilting point, especially of early stage seedlings and saplings – a fundamental trait that we excluded from this analysis since it would clearly out rule the other traits at stake in the simulated dryland system. The response of the root distribution trait is similar to the response of perennial grasses, but less pronounced. The explanation for the unimodal response is likely the same: only under rainfall for which the upper soil is the most reliable source of water availability, it is beneficial to invest into a dense rooting system in this part of the soil.

*Annuals*

Our results indicate that those annual sub-PFTs that foster their opportunistic life-history strategy by maximizing growth rates perform best throughout all scenarios but the most humid

one. The general increase of annuals towards the dry and heavily grazed end of the two dimensional gradient is further underlining this idea: An opportunistic type plant will be favoured by harsh and unpredictable conditions (e.g. compare with CSR theory of Grime 2001). Only under the most humid scenario, the most successful annual sub-PFT is the one that sacrifices its growth and mortality rate for the sake of its grazing resistance trait. This might actually be a model artefact resulting from extremely low cover values ($< 1.5\%$) of annual grasses under more humid conditions).

### 2.4.3 Implications for theoretical ecology and dryland vegetation modelling

This study is the first systematic modelling study on the response of sub-PFTs in savannas towards environmental conditions, here grazing intensity and mean annual precipitation. From our results, we can make two very general statements, both of which can stimulate future research on savanna dynamics, and that we would like to discuss in the following: (i) the traits of successful plants shift along environmental gradients, and (ii) meta-PFTs differ in their successful traits and in their response to environmental conditions. Our findings allow for integrating savanna systems into other conceptual approaches, since we can now systematically compare responses of savanna vegetation with other systems under different environmental settings.

For our simulated arid savannas with a MAP below 500 mm, the convergence model is helpful to predict community trait responses of the non-woody plants with regard to both, grazing and aridity. The explanation for this is that shrubs show a rather low abundance in these arid environments (Sankaran et al., 2005) where their establishment is limited by water availability (Joubert et al., 2008) and hence competitive interactions between meta-PFTs are of relatively low importance from the perspective of perennial grasses when compared to the effects of aridity and grazing. Under more mesic conditions, however, water availability allows for woody plants to establish and persist and they are only limited if they are either directly suppressed by the presence of grass (Riginos, 2009; D'Onofrio et al., 2015) or supressed due to the indirect effects of grass cover on woody plants via fire (Midgley et al., 2010). Wrapped up, we propose that the convergence model does only apply in savannas below a certain MAP threshold. Consequently, empirical studies from rather humid systems are at risk to produce misleading hypothesis if based on the assumptions of the convergence model. This demonstrates a difficulty described by several other studies, too: The traits responsible for the response of a species to drivers like grazing and aridity are not universal, i.e. at contrasting ends of a gradient, different traits might determine the success of a species. Therefore, it is challenging or maybe

not possible to identify universal traits that are helpful across larger gradients (Vesk et al., 2004; De Bello et al., 2005; Díaz et al., 2007). However, by simulating vegetation dynamics with randomly assembled trait combinations and non-superimposed trade-offs, we received a set of emerging trait combinations that were most successful under the respective environmental conditions. These trait responses varied between the meta-PFTs in our model as well as in empirical data (McIntyre et al., 1999; McIntyre and Lavorel, 2001), showing the importance of considering a broad variety of traits in studies across environmental conditions.

Our results show a very complex pattern and clearly interdependencies between traits i.e. trade-offs but also correlations between traits depend on both, precipitation and grazing intensity. In addition, we see that the plant communities shift along the grazing and aridity gradient at the sub-PFT level. Such responses will clearly impact the overall community level response to land use and climate change. This perspective is quite common in other ecosystems like e.g. temperate grasslands (May et al., 2013; Weiss et al., 2014) and has also been shown for grasses and herbs of dry and open Australian woodlands (McIntyre and Lavorel, 2001). Hence, we suggest that our approach to include trait variability within coarse meta-PFTs is the way forward for future savanna research. In this context, it is important to define the traits and the level of species aggregation that actually matter with regard to the drivers of interest. However, this can be a challenging task as shown in a study by Linstädter et al. (2014), who aimed at identifying the appropriate level of species aggregation into PFTs in order to detect indicators of grazing impacts but struggled with numerous confounding sources of environmental variability, such as nutrient availability, that are masking grazing and aridity effects. A way forward in this sense could be analyses by system specific process-based dryland vegetation models like the one presented here. Recently, it has been shown that also large-scale dynamic global vegetation models (DGVMs) can account for trait variability within broader meta-PFTs, and that this trait variability can impact the systems response to climatic changes (Scheiter et al., 2013; Sakschewski et al., 2015; Sakschewski et al., 2016). These studies showed that the projected responses of an ecosystem to changes in climate and/or land use might differ significantly if trait variations and hence the adaptive potential of the vegetation are taken into account. However, until now grazing, worldwide being a main driving force in grassland systems is lacking a thorough (if any) representation in DGVMs (Díaz et al., 2001; Diaz et al., 2007), because of a general lack in trait-based understanding of grazing effects. In this work, we could show that grazing intensity indeed leads to a shift in successful traits and thus community composition. Therefore, we strongly argue for explicitly including livestock behaviour into future DGVMs.

## 2.5 Conclusion

We conclude that vegetation models, both for the simulation of single biomes like in our approach and for broader DGVMs, should allow for a certain variability within PFTs, to allow the multitude of responses that ecosystems show in response to multi-dimensional environmental gradients. In this context, models and empirical research can complement each other: models are directly dependent on databases such as TRY (Kattge et al., 2011)(https://www.try-db.org/) and empirical research to parameterise traits and to gain understanding of ecosystem processes. However, future empirical research can also be guided by insights from model results, for example which traits vary most across environmental conditions and are thus of high importance, and which processes are governed by these traits.

## 2.6 Appendix 2.A

## Model rules

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. In the hydrological sub-model daily soil moisture in two layers (upper: 0-20 cm; lower: 20-80 cm) is calculated (Tietjen et al., 2009). In addition to earlier versions of the model (Lohmann et al 2014 and earlier), we now separate 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 sub-model and a full description thereof can be found in Tietjen *et al.* (2009). In the vegetation sub-model biweekly growth of three plant functional types (PFTs), namely shrubs, perennial grasses and annual grasses, is calculated (Tietjen et al., 2010; Lohmann et al., 2012; Guo et al., 2016).

Two tables with the description, value and source of all model parameters are given for the hydrological (table S1) and the vegetation sub-model (table S2) respectively. Parameter and variable names directly relate to the description in Tietjen *et al.* (2009, 2010), Lohmann *et al.* (2012) and Guo *et al.* (2016).


## 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 $(\overline{T}, T_{min} \text{ and } T_{max})$ [°C], extraterrestrial radiation($R_a$), slope($sl$)and aspect effects($af$). The potential evapotranspiration function is (according to Tietjen et al., 2009):

$$ET_{pot} = 0.0023 * (\overline{T} + 17.8) * (T_{max} - T_{min})^{0.5} * R_a * af * \cos(sl) \qquad \text{Eq. 1}$$

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 ($ET_{L1} \text{ and } ET_{L2}$) using the volumetric soil moisture ($W_{Lx}$) [$m^3/m^3$], stomata closing point, the cover of annual grasses, perennial grasses and shrubs ($c\_total_{ag}, c\_total_{pg}, c\_total_s$) and the cover of each sub-PFT ($c_{veg}$) (Tietjen, 2009). As in the version in 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 ($root_{veg,Lx}$). The calculation functions of surface, upper and lower actual evapotranspiration are (according to Tietjen et al., 2009):

$$ET_{surf} = ET_{pot} * (1 - 0.5 * \sum_{veg} c\_total_{veg}) \; [mm/d]$$

$$ET_{L1} = ET_{pot} * \left(\frac{W_{L1}}{wsc}\right)^2 * g_1 \; [mm/d]$$

$$g_1 = 1.2 - 0.2 * (\sum_{veg} c\_total_{veg}) \; [dimonsionless]$$

$$ET_{L2} = ET_{pot} * \left(\frac{W_{L2}}{wsc}\right)^2 * g_2 \; [mm/d]$$

with

$$g_2 = \sum_{veg \; in \; perennial \; grasses, shrubs} root_{veg,L2} * c_{veg} \; [dimensionless]$$

$$ET_{act} = ET_{surf} + ET_{L1} + ET_{L2} \; [mm/d] \qquad \qquad \text{Eq. 2}$$

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 ($T_{L1}/ET_{L1}$) 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 ($T_{L2}$).:

$$E = E_{L0} + E_{L1}$$

$$E_{L0} = ET_{surf}$$

$$T = T_{L1} + T_{L2}$$

$$ET_{L1} = T_{L1} + E_{L1}$$

$$\frac{T_{L1}}{ET_{L1}} = \begin{cases} 1.05 * c\_total - 0.04 & if \; c_{total} > 4\% \\ 0 & else \end{cases} \; [dimensionless]$$

$$ET_{L2} = T_{L2} \qquad \qquad \text{Eq. 3}$$

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. 4). The

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

$$U_{veg,Lx} = \frac{\theta_{veg} * root_{veg,Lx}}{\sum_{veg} \theta_{veg} * root_{veg,Lx} * c_{veg}} \ [dimensionless] \qquad\qquad \text{Eq. 4}$$

$$T_{veg,Lx} = T_{Lx} * c_{veg} * U_{veg,Lx} \ [mm/day] \qquad\qquad \text{Eq. 5}$$

**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. 6) is hereby based on a logistic behaviour and calculated separately for each 5m x 5m 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 ($c\_total_{\neg veg}$) 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. 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):

$$gr_{veg,Lx} = T_{veg} * r_{veg} * \left(1 - \frac{c\_total_{veg}}{cmax_{veg} - \left(c\_total_{\neg veg} * (1 - lap)\right)}\right) [yr^{-1}] \qquad \text{Eq. 6}$$

$$gr_{ag} = min(1 * avW_{ag,L1}, 1) * r_{ag} * \left(1 - c\_total_{pg} - c\_total_s * (1 - lap) - c\_total_{ag} - c_{mor}\right)[yr^{-1}]$$
$$\text{Eq. 7}$$

*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. 4) and depends on a drought mortality rate $mr_{veg}$, the average available water content in both soil layers during the growing season ($avW_{veg,Lx}$) and the relative water uptake rate ($U_{veg,Lx}$).

$$md_{veg,Lx} = mrd_{veg} * c_{veg} * \left[ \left( 1 - min(U_{veg,Lx} * avW_{veg,Lx}, 1) \right) * \frac{root_{veg,Lx}}{\sum_i root_{veg,Li}} \right] \ [yr^{-1}] \qquad \text{Eq. 8}$$

Second, we introduced stochastic age based mortality ($ma_s$) for woody plants, referring to empirical data on *Acacia mellifera* L. from a semi-arid savannah 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 $ScenAge$ age are completely cleared from woody vegetation with an annual probability ($mp_{age}$).

*Plant grazing*

To allow for different sub-PFTs within the meta-PFTs, we slightly revised the grazing algorithm developed by Lohmann *et al.* (2012). The changes in the grazing process were mainly implemented in two terms compared to earlier version.

First, we introduced a new grazing related functional trait to the description of our PFTs (grazing preference) to represent the palatability of each PFT (e.g. how much grazing ungulates would prefer this type relative to others). Thereafter we consolidated the calculation of the relative grazed biomass ($RGB_{veg}$) for each PFT instead of differentiating the grazing calculation between woody plants and grasses only. The relative grazed biomass of each PFT ($RGB_{type,veg}$) depends on the number of PFTs ($veg\_Nr$), the available edible biomass ($BMedible_{veg}$) and the grazing preference of each PFT ($GP_{veg}$). It means that a PFT with higher grazing preference and more available edible biomass is prone to be eaten by cattle. The second amendment to the grazing algorithm refers to the inclusion of dead plant biomass. For annual grasses and perennial grasses, at the end of growing season of each year, green shoot biomass (alive biomass) is assumed to die and turn into standing dead biomass (reserve biomass). Shrubs were assumed to have no reserve biomass. In addition, we assumed a

limited maximum fraction of the given biomass of each PFT to be available, because cattle cannot graze the biomass at the soil surface and not all parts of the different plants are edible. Further, there is a fractional decay of reserve biomass from year to year according to a constant rate of decay ($Resbio\_L_{veg}$). We calculated the removal amount of reserve biomass and alive biomass by cattle based on the ratio of both biomass fractions in one cell.

$$RGB_{type,veg} = \frac{GP_{veg}}{\frac{\sum_{veg} GP_{veg}}{veg\_Nr}} * \left( \frac{BMedible_{type,veg}}{\sum_{type} \sum_{veg} BMedible_{type,veg}} \right) [dimensionless] \qquad \text{Eq. 9}$$

*Dispersal and seedling establishment*

Dispersal and establishment were simulated as addition to the cover of a respective growth form ($ds_{veg}$) to certain cells in the grid. This is rather representing seedling dispersal than seed dispersal. Germination and seedling/juvenile survival were 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 2 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 semi-arid 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 ($W_{L1,mean} > m_{est} * W_{wp,s}$). 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), we added a grazing dependent factor 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 ($distConst(SR)$) and the maximum dispersal distance ($distmax_s(SR)$).

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:

$$ds = c_{s\_source} * est_s * dist_0 * e^{-distConst(SR)*dist} * max(1 - c\_total_s - c\_total_{pg}; 0) \ [dimensionless]$$

<div align="right">Eq. 10</div>

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 impact on the dispersal kernel is given by the following linear relation being a function of the stocking rate ($SR$):

$$distConst(SR) = dc_a + (dc_b * SR) \ [dimensionless]$$ <div align="right">Eq. 11</div>

The maximum dispersal distance $distmax_s(SR)$ is calculated so that the added cover $ds$ is at least 1% of the maximum possible value of $ds$ at the center of the source cell ($dist = 0$).

## Model parameters

Table A1 Standard parameters of the hydrological sub-model (for further details see Tietjen et al., 2009)

| Name | Description | Value | Unit | Source/Parameterization |
|---|---|---|---|---|
| $growStart$ | first day of growing season | 150 | d | Tietjen et al., 2010 |
| $growEnd$ | last day of growing season | 330 | d | Tietjen et al., 2010 |
| $rw$ | residual water content during the dry season | 3.5 | vol% | Rawls et al., 1992 |
| $wsc$ | water content at capillary pressure of 15 bar (-1500kpa) | 4.1 | vol% | Rawls et al., 1992 |
| $fc$ | water content capillary pressure of 0.33 bar (-33kpa) | 16.7 | vol% | Rawls et al., 1992 |
| $S_f$ | effective suction at wetting front | 61.3 | mm | Rawls et al., 1992 |
| $K_s$ | saturated hydraulic conductivity | 59.8 | mm/h | Rawls et al., 1992 |

| | | | | |
|---|---|---|---|---|
| $d$ | water balancing constant between layers | 0.05 | - | Tietjen et al., 2009 |
| $depth_{L1}$ | depth of upper layer | 200 | mm | Tietjen et al., 2009 |
| $depth_{L2}$ | depth of lower layer | 600 | mm | Tietjen et al., 2009 |

Table A2 Standard parameters of the vegetation sub-model (for further details see Tietjen et al., 2010; Lohmann et al., 2012; Guo et al., 2016)

| Name | Description | Value | Unit | Source/Parameterization |
|---|---|---|---|---|
| $sclim$ | cover boundary for shrub (differentiate shrub and non-shrub) | 0.001 | - | Lohmann et al., 2012 |
| $scrlim$ | cover boundary for shrub (differentiate juvenile and adult) | 0.1 | - | Lohmann et al., 2012 |
| $lap$ | cover overlapping between grass and shrub | 0.2 | - | Tietjen et al., 2010 |
| $bm\_c\_rain$ | constant for impact of precipitation on the biomass per unit of cover | 0.35 | - | Lohmann et al., 2012 |
| $ga$ | constant for shaping quadratic function of grazing damage | 0.8 | - | Lohmann et al., 2012 |
| $gb$ | constant for shaping quadratic function of grazing damage | 0.1 | - | Lohmann et al., 2012 |
| $EnScov$ | cover boundary for shrub encroachment | 0.4 | - | Sankaran et al., 2005 |
| $\theta_{BM,pg}$ | relative uptake rate per perennial grass biomass | 0.9 | $mm \, (yr * g)^{-1}$ | Tietjen et al., 2010 |
| $\theta_{BM,s}$ | relative uptake rate per shrub biomass | 0.5 | $mm \, (yr * g)^{-1}$ | Tietjen et al., 2010 |
| $\theta_{BM,ag}$ | relative uptake rate per annual grass biomass | 0.2 | $mm \, (yr * g)^{-1}$ | Guo et al., 2016 |
| $root_{pg,L1}$ | fraction of roots in the upper layer for perennial grass | 0.63 | - | Tietjen et al., 2010 |
| $root_{s,L1}$ | fraction of roots in the upper layer for shrub | 0.36 | - | Tietjen et al., 2010 |
| $r_{ag}$ | potential growth rate of annual grass | 1.5 | $mm^{-1} * yr^{-1}$ | Tietjen et al., 2010 |
| $r_{pg}$ | potential growth rate of perennial grass | 0.5 | $mm^{-1} * yr^{-1}$ | Guo et al., 2016 |
| $r_s$ | potential growth rate of shrub | 0.15 | $mm^{-1} * yr^{-1}$ | Guo et al., 2016 |
| $mrd_{pg}$ | mortality rate dependent on soil moisture for perennial grass | 0.54 | $mm^{-1} * yr^{-1}$ | Tietjen et al., 2010 |
| $mrd_s$ | mortality rate dependent on soil moisture for shrub | 0.12 | $mm^{-1} * yr^{-1}$ | Tietjen et al., 2010 |
| $mrd_{ag}$ | mortality rate dependent on soil moisture for annual grass | 0.8 | $mm^{-1} * yr^{-1}$ | Tietjen et al., 2010 |
| $W_{wp,pg}$ | specific wilting point for perennial grass | 3.6 | vol% | Neilson, 1995 and Sala et al., 1989 |

| | | | | |
|---|---|---|---|---|
| $W_{wp,s}$ | specific wilting point for shrub | 3.6 | vol% | Neilson, 1995 and Sala et al., 1989 |
| $W_{wp,ag}$ | specific wilting point for annual grass | 3.9 | vol% | Neilson, 1995 and Sala et al., 1989 |
| $cmax_{pg}$ | maximum cover for perennial grass | 1.0 | - | Tietjen et al., 2010 |
| $cmax_s$ | maximum cover for shrub | 0.8 | - | Sankaran et al., 2005 |
| $conv\_c\_bm_{pg}$ | biomass at 100% cover for perennial grass | $1.9*10^6$ | $g*ha^{-1}$ | Lohmann et al., 2012 |
| $conv\_c\_bm_s$ | biomass at 100% cover for shrub | $2.1*10^7$ | $g*ha^{-1}$ | Lohmann et al., 2012 |
| $conv\_c\_bm_{ag}$ | biomass at 100% cover for annual grass | $1.7*10^6$ | $g*ha^{-1}$ | Lohmann et al., 2012 |
| $gLim_{pg}$ | non edible biomass fraction for perennial grass | 0.15 | - | Lohmann et al., 2012 |
| $gLim_s$ | non edible biomass fraction for shrub | 0.9 | - | Lohmann et al., 2012 |
| $gLim_{ag}$ | non edible biomass fraction for annual grass | 0.05 | - | Lohmann et al., 2012 |
| $GP_{pg}$ | grazing preference for perennial grass | 1 | - | Rothauge, 2006 |
| $GP_s$ | grazing preference for shrub | 0.3 | - | Rothauge, 2006 |
| $GP_{ag}$ | grazing preference for annual grass | 0.6 | - | Rothauge, 2006 |
| $est_{pg}$ | rate of successful establishment for perennial grasses | 0.05 | $yr^{-1}$ | Tietjen et al., 2010 |
| $est_s$ | rate of successful establishment for shrub | 0.005 | $yr^{-1}$ | Tietjen et al., 2010 |
| $m_{est,pg}$ | factor determining minimum mean soil moisture content for establishment for perennial grass | 1.05 | - | Joubert et al., 2008 |
| $m_{est,s}$ | factor determining minimum mean soil moisture content for establishment for shrub | 1.205 | - | Joubert et al., 2008 |
| $dist_0$ | constant for exponential dispersal decline with distance for Shrub | 0.5 | - | Tietjen et al., 2010 |
| $dc_a$ | constant for exponential dispersal decline with distance for Shrub | 0.1 | - | Lohmann et al., 2012 |
| $dc_b$ | constant for exponential dispersal decline with distance for shrub | 0.0125 | - | Lohmann et al., 2012 |
| $Resbio\_L_{pg}$ | fraction of reserved biomass that cannot be grazed for perennial grass | 0.15 | - | Lohmann et al., 2012 |
| $Resbio\_T_{pg}$ | fraction of alive biomass that is transformed into reserved biomass for perennial grass | 0.25 | - | Lohmann et al., 2012 |

| | | | | |
|---|---|---|---|---|
| $Resbio\_L_{ag}$ | fraction of reserved biomass that cannot be grazed for annual grass | 0.05 | - | Lohmann et al., 2012 |
| $Resbio\_T_{ag}$ | fraction of alive biomass that is transformed into reserved biomass for annual grass | 0.1 | - | Lohmann et al., 2012 |

Table A3 Standard trait parameters of perennial grasses, shrubs and annual grasses

| Parameter / Trait | Description | perennial grasses | shrubs | annual grasses |
|---|---|---|---|---|
| r | potential growth rate [mm-1 * yr-1] | 0.5 | 0.15 | 1.5 |
| mrd | Mortality rate dependent on soil moisture [mm$^{-1}$ * yr$^{-1}$] | 0.54 | 0.12 | 0.8 |
| root | fraction of roots in the upper soil layer [-] | 0.63 | 0.36 | 1 |
| Ɵ | relative uptake rate per biomass [mm * (yr * g) $^{-1}$] | 0.9 | 0.5 | 0.2 |
| e | rate of successful establishment [yr$^{-1}$] | 0.05 | 0.005 | - |
| GP | grazing preference [-] | 1 | 0.3 | 0.6 |
| glim | non-edible biomass fraction [-] | 0.15 | 0.9 | 0.05 |
| W | specific wilting point [vol%] | 3.6 | 3.6 | 3.9 |
| m_est | factor determining minimum mean soil moisture content for establishment [-] | 1.05 | 1.205 | - |
| conv_c_bm | biomass at 100% cover [g * ha$^{-1}$] | $1.9 * 10^6$ | $2.1*10^7$ | $1.7*10^6$ |

# Sensitivity analysis
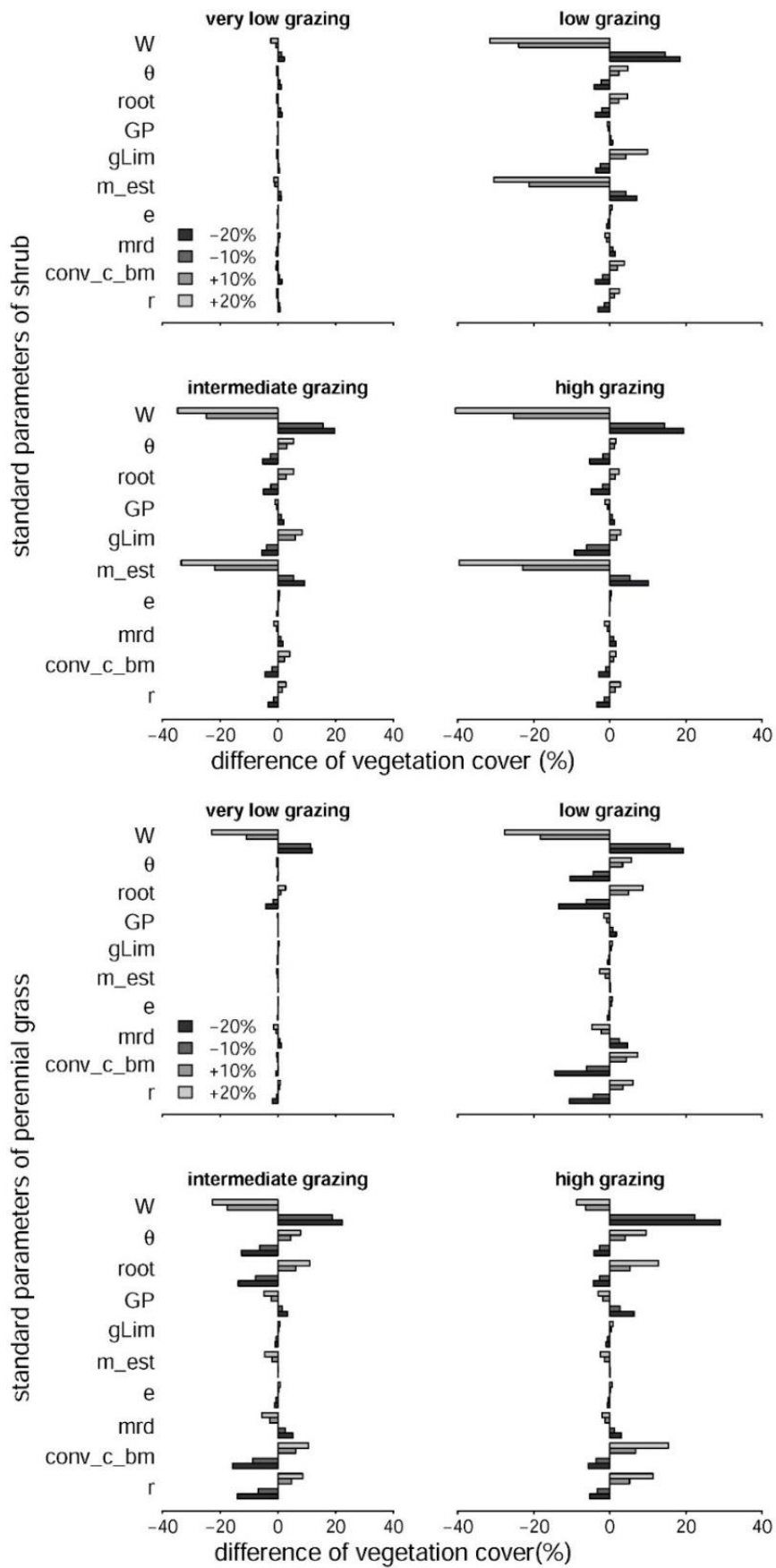
Fig A1 Sensitivity analysis of standard trait parameters of shrubs and perennial grasses under mean annual precipitation of 500 mm and different grazing intensities (very low: 2 LSU/100 ha; low: 5 LSU/100 ha; intermediate: 6.25 LSU/100 ha; high grazing: 8.33 LSU/ 100 ha)

Before we conducted our actual simulations, we have performed a local sensitivity analyses for the parameters describing the perennial and woody meta-PFTs. For the woody plant type two parameters are disproportionately sensitive: the wilting point (W) and the soil water content at which establishment of seedlings is possible (m_est). A decrease in both W and m_est leads to an increase in shrub cover. Further, it is very clear that under very low grazing none of the parameters has a very strong influence on the resulting shrub cover after 100 years. For the perennial grass meta-PFT the wilting point (W) is also the single most important parameter leading to disproportionate effects on the vegetation cover after 100 years of simulated vegetation dynamics. It is visible that also other parameters are quite sensitive, however the resulting response in grass cover never exceeds the magnitude of change that the parameter itself experienced.

From these results we concluded that using the wilting point and the soil moisture threshold for establishment in our experiment would not lead to useful results, since clearly the variations of these very parameters would mask all other adaptations.

# Link to Chapter 3

In chapter 2, I identified trait responses to mean annual precipitation (MAP) and grazing intensity of three meta plant functional types (PFT) in savannas, namely perennial grass, shrub and annual grass. Moreover, the effect of both drivers on the vegetation community composition was assessed. My simulations indicate that precipitation and grazing have a convergent effect on the functional trait composition of respective dominant meta-PFT under arid conditions (MAP < 500 mm). While precipitation, rather than grazing, leads to a shift in trait composition under moist conditions (MAP > 500 mm). In contrast, increasing grazing intensity leads to a transition from a perennial grass dominated to a woody dominated plant community which is in good agreement with empirical studies.

Results indicate that growth rate is of great importance for the competitiveness of the annual grass PFTs. For perennial grasses and shrubs, the importance of traits for their respective competitiveness strongly depends on environmental conditions and displays a more diverse pattern. While traits like growth rate and water uptake rate have a strong effect on the competitiveness of perennial grasses, traits like non-edible biomass fraction only play a minor role in an arid and high grazing environment. For shrubs, under moist conditions, a higher seed establishment rate is important while the effect of non-edible biomass is negligible. Those results demonstrate how important considering functional diversity is for quantifying the response of savanna ecosystems to environmental factors. On the other hand, I identified mechanisms by which savanna vegetation may adapt to climatic and land use conditions.

Besides precipitation and grazing, soil conditions are another important factor in shaping vegetation diversity and ecosystem functioning in savannas. Landscapes in these ecosystems are often characterized by a high local difference of edaphic conditions. However, traditional savanna models mostly ignore this landscape heterogeneity. Thus, explicitly simulating heterogeneous landscapes with respect to soil properties allows for a quantification of their impact on plant functional diversity and ecosystem functioning across spatial scales. Moreover, it will assist in determining how the effects of landscape heterogeneity might be modulated by precipitation and grazing.

In the following chapter, I analyze how landscape heterogeneity affects vegetation functional diversity and ecosystem functioning in semi-arid savannas. To this end, I calibrated the EcoHyD model with landscapes composed of different soil properties. In particular, I simulated the plant assembly based on adaptations to specific edaphic conditions in order to

assess the relationship between landscape heterogeneity and vegetation functional diversity. I further demonstrate how precipitation and grazing intensity modulate the effects of landscape heterogeneity on the functioning of savanna ecosystems.

# Chapter 3

# The role of landscape heterogeneity in regulating plant functional diversity under different precipitation and grazing regimes in semi-arid savannas

**Summary**

· Savanna systems exhibit a high plant functional diversity. While the level of aridity and grazing intensity has been widely discussed as drivers of savanna vegetation composition, physical soil properties have received less attention. Since savannas can show local differences in soil properties, these might act as environmental filters and affect plant diversity and ecosystem functioning at the patch scale. However, research on the link between savanna diversity and ecosystem function is widely missing.

· In this study, we aim at understanding the impact of local heterogeneity in the soil conditions on plant performance, on plant diversity and on ecosystem functions. For this, we used the ecohydrological savanna model EcoHyD. The model simulates the fate of multiple plant functional types and their interactions with local biotic and abiotic conditions. We applied the model to a set of different landscapes under a wide range of grazing and precipitation scenarios to assess the impact of local heterogeneity in soil conditions on the composition and diversity of plant functional types and on ecosystem functions.

· Comparisons between homogeneous and heterogeneous landscapes revealed that landscape heterogeneity allowed for a higher functional diversity of vegetation under low but not under high grazing stress. However, landscape heterogeneity did not have this effect under low grazing stress in combination with high mean annual precipitation (MAP). Further, landscape heterogeneity led to a higher community biomass in different precipitation and grazing scenarios. However, the increase did not show a clear pattern with respect to MAP and grazing stress. Plant transpiration of the community was found to decrease in heterogeneous landscapes under arid conditions.

· This study highlights that local soil conditions interact with precipitation and grazing in driving savanna vegetation. It clearly shows that vegetation diversity and resulting ecosystem functioning can be driven by landscape heterogeneity. We therefore suggest

that future research on ecosystem functioning of savanna systems should focus on the links between local environmental conditions via plant functional diversity to ecosystem functioning.

**3.1 Introduction**

Savannas cover approximately 20% of the global land surface and account for 30% of the terrestrial net primary production (Sankaran et al., 2005; Grace et al., 2006). They can be found in regions with a rather limited water availability and highly variable annual precipitation (D'Onofrio et al., 2015). The savanna biome is characterized by a matrix of abundant perennial grasses and scattered woody plants (Scholes and Archer, 1997). Locally, plant coverage and species composition vary (Asner et al., 1998; Augustine, 2003). In addition, the plant species differ in their morphological, biophysical and phenotypic characteristics. As a result, savanna vegetation exhibits a high functional diversity (Cowling et al., 1994; Busso et al., 2001; Kos and Poschlod, 2010; Batalha et al., 2011).

The high temporal and spatial variability of environmental conditions in savannas is assumed to be a major driver for this high functional diversity because it enables the coexistence of plants with different strategies. For example, high intense precipitation events can lead to deep soil infiltration, which facilitates woody plants with a deeper rooting system. In contrast, less intense precipitation events benefit species with a shallow rooting system (Walter, 1954). Accordingly, if mean annual precipitation increases, vegetation composition will shift towards more woody plant cover (Sankaran et al., 2005). Grazing is another important factor affecting vegetation distribution and diversity (Adler et al., 2001). It can increase the spatial heterogeneity of vegetation leading to long term changes in the community composition. In savannas, the shrub encroachment rate has been found to be very sensitive to grazing patterns (Weber et al., 1998). While moderate-level grazing intensity can increase vegetation diversity by creating mosaics of microhabitats (Oba et al., 2001), high grazing can cause a decline in plant diversity as it reduces the abundance and the biomass of most plant species (Mysterud, 2006). Another key factor for vegetation diversity in savannas is landscape heterogeneity (San Jose et al., 1998; Augustine, 2003). In this context, we define heterogeneous landscapes as a mosaic of patches with different resource availabilities in terms of nutrients, water or soil properties. Landscape heterogeneity can act as a buffer mechanism against adverse environmental conditions (Jeltsch et al., 2000) through the provision of refuge sites. In addition it can create a high number of ecological niches hosting a more diverse plant species assemblage than homogeneous landscapes (Stein et al., 2014). Although such effects are well known (Kneitel and Chase, 2004; Melbourne et al., 2007; Lundholm, 2009), the spatial heterogeneity of soil conditions has so far received very little attention in the savanna ecology literature in general and in modelling studies in particular.

Empirical studies and remote sensing data reveal that savanna landscapes show a high spatial

variability of soil conditions (Williams et al., 1996; Fuhlendorf and Smeins, 1998; Bestelmeyer et al., 2009; Bestelmeyer et al., 2011; Zhou et al., 2017) and topographic conditions (Ben Wu and Archer, 2005). The soil conditions differ in soil texture and soil depth (Williams et al., 1996; Fuhlendorf and Smeins, 1998; Zhou et al., 2017). The differences in these conditions have multiple effects on vegetation. *Soil texture* results from the composition of soil particle sizes and determines major physical properties of the soil such as hydrological processes. By impacting infiltration and water holding capacity it determines plant water availability (Fernandez-Illescas et al., 2001). Coarse textured soils such as sand facilitate water infiltration into deeper soil layers (McClaran and Van Devender, 1997) thus increasing the water availability for deep rooted plants. *Soil depth* determines the vertical water distribution as well as space that is available for rooting and thus determines the amount of water available for plant growth (Peterman et al., 2014). Besides variability in soil conditions, *topography* is another aspect of spatial heterogeneity. It mainly influences lateral water fluxes by runoff and soil erosion (Tietjen, 2016). This impacts the surface water budget and vegetation patterns at different spatial scales (Bergkamp, 1998).

In summary, heterogeneous soil conditions and topography in savanna landscapes will affect the hydrology and thus the abundance and distribution of plant species. Therefore, it will ultimately change the vegetation functional diversity.

Unravelling the impact of landscape soil heterogeneity on plant functional diversity can improve our understanding of system level changes. Different soil conditions in the landscape will affect ecosystem functioning such as nutrient cycling (Cable et al., 2008). Thus, a better understanding of landscape heterogeneity will allow more insights into ecosystem functioning in different landscapes. Soil conditions have been found to influence the resilience of savanna vegetation, i.e. whether they tend to change from a grass dominated to a woody state (Wonkka et al., 2016). Therefore the assessment of spatial heterogeneity of soils and topography can be used to identify landscapes that are vulnerable to transitions to a less desirable state (Bestelmeyer et al., 2011).

The effects of landscape soil heterogeneity on plant diversity and functioning might be modulated by drivers such as precipitation and land use in savanna ecosystems since different soil parameters, e.g. soil texture and soil depth, can interact with those drivers (Williams et al., 1996; Fuhlendorf and Smeins, 1998). For example, increased soil clay content and decreased rainfall have been found to reduce the woody species richness and tree cover in Australian tropical savannas (Williams et al., 1996). Another example is the larger decline of shrub cover on shallow soils than on deep soils during droughts (Munson, 2013). The co-occurrence of

dominant grasses may be facilitated by spatial difference of habitats caused by soil texture and grazing in the Serengeti savanna (Anderson et al., 2006). Increased precipitation shifted the effect of herbivore grazing on soil organic carbon from negative to positive with coarser-textured soils (McSherry and Ritchie, 2013). So far, many studies of savanna ecosystems assessed the interactive role of precipitation and grazing with single soil parameters. However, to our knowledge, there is no study that considers the effects of landscape soil heterogeneity on plant functional diversity and ecosystem functioning comprehensively, and that also accounts for its interaction with precipitation and grazing intensity.

Simulation models are a successful approach to disentangle multiple effects of landscape heterogeneity in drylands. Some models, e.g. the trigger-transfer-reserve-pulse model (Ludwig et al., 2005), assessed the influence of spatial resource heterogeneity such as water distribution on the biomass production of savanna vegetation. Other spatially explicit models were built to simulate emergence of heterogeneous vegetation patterns in drylands (Rietkerk et al., 2004; Meron, 2011; Ursino and Callegaro, 2016). These patterns were further studied with remote sensing data (Hill, 2013; Meyer and Okin, 2015). Simulations of patchy vegetation across the landscape were also used to assess vegetation dynamics and productivity (Caylor and Shugart, 2004; Montaldo et al., 2008). However, to our knowledge there is no savanna model that explicitly considers the spatial heterogeneity of physical soil properties such as soil texture and soil depth.

In this study, we extended the ecohydrological dryland model EcoHyD (Tietjen et al., 2009; Tietjen et al., 2010; Lohmann et al., 2012; Guo et al., 2016) to assess the impact of landscape heterogeneity in terms of soil properties under different precipitation and grazing regimes in semi-arid savannas. We simulated a functionally diverse plant community and addressed the following questions:

(1) How does landscape heterogeneity affect plant functional diversity and ecosystem functioning?

(2) Is the impact of landscape heterogeneity on functional diversity dependent on the spatial scale of observation?

(3) How does the effect of landscape heterogeneity interact with precipitation and grazing intensity?

## 3.2 Methods

We used an ecohydrological model to simulate the impact of spatial heterogeneity of soils on ecosystem function in savanna landscapes. The soils differ in their soil depth and soil texture.

We studied the vegetation cover that emerged in artificial heterogeneous and homogeneous landscapes, and evaluated plant functional type (PFT) diversity and composition, and resulting ecosystem functioning for different grazing and precipitation scenarios. In the following, we describe the simulation model, the experimental setup of the simulated landscapes and PFTs and how we evaluated the results.

### 3.2.1 Model overview

The process-based savanna model EcoHyD was used in this study (Tietjen et al., 2009; Tietjen et al., 2010; Lohmann et al., 2012; Guo et al., 2016). EcoHyD calculates soil moisture in two layers and dynamics of vegetation cover and biomass. This model is designed in a moderate-level complexity and includes basic hydrological and vegetation processes, which are dynamically linked (see conceptual overview in Fig. 1). All processes are simulated on a grid cell level with a resolution of 5 by 5 m². In this study, the landscape comprises 60 by 60 grid cells with a total size of 90,000 m². Hydrological processes are detailedly described in Tietjen *et al.* (2009) and are calculated in an hourly to daily resolution and include potential evapotranspiration, soil evaporation, plant transpiration, water fluxes in the upper and lower soil layer, and water run-on and run-off on the soil surface. The potential evapotranspiration is determined by daily temperature, solar radiation and topographical parameters. The actual evapotranspiration is separated into soil evaporation and plant transpiration (Guo et al., 2016). Evaporation is assumed to play an important role in the surface soils and upper soil layer, which can be negligible in the lower soil layer. Transpiration of both soil layers is determined by the actual vegetation in a grid cell and its rooting (Guo et al., 2016). Soil hydrological parameters such as soil water potential, hydraulic conductivity, and field capacity largely control the infiltrative flux between layers (Tietjen et al., 2009). Vegetation processes (Tietjen et al., 2010; Lohmann et al., 2012; Guo et al., 2016) include growth, mortality, seed dispersal, establishment, and grazing by animals in a biweekly or annual temporal resolution. The vegetation composition consists of three main plant functional types (PFT) in savanna ecosystems, namely shrubs, perennial and annual grasses. Growth of perennial grasses and shrubs is based on the logistic behavior (Tietjen et al., 2010) and is related to the transpirational flux (Guo et al., 2016). Growth of annual plants does not include any competition for available soil water and annual grasses exclusively invest into a rooting system in the upper soil layer (Lohmann et al., 2012). We simulate the drought-induced mortality of three main PFTs and particularly age-based mortality of woody plants (Tietjen et al., 2010; Lohmann et al., 2012). Dispersal distance of perennial grasses is not assumed to be limited at the simulated spatial scale, and establishment

depends on top-soil water availability (Tietjen et al., 2010). Seeds of annual grasses are assumed to be omnipresent, but can only germinate and establish if competition is low (Lohmann et al., 2012). In contrast, shrub dispersal is limited to the local surrounding of the mother plant, but can be extended by grazing animals (Tietjen et al., 2010; Lohmann et al., 2012). Livestock grazing leads to a reduction of plant biomass. The selection of fodder plants is determined by the palatability, distribution and amount of available biomass of each PFT (Lohmann et al., 2012). All model processes and the related model parameters are given in detail in the supplementary materials (see the Appendix 3.A).
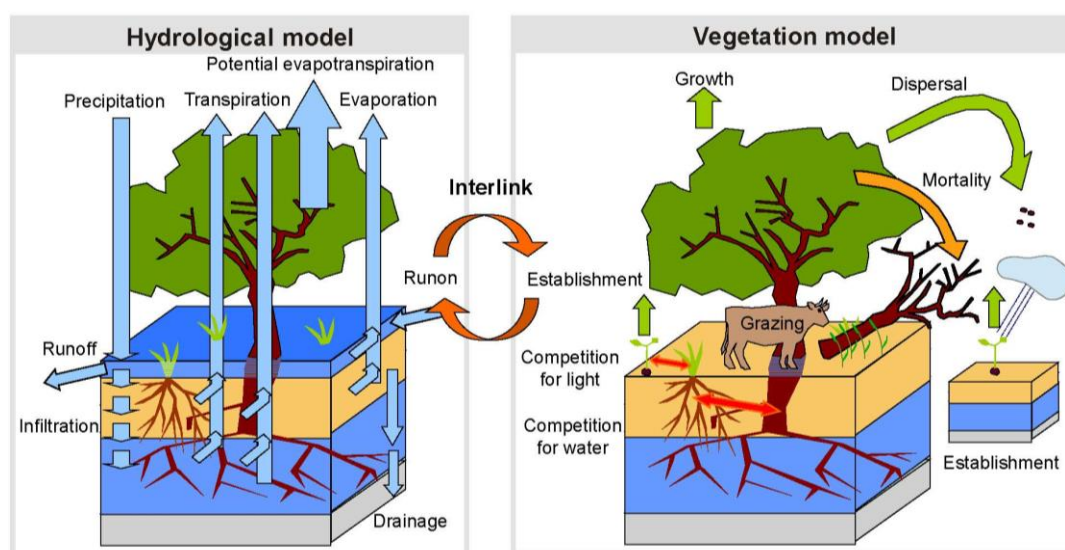


Fig. 1 Overview of the hydrological and vegetation processes in model EcoHyD, after Tietjen, 2016

### 3.2.2 Landscape heterogeneity

We studied landscape heterogeneity in two characteristics: soil texture and soil depth. For this, we first constructed nine homogeneous landscapes in a full factorial design with one of three common soil textures (sand, loamy sand and sandy loam) and one of three soil depths of the lower soil layer (400, 600 and 800 mm), with a fixed depth of the upper soil layer (200 mm). Only then, we constructed the heterogeneous landscapes by randomly assigning each set of neighboring 3 by 3 grid cells to one of the nine combinations of soil texture and depth with the same probability for each combination. Details were provided in the Appendix 3.A. The mean slope of the landscape was set to 0.5% in all simulations with local slopes between 0.001% and 12.32% (based on Tietjen, 2016).

### 3.2.3 Plant functional type assemblage

EcoHyD assesses the fate of three broad plant functional types (PFTs), namely shrubs, perennial grasses, and annual grasses, called meta-PFT in the following. These meta-PFTs differ in their

plant life forms (woody vs. herbaceous plants) and their life cycle (perennial vs. annual). Each meta-PFT was sub-divided into sub-PFTs differing in seven plant traits (annual grasses: five traits). We first constructed a species pool containing all theoretically possible sub-PFTs. Each trait of the sub-PFTs could take a low, a medium and a high value, and to enforce trade-offs only trait combinations were allowed in which these values were balanced (see the Appendix 3.A). Out of this total species pool of 353 sub-PFTs for perennial and woody species and 51 sub-PFTs for annual species we determined the two sub-PFTs that were most successful in a given combination of soil texture and soil depth for low grazing (5 large stock units LSU per 100 ha) and moderate mean annual precipitation (500 mm). For this, we randomly chose ten shrubs, ten perennial grasses and five annual sub-PFTs from the total species pool, leading to a PFT assemblage of 25 sub-PFTs in total. We simulated the fate of this PFT assemblage in a given landscape. This was repeated for each homogeneous landscape 50 times, each with three rainfall time series. For each simulation, we determined the two dominant sub-PFTs of each meta-PFT (only one for annual grasses) in year 50 to 100, i.e. those sub-PFTs that showed the highest mean cover during this period. We then calculated the mean value of each trait of both dominant sub-PFTs separately for each meta-PFT over all 150 repetitions (50 repetitions for random sub-PFT selection and 3 precipitation repetitions). We then constructed the total species pool out of these artificial dominant sub-PFTs leading to a pool of 18 shrub sub-PFTs, 18 perennial grass sub-PFTs, and 9 annual grass sub-PFTs. Optimal trait combinations showed clear differences across the soil properties (see the Appendix 3.A).

For all following simulations, we initialized the vegetation in a way that all sub-PFTs of the optimal species pool were initially present. The initial distribution of the sub-PFTs within the landscape followed the same rule for every simulation: Shrubs were assumed to be present in 20% of the grid cells (here called woody cells), with a cover of 60% in each woody cell. For this, one of the 18 shrub sub-PFTs was randomly assigned to a woody cell. In woody cells, perennial cover was set to 5% (five perennial sub-PFTs, each with a cover of 1%), and in non-woody cells, perennial cover was set to 90% (ten perennial sub-PFTs, each with a cover of 9%). Annual grasses were not initialized because they are assumed to emerge as soon as conditions are appropriate.

### 3.2.4 Grazing and precipitation scenarios

We tested the effect of landscape heterogeneity on functional diversity and ecosystem functioning along a rainfall gradient under two scenarios of grazing intensity. Mean annual rainfall was set to 400, 500 and 600 mm using a time-series of precipitation generated by the

rainfall simulator Namrain (Köchy, 2010). Grazing intensity was set to low (5 LSU/100 ha) and high (8.33 LSU/100 ha). Each landscape setting was replicated three times with a different initial distribution of plant functional types and soil conditions (for heterogeneous landscapes). Each scenario of mean annual precipitation was replicated five times, leading in total to 15 replicates for each combination of grazing and rainfall.

### 3.2.5 Evaluation of PFT diversity and ecosystem functioning

We evaluated functional diversity of plants by reporting the number of coexisting sub-PFTs and the Shannon index. Only those sub-PFTs were included in the coexistence analysis that are present in at least one grid cell with at least 5 % cover within the landscape. We chose this threshold to exclude the impact of very rare sub-PFTs, which allowed us to better detect differences in plant coexistence among scenarios. To investigate the diversity of sub-PFTs at different spatial extents, we selected different sizes of sampled area in each landscape scenario. The smallest sampled area is composed of 6 by 6 grid cells. Thus it can include a mixture of soil properties in heterogeneous landscapes. Thereafter we extended the size of sampled area by 3 grid cells for each side until the last sampled area fully covers the whole landscape (i.e. 6 by 6, 12 by 12, 18 by 18, …, 48 by 48). Thus in total we obtained 8 sampled areas.

To assess the diversity we calculated the Shannon index *H*. It integrates the occurrence as well as the abundance of coexisting sub-PFTs (Spellerberg and Fedor, 2003):

$$H = (\frac{cover_{PFT,area}}{\sum_{n=1}^{45} cover_{PFT,area}}) * \ln\left(\frac{cover_{PFT,area}}{\sum_{n=1}^{45} cover_{PFT,area}}\right) \qquad Eq.1$$

Ecosystem functioning was estimated by calculating biomass and transpiration of the community. To study the difference in ecosystem functioning between homogeneous and heterogeneous landscapes, we related the functioning of the heterogeneous landscape to the average functioning of all nine homogeneous landscapes. We used the mean value of all the grid cells to present the ecosystem functioning in a given landscape.

We applied the Wilcoxon signed-rank test to assess whether landscape heterogeneity significantly affects functional diversity or ecosystem functioning using R software (R-Core-Team, 2013). All model outcomes were evaluated for the central zone (48 x 48 grid cells) of the overall landscape (60 x 60 grid cells) to exclude border effects through processes such as seed dispersal and lateral water flow (see the Appendix 3.A).

### 3.3 Results

### 3.3.1 Functional diversity in heterogeneous and homogeneous landscapes

We found that the number of coexisting sub-PFTs were very similar among the scenarios of different soil depths (see the Appendix 3.A). Thus, we pooled the results of all soil depths by soil textures to work with a higher number of replicates for soil texture scenarios. Comparing homogeneous and heterogeneous landscapes under a low grazing intensity and mean annual precipitation (MAP) of 500 mm we found that heterogeneity significantly increased the number of coexisting sub-PFTs (Fig. 2a). On average, nearly 80% of the 45 constructed sub-PFTs coexisted in heterogeneous landscapes. All of the 18 shrub sub-PFTs were present in all landscapes. The number of present perennial grass sub-PFTs differed between landscapes. Annual grass sub-PFTs were rated absent in the coexisting community, because of their low mean cover. The lowest number of sub-PFTs (21 sub-PFTs) was found in landscapes with sandy loam soils, and all of these sub-PFTs were also present in sandy soils and loamy sand soils (Fig. 2b). There was one sub-PFT that was exclusively present in sandy soils compared to loamy sand soils. All sub-PFTs that were present in homogeneous landscapes coexisted also in heterogeneous landscapes.
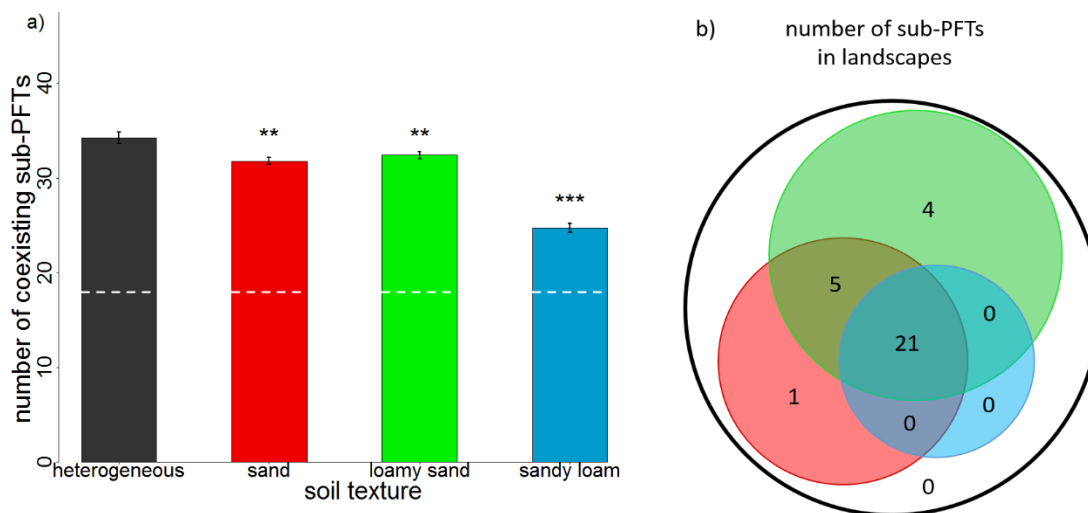


Fig. 2 Number of coexisting sub-PFTs and their overlap. The left panel (a) shows the mean number of coexisting sub-PFTs in the heterogeneous landscape and homogenous landscapes. We used the mean value of three soil depths (400 mm, 600 mm, 800 mm) for each soil texture scenario. Error bars represent the standard error. Asterisks indicate significance level of the Wilcoxon signed rank test (***: $< 0.001$; **: $< 0.01$; *: $< 0.05$; n.s.: $> 0.05$). The white dotted line indicates the number of shrubs (below line) and perennial grasses (above line). The right panel (b) shows the total number of sub-PFTs that are robustly present in all model repetitions for each landscape scenario. First we calculated the co-occurring number of sub-PFTs that were present for a given soil texture based on 45 replicates (three soil depth * three landscape replicates * five precipitation replicates). The numbers in the

colored circles indicate how many PFTs are present in only one (non-overlapping case), two (overlap between two circles) or all (overlap between three circles) landscapes with a given soil texture; the additional black circles would indicate the presence in heterogeneous landscapes only.

### 3.3.2 Impact of landscape heterogeneity across spatial scales

We assessed how the effect of landscape heterogeneity on functional diversity changes with the spatial scale at which the functional diversity is reported (Fig. 3). The Shannon index increased with an increasing sampling area, but this increase levelled off for areas larger than $10^4$ m$^2$. The lower the sand content of the soil, the lower the Shannon index and the larger the sampling area had to be to reach the maximal Shannon index. For sizes of the sampling area at which the Shannon index was still increasing ($< 10^3$ m$^2$), most homogeneous landscapes showed a higher Shannon index. In contrast, heterogeneous landscapes had a higher Shannon index for larger sampling areas. The standard error of the Shannon index decreased with increasing size of the sampling area, indicating higher variability in the functional composition of the plant community for small sampling areas.
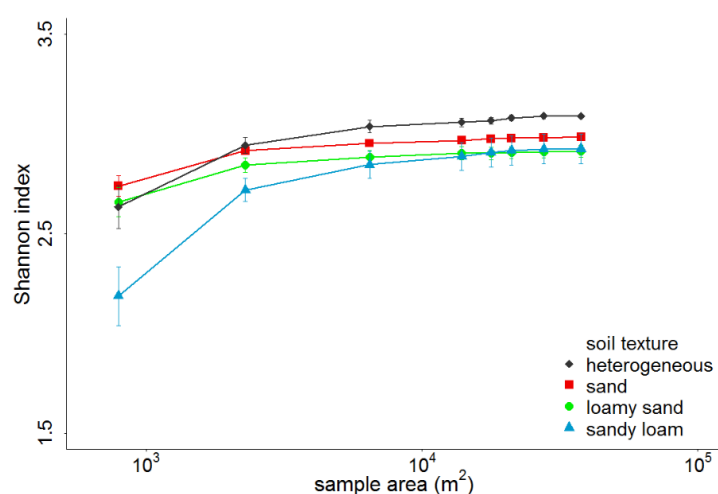


Fig. 3 Shannon index dependent on the size of the sampling areas for homogeneous and heterogeneous landscapes. We used the mean value of three soil depths (400 mm, 600 mm, 800 mm) for each soil texture. Values are based on vegetation cover of the sub-PFTs during the year 50-100, and show mean (lines) and standard error (error bars) of the Shannon index. Simulations were replicated 45 times (three soil depths * three landscape replicates * five precipitation replicates) and refer to a scenario of intermediate mean annual precipitation (500 mm) and low grazing intensity (5.0 large stock unit per 100 ha).

### 3.3.3 Effect of landscape heterogeneity on functional diversity under different environmental conditions

The impact of landscape heterogeneity on the functional diversity was affected by the mean

annual precipitation as well as by the grazing intensity (Fig. 4). At a low grazing intensity, landscape heterogeneity led to a significantly higher number of coexisting sub-PFTs at precipitation levels of 400 and 500 mm/a, but not for 600 mm/a with the exception of sandy loam soils. This was in contrast with the effects of landscape heterogeneity under high grazing intensity. Heterogeneity led to lower or similar diversity compared to homogeneous landscapes for landscapes with sandy soils or loamy sand soils. Again, sandy loam soils showed the lowest diversity, which was significantly lower for $MAP \geq 500$ mm than for heterogeneous landscapes. All shrub sub-PFTs coexisted at each soil texture independent on grazing intensity and MAP. Annual grass sub-PFTs were absent in all landscapes, again due to their overall very low mean cover across years. In the scenario of high grazing and low precipitation, perennial grass sub-PFTs were only present in the sand textured landscape. Generally, higher rainfall and low grazing led to higher functional diversity.
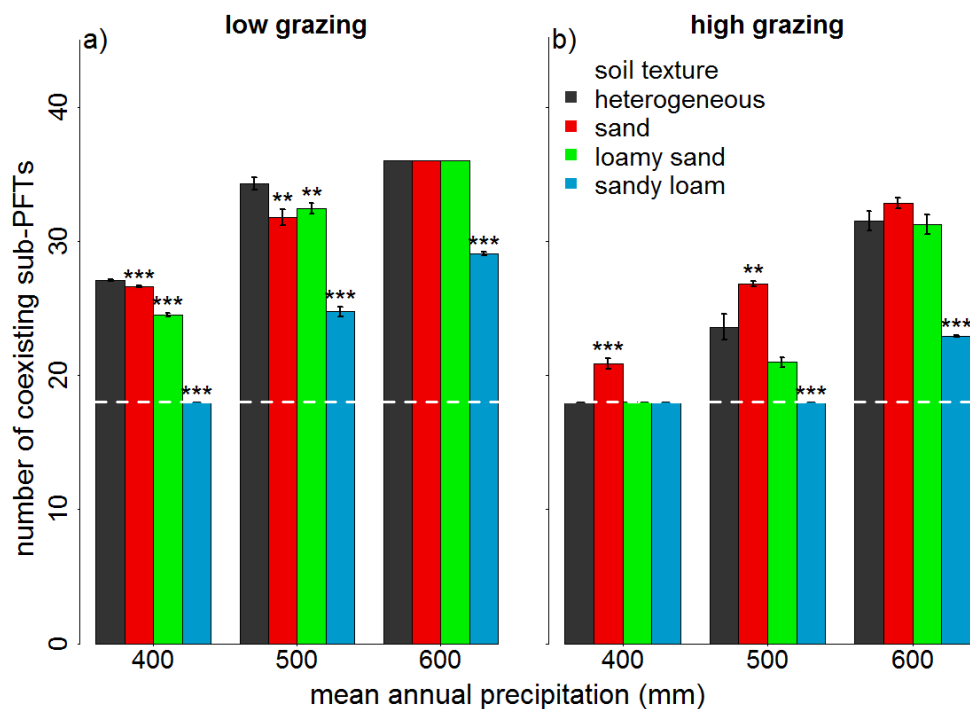


Fig. 4 Number of coexisting sub-PFTs for homogeneous and heterogeneous landscapes. We used the mean value of three soil depths (400 mm, 600 mm, 800 mm) for each soil texture. The white dotted line indicates the number of shrubs (below line) and perennial grasses (above line). For low (a) and high (b) grazing intensity, the number of coexisting sub-PFTs is shown for different landscapes and scenarios of mean annual precipitation (x-axis). Results refer to mean values (bars) and standard error (error bars) of 45 model replicates (three soil depths * three landscape replicates * five precipitation replicates) during the year 50-100. Asterisks indicate significance level of the Wilcoxon signed rank test (***: < 0.001; **: < 0.01; *: < 0.05; n.s.: > 0.05).

### 3.3.4 Effect of landscape heterogeneity on ecosystem functioning

In addition to the number of coexisting sub-PFTs, landscape heterogeneity impacted ecosystem functioning, here measured as biomass and transpiration. The effect of landscape heterogeneity on the total community biomass as well as on the total community transpiration depended on mean annual precipitation and grazing intensity (Fig. 5). For all environmental conditions, landscape heterogeneity increased total community biomass, however, the magnitude did not show a clear pattern: The only significant and biggest relative increases in biomass were found for a MAP of 400 mm and low grazing as well as for a MAP of 500 mm and high grazing pressure. Despite higher biomass, plant transpiration was lower for 400 mm MAP (significantly only for high grazing pressure). For a MAP of 500 mm transpiration was slightly, but non-significantly higher, and we did not observe a change in transpiration for 600 mm of rainfall.
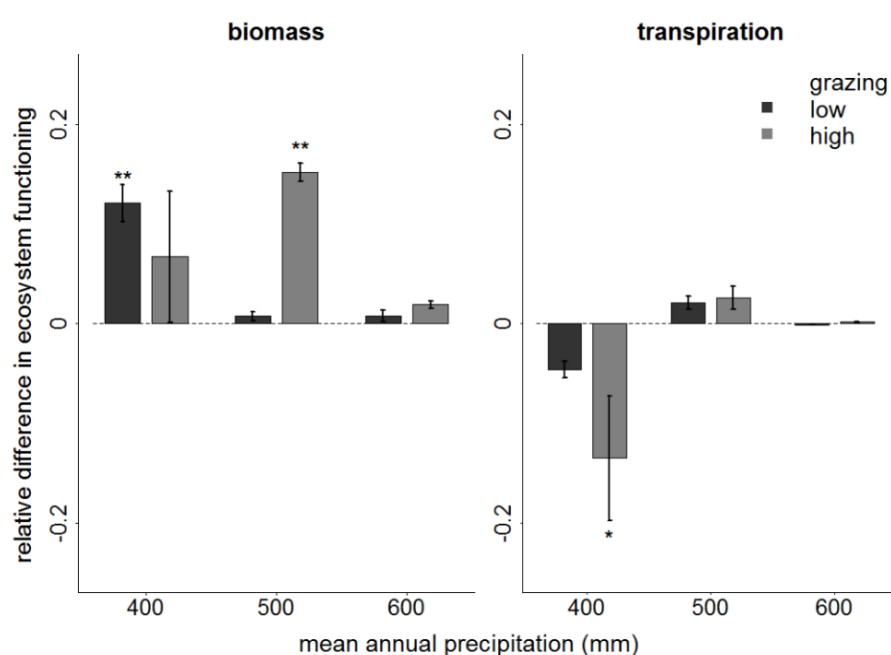


Fig. 5 Difference in biomass and transpiration between homogeneous and heterogeneous landscapes. The graphs show the relative difference in mean biomass (left) and transpiration (right) as a result of landscape heterogeneity along the precipitation gradient for low (black) and high (grey) grazing intensity. Results refer to 45 model replicates (three soil depths * three landscape replicates * five precipitation replicates) during the year 50-100. Asterisks indicate significance levels using the Wilcoxon signed rank test (***: < 0.001; **: < 0.01; *: < 0.05; n.s.: > 0.05).

## 3.4 Discussion

In this study, we used the ecohydrological model EcoHyD (Tietjen et al., 2009; Tietjen et al., 2010; Lohmann et al., 2012; Guo et al., 2016) to simulate the fate of multiple plant functional types in semi-arid savannas. Our goal was to assess the effects of landscape heterogeneity on functional vegetation diversity and ecosystem functioning. We simulated landscapes composed of a variety of soil textures and soil depths.

To summarize our results: We did not observe an effect of soil depth. In contrast, soil texture clearly impacted plant functional diversity and partly also ecosystem functioning. Simulation results showed that heterogeneous landscapes sustained a higher functional diversity. However, this positive effect was only found for low grazing intensity and under more arid conditions. At the level of the whole community, the impact of landscape heterogeneity on total biomass and total transpiration depended on the mean annual precipitation and grazing intensity. In addition, we found that the size of the sampling area determined whether landscape heterogeneity had a positive or negative effect on functional diversity. In the following, we will discuss these findings in more detail.

### 3.4.1 The effect of landscape heterogeneity on functional diversity

We found that soil depth did not significantly affect plant coexistence. In our simulation experiments on soil depth, we exclusively changed the soil depth of the lower layer. In the lower layer, the relative soil moisture was generally lower than in the upper layer, but also the root density of plants was lower. Therefore, changing soil depth did not affect plant access to soil water. As a result, we did not see any response of plants or plant diversity in our simulations. Consequently, we used mean values of simulation results for soil depths in all further assessments to increase our number of replicates.

In contrast to soil depth, soil texture and its heterogeneity strongly affected plant coexistence. Soil texture influences most soil hydrological parameters such as wilting point, water potential and hydraulic conductivity (Maidment, 1993). Because of their impact on soil water availability, these parameters also indirectly affect vegetation processes such as plant growth, mortality and seed establishment. Empirical studies also show that soil texture has a strong filtering effect on plant functional traits. Plants in water-limited environments potentially have longer roots in coarser textured soils because such soil properties hardly hold water which means a stronger infiltration into deeper layers (Schenk and Jackson, 2002). Our results showed that landscapes with heterogeneous soil conditions hosted more plant functional types in a given community than landscapes with homogeneous soil conditions. This is in line with empirical studies (Deutschewitz et al., 2003; Kumar et al., 2006; Lundholm, 2009) and theoretical expectations (Kneitel and Chase, 2004; Melbourne et al., 2007). The reason for this finding is that diverse edaphic conditions provide more diverse conditions for plants, and can thus host more diverse plants with specialized traits. We found that all simulated shrub sub-PFTs coexisted regardless of the landscape type, i.e. as well for all homogenous soil texture conditions as for the heterogeneous landscape. In the model, shrubs were dispersed scattered across the landscape,

i.e. many grid cells contained no shrubs. Our shrub sub-PFTs might not be different enough to outcompete any other present shrub. Therefore, in our setting the size of observation rather than the landscape heterogeneity determined the richness of woody plants. In contrast to highly diverse shrubs, all annual grasses were evaluated as absent in all landscape settings. The reason is that the mean total cover of annual grass over time was very low, since annual grass species appeared only in years with high rainfall in landscapes holding very low cover of perennial species.

Since neither shrub diversity nor annual grass diversity was affected by landscape heterogeneity or grazing intensity and MAP, the diversity effects that we will discuss in the next paragraphs are results of changes in perennial grass diversity.

Generally, landscapes with high precipitation led to higher coexistence of perennial grasses while those with high grazing decreased the diversity of perennial grasses, which is consistent with empirical findings (Busso et al., 2004; Adler and Levine, 2007). In addition, our results also clearly showed that the interactions between grazing intensity and precipitation modulated the effects of landscape heterogeneity. Perennial grass coexistence was higher in heterogeneous landscapes than in homogeneous landscapes under low grazing stress. On the other hand, at high grazing intensity heterogeneity did not facilitate a higher functional diversity. The reason for this contrasting effect of landscape heterogeneity under low and high grazing is, that high grazing strongly decreased total plant biomass and created more empty space for plants to colonize. Therefore, inter-specific competition decreased, and specialized plants did not benefit from landscape diversification. Generally, mean annual precipitation (MAP) influenced the impact of landscape heterogeneity on functional biodiversity less than grazing intensity. However, for the highest rainfall scenario with 600 mm MAP, landscape heterogeneity did not increase functional diversity, except for a comparison with sandy loamy soils. The reason might be that the difference in water stress under different soil texture conditions decreased (see also analyses on soil texture effects on water stress in Tietjen, 2016), because water availability was generally higher, except for more infiltration limited sandy loamy soils. Therefore, the landscape was perceived less heterogeneous by plants than under more arid conditions. In our simulations, we analyzed the rather sandy end of soil texture condition. We found highest diversity of perennial plants under loamy sandy and sandy conditions (for 500 mm MAP and low grazing) with 4 perennial sub-PFTs exclusively being present in the landscape with loamy sand (sand: 1 perennial sub-PFT) and only few perennial sub-PFTs present in the landscape with sandy loamy soil texture. Empirical findings from Australian tropical savannas showed similar effects of reduced infiltration at soils with finer grain size on plant diversity, where an

increase in soil clay content reduced woody species richness (Williams et al., 1996).

### 3.4.2 The response of ecosystem functioning to landscape heterogeneity

Generally, vegetation diversity has been found to increase ecosystem functioning across biomes such as grasslands (Tilman et al., 1997; Loreau et al., 2001) and drylands (Maestre et al., 2012). Our results showed a similar response in the change of two indicators of ecosystem functioning to landscape heterogeneity: for arid conditions and low grazing, landscape heterogeneity led to a higher community biomass. Arid landscapes are often characterized by strong facilitation among plants (Moustakas et al., 2013; Synodinos et al., 2015) leading to heterogeneous vegetation patterns with mosaics of bare patches and vegetated patches differing in their resource availability (Meron et al., 2004; Rietkerk et al., 2004). This has been found to increase net primary production, since water can be more efficiently used by plants (Ludwig et al., 1999). In our case, landscape heterogeneity in terms of soil texture seems to promote this aspect, since especially under dry conditions, total biomass is higher and can be sustained by less water losses. This mechanism seems to level off under less arid conditions, where competition plays a more important role. For MAP of 500 mm, we only found a significant increase in biomass for landscapes with high grazing intensity, i.e. for sites with low competition. For sites receiving more rainfall, landscape heterogeneity did not significantly increase biomass. For these more humid sites, we also found a very low effect of landscape heterogeneity on the number of coexisting sub-PFTs.

Although, we found an increase in plant biomass in response to landscape heterogeneity under arid conditions (400 mm), water losses by transpiration were lower. That is, a higher biomass was sustained by less water extraction. The reason might be that landscape heterogeneity facilitated the presence of drought-resistant plant types. These plant types can use water more efficiently and maintain the biomass of plant community (Guenni et al., 2002). For higher rainfall, we did not find any significant change in transpiration.

### 3.4.3 The role of landscape heterogeneity: spatial scale matters

Literature indicates that the relationship between landscape heterogeneity and plant diversity positively related to the spatial scale (Stein et al., 2014). Our simulation experiments show the same relationship, in our case for the Shannon index dependent on the scale of observation: the scale of observation even reversed the impact of landscape heterogeneity. While we found a negative effect of landscape heterogeneity on functional diversity at small scales ($< 10^3$ m$^2$), the effect turned positive at a larger scale. A large area containing heterogeneous soil conditions

includes more different soil texture, leading to a higher number of ecological niches, and random effects are less likely. For small areas, random effects are less important for homogeneous landscapes, leading to the higher functional diversity of these landscapes at small scales.

The change in functional diversity with increasing spatial scale was similar for all landscape settings: after a strong increase in diversity at a small scale the increase leveled off, which is well in agreement with the species-area relationship (Ibáñez et al., 2006). The reason is that a larger landscape includes diverse habitat types, such as patches with very low or very high plant cover. While patches with low cover favor fast growing and less competitive species, patches with high cover contain more species with a high competitive ability (Grime, 2001), leading overall to higher diversity.

### 3.4.4 Significance of understanding landscape heterogeneity

Landscape heterogeneity can play an essential role for plant biodiversity and ecosystem functioning in savannas. It can affect the demographical processes of plants e.g. seed dispersal and establishment, water-vegetation feedbacks and the response to grazing animals (Scoones, 1995; Breshears and Barnes, 1999; Maestre et al., 2003; Fortin et al., 2015). However, in savannas, the role of spatial heterogeneity in soil morphological conditions has mostly been disregarded (Zhou et al., 2017). Therefore a mechanistic understanding of the interactions of landscape heterogeneity with climatic conditions or land management is widely missing.

In this study, we systematically evaluated landscapes with homogeneous and heterogeneous conditions in their soil depth and soil texture. While our simulation layout was certainly somewhat artificial, our chosen range of settings well matches field conditions. For example, our maximal chosen difference in soil depth between patches does not exceed 400 mm as in (Fuhlendorf and Smeins, 1998). Rather sandy soils are quite typical for many savannas (Wilson and Witkowski, 1998; Bestelmeyer et al., 2011). Differences between neighboring patches might further determine spatial processes, which we did not explicitly evaluate in this study. For example, the dispersal distance of seeds from woody plant species has been found to be limited (Joubert et al., 2008), dependent on the suitability of the neighboring patch for establishment, this could strongly impact recruitment success of the woody vegetation.

### 3.5 Conclusion

Our results clearly show that landscape heterogeneity is an important factor driving savanna vegetation. It interacts with other factors such as precipitation and grazing that have received

more attention so far. Our approach of process-based modelling allows us to simulate a system multiple interaction drivers that simultaneously affect hydrological and vegetation processes. This further highlights the role of process-based models as a useful tool to study the complex savanna biome.

In addition, we could show that soil conditions in savannas and their spatial configuration can be essential, even at the local scale. Current threats to biodiversity and ecosystem service provision in savannas, such as reduced precipitation through climate change or overgrazing will leave some regions more vulnerable than others because of their predetermined environmental conditions. Thus to optimize conservation efforts we need to study which regions require more effort, respectively in which locations management interventions have the potential to succeed and where they may be overridden by the predetermined natural conditions.

### 3.6 Appendix 3.A

**Model rules**

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. In the hydrological sub-model daily soil moisture in two layers (upper: 0-20 cm; lower: 20-80 cm) is calculated (Tietjen et al., 2009). In addition to earlier versions of the model (Lohmann et al 2014 and earlier), we now separate 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 sub-model and a full description thereof can be found in Tietjen *et al.* (2009). In the vegetation sub-model biweekly growth of three plant functional types (PFTs), namely shrubs, perennial grasses and annual grasses, is calculated (Tietjen et al., 2010; Lohmann et al., 2012; Guo et al., 2016).

Two tables with the description, value and source of all model parameters are given for the hydrological (table A1) and the vegetation sub-model (table A2) respectively. Parameter and variable names directly relate to the description in Tietjen *et al.* (2009, 2010), Lohmann *et al.* (2012) and Guo *et al.* (2016).

**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 $\overline{(T}, T_{min} \text{ and } T_{\max})$ [°C] , extraterrestrial radiation ($R_a$) , slope ($sl$) and aspect effects ($af$) . The potential evapotranspiration function is (according to Tietjen et al., 2009):

$$ET_{pot} = 0.0023 * \left(\overline{T} + 17.8\right) * (T_{max} - T_{min})^{0.5} * R_a * af * \cos(sl) \qquad \text{Eq. 1}$$

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 ($ET_{L1} \text{ and } ET_{L2}$) using the volumetric soil moisture ($W_{Lx}$) [$m^3/m^3$] , stomata closing point, the cover of annual grasses, perennial grasses and shrubs ($c\_total_{ag}, c\_total_{pg}, c\_total_{s}$) and the cover of each sub-PFT ($c_{veg}$) (Tietjen, 2009). As in the version in 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 ($root_{veg,Lx}$). The calculation functions of surface, upper and lower actual evapotranspiration are (according to Tietjen et al., 2009):

$$ET_{surf} = ET_{pot} * (1 - 0.5 * \sum_{veg} c\_total_{veg}) \ [mm/d]$$

$$ET_{L1} = ET_{pot} * \left(\frac{W_{L1}}{wsc}\right)^2 * g_1 \ [mm/d]$$

$$g_1 = 1.2 - 0.2 * (\sum_{veg} c\_total_{veg}) \ [dimonsionless]$$

$$ET_{L2} = ET_{pot} * \left(\frac{W_{L2}}{wsc}\right)^2 * g_2 \ [mm/d]$$

with

$$g_2 = \sum_{veg\ in\ perennial\ grasses, shrubs} root_{veg,L2} * c_{veg} \ [dimensionless]$$

$$ET_{act} = ET_{surf} + ET_{L1} + ET_{L2} \ [mm/d] \qquad \text{Eq. 2}$$

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 ($T_{L1}/ET_{L1}$) 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 ($T_{L2}$).:

$$E = E_{L0} + E_{L1}$$
$$E_{L0} = ET_{surf}$$
$$T = T_{L1} + T_{L2}$$
$$ET_{L1} = T_{L1} + E_{L1}$$
$$\frac{T_{L1}}{ET_{L1}} = \begin{cases} 1.05 * c\_total - 0.04 & if\ c_{total} > 4\% \\ 0 & else \end{cases} \ [dimensionless]$$
$$ET_{L2} = T_{L2} \qquad \text{Eq. 3}$$

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. 4). The relative

uptake rate of each sub-PFT ($U_{veg,Lx}$) is calculated based on the potential water uptake rate per biomass ($\theta_{veg}$) [mm * yr⁻¹], vegetation cover ($c_{veg}$) and the fraction of roots ($root_{veg,Lx}$) in the respective layer.

$$U_{veg,Lx} = \frac{\theta_{veg} * root_{veg,Lx}}{\sum_{veg} \theta_{veg} * root_{veg,Lx} * c_{veg}} \ [dimensionless] \qquad \text{Eq. 4}$$

$$T_{veg,Lx} = T_{Lx} * c_{veg} * U_{veg,Lx} \ [mm/day] \qquad \text{Eq. 5}$$

**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. 6) is hereby based on a logistic behaviour and calculated separately for each 5m x 5m 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 ($c\_total_{\neg veg}$) 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. 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):

$$gr_{veg,Lx} = T_{veg} * r_{veg} * \left(1 - \frac{c\_total_{veg}}{cmax_{veg} - \left(c\_total_{\neg veg} * (1 - lap)\right)}\right) [yr^{-1}] \qquad \text{Eq. 6}$$

$$gr_{ag} = min\left(1 * avW_{ag,L1}, 1\right) * r_{ag} * \left(1 - c\_total_{pg} - c\_total_{s} * (1 - lap) - c\_total_{ag} - c_{mor}\right)[yr^{-1}]$$
$$\text{Eq. 7}$$

*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. 4) and depends on a drought mortality rate $mr_{veg}$, the average available water content in both soil layers during the growing season ($avW_{veg,Lx}$) and the relative water uptake rate ($U_{veg,Lx}$).

$$md_{veg,Lx} = mrd_{veg} * c_{veg} * \left[\left(1 - min(U_{veg,Lx} * avW_{veg,Lx}, 1)\right) * \frac{root_{veg,Lx}}{\sum_i root_{veg,Li}}\right] [yr^{-1}] \qquad \text{Eq. 8}$$

Second, we introduced stochastic age based mortality ($ma_s$) for woody plants, referring to empirical data on *Acacia mellifera* L. from a semi-arid savannah 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 $ScenAge$ age are completely cleared from woody vegetation with an annual probability ($mp_{age}$).

*Plant grazing*

To allow for different sub-PFTs within the meta-PFTs, we slightly revised the grazing algorithm developed by Lohmann *et al.* (2012). The changes in the grazing process were mainly implemented in two terms compared to earlier version.

First, we introduced a new grazing related functional trait to the description of our PFTs (grazing preference) to represent the palatability of each PFT (e.g. how much grazing ungulates would prefer this type relative to others). Thereafter we consolidated the calculation of the relative grazed biomass ($RGB_{veg}$) for each PFT instead of differentiating the grazing calculation between woody plants and grasses only. The relative grazed biomass of each PFT ($RGB_{type,veg}$) depends on the number of PFTs ($veg\_Nr$), the available edible biomass ($BMedible_{veg}$) and the grazing preference of each PFT ($GP_{veg}$). It means that a PFT with higher grazing preference and more available edible biomass is prone to be eaten by cattle.

The second amendment to the grazing algorithm refers to the inclusion of dead plant biomass. For annual grasses and perennial grasses, at the end of growing season of each year, green shoot biomass (alive biomass) is assumed to die and turn into standing dead biomass (reserve biomass). Shrubs were assumed to have no reserve biomass. In addition, we assumed a limited maximum fraction of the given biomass of each PFT to be available, because cattle cannot graze the biomass at the soil surface and not all parts of the different plants are edible. Further, there

is a fractional decay of reserve biomass from year to year according to a constant rate of decay ($Resbio\_L_{veg}$). We calculated the removal amount of reserve biomass and alive biomass by cattle based on the ratio of both biomass fractions in one cell.

$$RGB_{type,veg} = \frac{GP_{veg}}{\frac{\sum_{veg} GP_{veg}}{veg\_Nr}} * \left( \frac{BMedible_{type,veg}}{\sum_{type} \sum_{veg} BMedible_{type,veg}} \right) [dimensionless] \qquad \text{Eq. 9}$$

*Dispersal and seedling establishment*

Dispersal and establishment were simulated as addition to the cover of a respective growth form ($ds_{veg}$) to certain cells in the grid. This is rather representing seedling dispersal than seed dispersal. Germination and seedling/juvenile survival were 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 2 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 semi-arid 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 ($W_{L1,mean} > m_{est} * W_{wp,s}$). 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), we added a grazing dependent factor 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 ($distConst(SR)$) and the maximum dispersal distance ($distmax_s(SR)$).

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:

$$ds = c_{s\_source} * est_s * dist_0 * e^{-distConst(SR)*dist} * max(1 - c\_total_s - c\_total_{pg}; 0) \ [dimensionless]$$

Eq. 10

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 impact on the dispersal kernel is given by the following linear relation being a function of the stocking rate ($SR$):

$$distConst(SR) = dc_a + (dc_b * SR) \ [dimensionless]$$

Eq. 11

The maximum dispersal distance $distmax_s(SR)$ is calculated so that the added cover $ds$ is at least 1% of the maximum possible value of $ds$ at the center of the source cell ($dist = 0$).

## Model parameters

Table A1 Standard parameters and soil specific parameters in the hydrological sub-model (for further details see Tietjen et al., 2009)

| Name | Description | Value | Unit |
|---|---|---|---|
| $growStart$ | first day of growing season | 150 | d |
| $growEnd$ | last day of growing season | 330 | d |
| $depth_{L1}$ | depth of upper layer | 200 | mm |
| $depth_{L2}$ | depth of lower layer | 600 | mm |

*Sandy texture*

| Name | Description | Value | Unit |
|---|---|---|---|
| $rw$ | Residual water content during the dry season | 2.0 | vol% |
| $wsc$ | Water content at capillary pressure of 15 bar (-1500kpa) | 2.2 | vol% |
| $fc$ | Water content capillary pressure of 0.33 bar (-33kpa) | 11.2 | vol% |
| $S_f$ | Effective suction at wetting front | 49.5 | mm |
| $K_s$ | Saturated hydraulic conductivity | 235.6 | mm/h |

*Loamy sand texture*

| Name | Description | Value | Unit |
|---|---|---|---|
| $rw$ | Residual water content during the dry season | 3.5 | vol% |
| $wsc$ | Water content at capillary pressure of 15 bar (-1500kpa) | 4.1 | vol% |
| $fc$ | Water content capillary pressure of 0.33 bar (-33kpa) | 16.7 | vol% |
| $S_f$ | Effective suction at wetting front | 61.3 | mm |
| $K_s$ | Saturated hydraulic conductivity | 59.8 | mm/h |

*Sandy loam texture*

| Name | Description | Value | Unit |
|---|---|---|---|
| $rw$ | Residual water content during the dry season | 4.1 | vol% |
| $wsc$ | Water content at capillary pressure of 15 bar (-1500kpa) | 7.0 | vol% |
| $fc$ | Water content capillary pressure of 0.33 bar (-33kpa) | 27.0 | vol% |
| $S_f$ | Effective suction at wetting front | 110.1 | mm |
| $K_s$ | Saturated hydraulic conductivity | 21.8 | mm/h |

Table A2 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 | - |
| $\theta_{BM,pg}$ | relative uptake rate per perennial grass biomass | 0.9 | $mm\,(yr*g)^{-1}$ |
| $\theta_{BM,s}$ | relative uptake rate per shrub biomass | 0.5 | $mm\,(yr*g)^{-1}$ |
| $\theta_{BM,ag}$ | relative uptake rate per annual grass biomass | 0.2 | $mm\,(yr*g)^{-1}$ |
| $root_{pg,L1}$ | fraction of roots in the upper layer for perennial grass | 0.63 | - |
| $root_{s,L1}$ | 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 | $mm^{-1}*yr^{-1}$ |
| $r_s$ | 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 | $mm^{-1}*yr^{-1}$ |
| $cmax_{pg}$ | maximum cover for perennial grass | 1.0 | - |
| $cmax_s$ | maximum cover for shrub | 0.8 | - |
| $conv\_c\_bm_{pg}$ | biomass at 100% cover for perennial grass | $1.9*10^6$ | $g*ha^{-1}$ |
| $conv\_c\_bm_s$ | biomass at 100% cover for shrub | $2.1*10^7$ | $g*ha^{-1}$ |
| $conv\_c\_bm_{ag}$ | biomass at 100% cover for annual grass | $1.7*10^6$ | $g*ha^{-1}$ |
| $gLim_{pg}$ | non edible biomass fraction for perennial grass | 0.15 | - |
| $gLim_s$ | non edible biomass fraction for shrub | 0.9 | - |
| $gLim_{ag}$ | non edible biomass fraction for annual grass | 0.05 | - |
| $GP_{pg}$ | grazing preference for perennial grass | 1 | - |
| $GP_s$ | grazing preference for shrub | 0.3 | - |
| $GP_{ag}$ | 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 | $yr^{-1}$ |
| $m_{est,pg}$ | 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 | - |
| $dist_0$ | constant for exponential dispersal decline with distance for Shrub | 0.5 | - |
| $dc_a$ | 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 | - |

*Sandy texture*

| Name | Description | Value | Unit |
|---|---|---|---|
| $W_{wp,pg}$ | Specific wilting point for perennial grass | 2.1 | vol% |
| $W_{wp,s}$ | Specific wilting point for shrub | 2.1 | vol% |
| $W_{wp,ag}$ | Specific wilting point for annual grass | 2.1 | vol% |

*Loamy sand texture*

| Name | Description | Value | Unit |
|---|---|---|---|
| $W_{wp,pg}$ | Specific wilting point for perennial grass | 3.6 | vol% |
| $W_{wp,s}$ | Specific wilting point for shrub | 3.6 | vol% |
| $W_{wp,ag}$ | Specific wilting point for annual grass | 3.9 | vol% |

*Sandy loam texture*

| Name | Description | Value | Unit |
|---|---|---|---|
| $W_{wp,pg}$ | Specific wilting point for perennial grass | 5.2 | vol% |
| $W_{wp,s}$ | Specific wilting point for shrub | 5.2 | vol% |
| $W_{wp,ag}$ | Specific wilting point for annual grass | 5.4 | vol% |

**Landscape heterogeneity**

The whole simulated landscape is composed of 60 by 60 grid cells, and is separated into a "central zone" and a "marginal zone" (Fig A1). The marginal zone consists of 6 grid cells in each side. We used it to deal with border effect in processes that affect neighboring cells (e.g. seed dispersal, lateral water flow). The size of marginal zone is chosen to be too small for sub-PFTs to establish their seeds in this region. The central zone consists of 48 by 48 grid cells. In the central zone the spatial heterogeneity of soil properties is simulated. Heterogeneous

magnitude within the landscape is considered because vegetation processes take place at different spatial extents in the model EcoHyD. Growth and mortality of plants were calculated within each grid cell while processes, like seed dispersal and grazing, determined plant interactions across cells. Every homogeneous patch in the central zone is composed of 3 by 3 grid cells, and is randomly assigned with one soil texture and one soil depth. Therefore, the central zone was divided into 256 same-size homogeneous patches. We kept the soil properties of grid cells in the marginal zone identical with that of neighboring cells in the central zone.
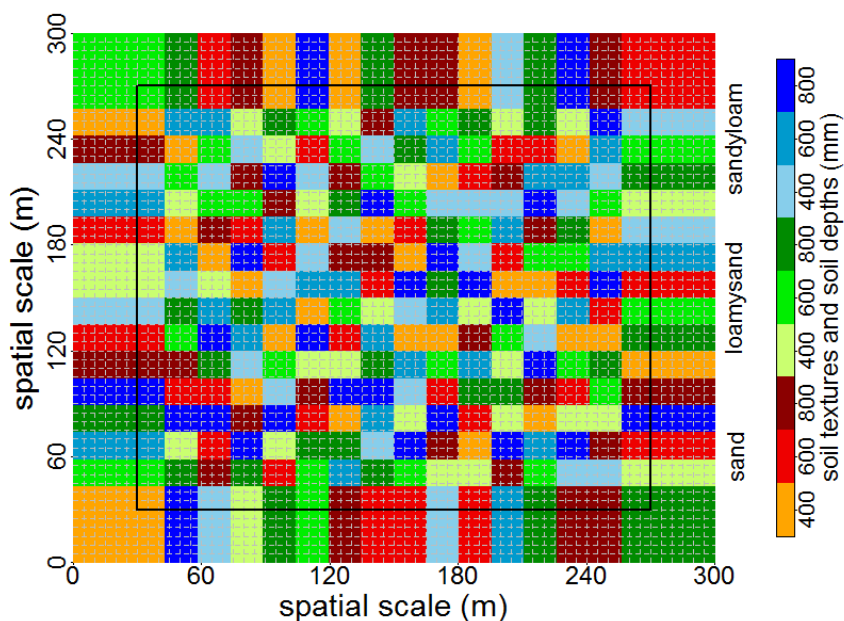


Fig A1 Spatial heterogeneity of soil properties within the landscape. The black solid line separates the landscape into central zone and marginal zone. Grey dashed line divides each patch into 3 by 3 cells

**Constructing the species pool**

We firstly constructed a species pool including all the qualified sub-PFTs. We implemented variability of seven traits for perennial grasses and shrubs. These traits are: growth rate, mortality rate, root distribution, dispersal fraction, water uptake rate per biomass, grazing preference and non-edible biomass fraction. In terms of annual grasses, it is assumed that roots exclusively distribute in the upper soil layer. Annual plants can grow rapidly after the first rain of the wet season and are omnipresent in savanna sites. Thus, the trait parameters root distribution and dispersal fraction were not considered in simulations of annual grass sub-PFTs. We used "trait indices" to represent variations of trait parameters based on their impacts on the vegetation cover of respective meta-PFTs. Positive values of the trait index mean that changes in one trait increase the vegetation cover of the meta-PFT, e.g., the index of increased growth rate was assigned "+1". In contrast the index was assigned "-1" in case the mortality rate

increases by +10%. We implemented the variability of all the selected trait parameters by changing the values ±10%. The protocol of constructing a new sub-PFT is that the sum of trait indices equals zero for each trait combination. Through this imposed trade-off we avoid the occurrence of super sub-PFTs that dominate all other sub-PFTs during the simulation.

## Trait distribution of optimal sub-plant functional types

Soil conditions are an important filter of plant traits. With respect to the optimal perennial plants, each trait showed different levels of variations across soil properties (Table A3). The traits such as root distribution and dispersal fraction were rather sensitive to the changes in soil conditions. In contrast, trait distribution slightly varied for the optimal annual plants.

Table A3 Varying range (%) of seven traits for the optimal perennial grasses, shrubs and annual grasses across soil properties

| Traits / PFT | growth rate r | mortality rate mrd | root distribution root | water uptake rate per biomass $\Theta$ | dispersal fraction e | grazing preference GP | non-edible biomass fraction gLim |
|---|---|---|---|---|---|---|---|
| perennial grasses | 1.4 ~ 6.6 | -2.0 ~ 3.0 | -6.0 ~ 5.0 | 1.0 ~ 7.4 | -7.4 ~ -1.8 | -0.2 ~ 2.2 | -6.4 ~ -1.8 |
| shrubs | 2.0 ~ 6.4 | -0.8 ~ 3.6 | -3.0 ~ 4.0 | -0.8 ~ 4.0 | -7.4 ~ 5.4 | -5.6 ~ -2.2 | -6.0 ~-0.6 |
| annual grasses | 8.6 ~ 8.8 | 0.4 ~ 0.8 | -- | -2.0 ~ -1.2 | -- | -5.0 ~ -4.2 | -3.4 ~ -2.6 |

## Distribution of sub-plant functional types in heterogeneous landscapes

We evaluated the occurrence of the optimal sub-PFTs within heterogeneous landscapes. The response of diversity of sub-PFTs to the sampled area is in line with the species - area curve (Fig A2). This curve assumes that species richness increases with an increasing spatial extent. Increment will slow down or level off when the given area is large enough (Ibáñez et al., 2006).
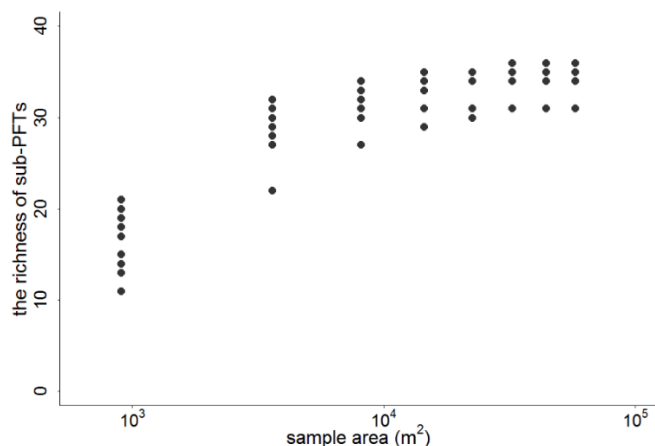
Fig A2 The relationship between the richness of sub-PFTs and the sampled area in heterogeneous landscapes under a mean annual precipitation of 500 mm and low grazing (5 LSU/100 ha). The richness was assessed based on the mean vegetation cover of respective sub-PFT during the year 50 - 100

The pattern of functional richness in a heterogeneous landscape did not obey a normal distribution ($p < 0.001$, Shapiro test) in the scenario of a MAP of 500 mm and low grazing (Fig A3). The vegetation pattern in the landscape was characterized by a diversity of sub-PFTs with different trait combinations. This simulation result is consistent with the findings on the distribution of phenological richness of perennial plants, which were studied in 10 m by 10 m quadrats in Venezuelan tropical savannas (Sarmiento, 1983).
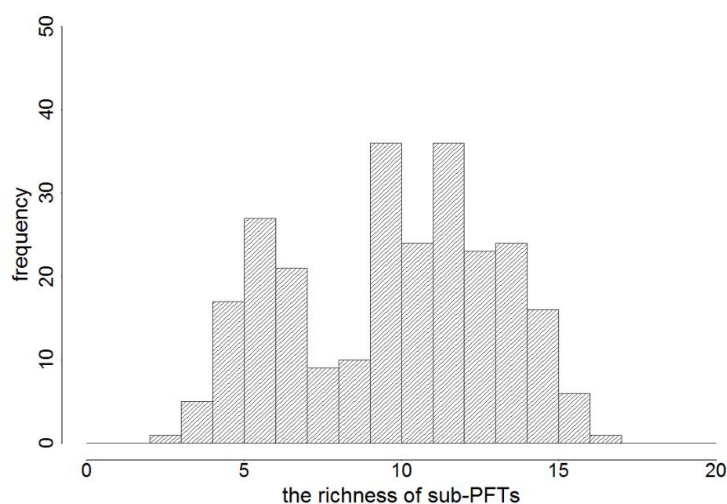


Fig A3 Distribution of functional richness per patch (3 by 3 grid cells, 15 m x 15 m) in a heterogeneous landscape during the year 50 - 100 in the scenario of a mean annual precipitation of 500 mm and low grazing

**Impact of soil depth on functional diversity**
We found that soil depth impacted the plant coexistence in the simulations only weakly. The number of coexisting sub-PFTs showed almost no change between soil depths in sandy and

sandy loam textured landscapes. and varied slightly in loamy sand textured landscapes along the gradient of soil depth (Fig A4).
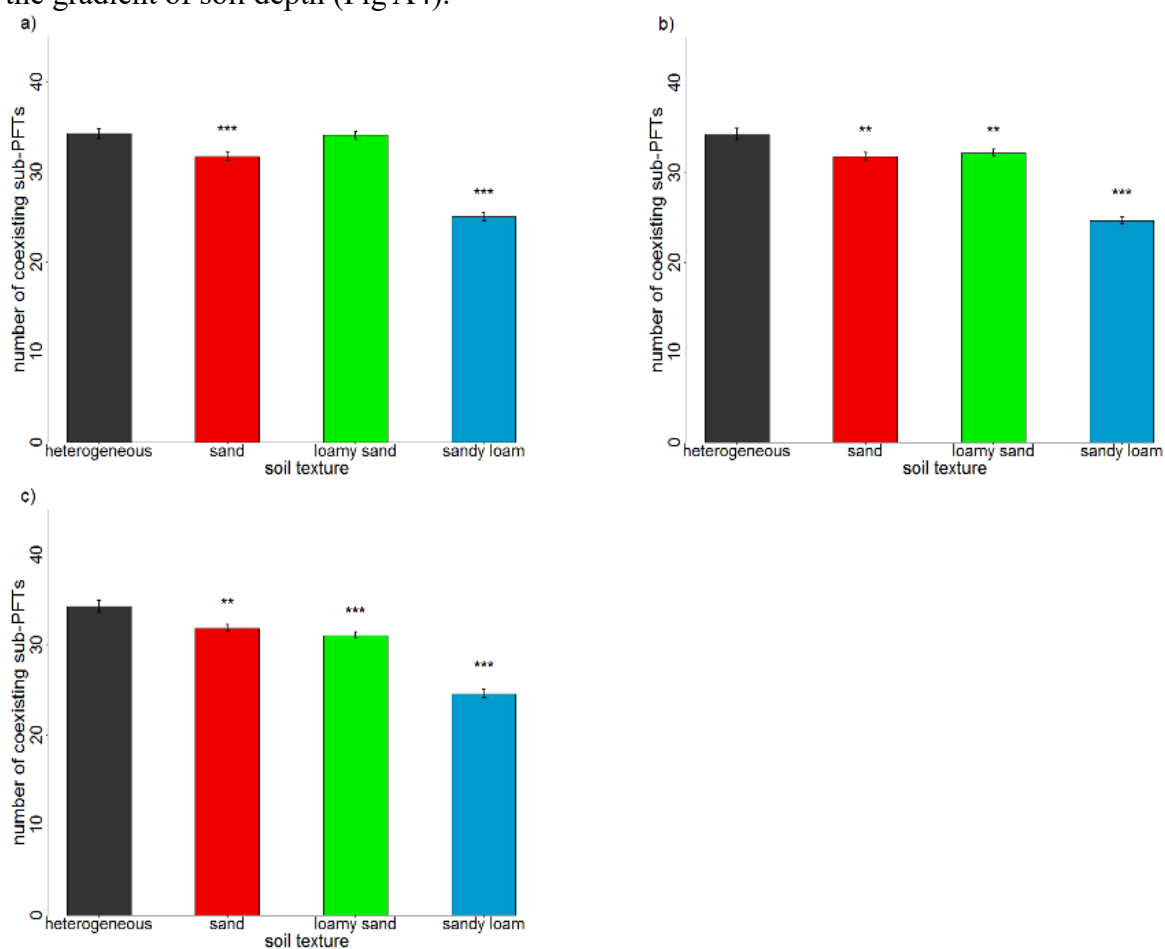


Fig A4 Number of coexisting sub-PFTs for homogeneous and heterogeneous landscapes in three soil depths. For soil depths 400 mm (a), 600 mm (b) and 800 mm (c), the number of coexisting sub-PFTs is shown for the scenario of a mean annual precipitation of 500 mm and low grazing. Results refer to 15 model replicates (three landscape replicates * five precipitation replicates) during the year 50-100. Asterisks indicate significance level of the Wilcoxon signed rank test (***: < 0.001; **: < 0.01; *: < 0.05; n.s.: > 0.05).

# Chapter 4

# General discussion

My PhD thesis focuses on how vegetation functional diversity and the most important drivers precipitation, grazing and soil heterogeneity affect vegetation composition and ecosystem functioning in semi-arid savannas. To investigate this, I first incorporated trait heterogeneity within the broad plant functional type (PFT) perennial grass into the ecohydrological savanna model EcoHyD (Tietjen et al., 2009; Tietjen et al., 2010; Lohmann et al., 2012) and assessed the effect of increased trait heterogeneity on ecosystem functioning for different combinations of annual precipitation and grazing intensity (see chapter 1). The main result is that diversification of perennial grasses generally increases the total vegetation cover and the water use efficiency of the plant community. However, besides the functional variability within perennial grasses (Busso et al., 2001), many empirical studies have shown that there is functional variability also within woody plants and annual grasses in savanna ecosystems (Kos and Poschlod, 2010; Batalha et al., 2011) and that this variability and thus the trait distribution of the plant community varies depending on environmental conditions (Díaz et al., 2007; Sandel et al., 2010; Harzé et al., 2016). In a second step, I therefore simulated functional trait diversity of three broad PFTs (also called meta-PFTs), namely shrubs, perennial and annual grasses under different precipitation and grazing conditions (see chapter 2). Simulation results indicate that annual precipitation markedly leads to shifts in the functional composition of the respective meta-PFTs at the trait level. In contrast, grazing causes a compositional change at the community level characterized by shifts between grass- and woody-dominated communities. Besides the variability of annual precipitation and different grazing intensities in semi-arid savannas, the landscapes in this biome are characterized by locally heterogeneous soil conditions (Williams et al., 1996; Fuhlendorf and Smeins, 1998; Zhou et al., 2017). In a last step, I therefore assessed the combined effects of landscape heterogeneity in terms of physical soil properties, precipitation and grazing on vegetation functional diversity and ecosystem functioning (see chapter 3). Landscape soil heterogeneity allows for a higher functional diversity under low grazing and less moist conditions. However, at a higher grazing intensity this positive effect was not present. Further, the effects of landscape heterogeneity on ecosystem functioning in terms of community level biomass and transpiration are dependent on mean annual precipitation and grazing intensity.

In the following, I will first discuss how functional trait compositions shift along gradients of annual precipitation and grazing intensity in semi-arid savanna ecosystems (see 4.1). Afterwards, I will shift the focus from the analysis of the vegetation composition to that of vegetation diversity. In particular, I will demonstrate how functional diversity is affected by heterogeneous landscapes under different environmental conditions and at different spatial extents (see 4.2). Further, I will discuss the effects of vegetation diversity and environmental conditions on ecosystem functioning (see 4.3). In addition, I will discuss the possible limitations of model simulations in terms of trait variability and give an outlook on how future research in this field could be continued (see 4.4). Finally, I will draw several conclusions from the overall findings of my thesis with respect to vegetation composition and diversity in semi-arid savannas (see 4.5).

## 4.1 Shifts of vegetation composition along environmental gradients

The results presented in this thesis indicate that both community level composition and functional trait composition are largely affected by different precipitation and grazing regimes (see chapter 1 and 2). Plant traits can be deemed as a functional link between vegetation composition and environmental impacts (Lavorel and Garnier, 2002). Thus, the response of individual plants or plant communities to different environmental conditions can be quantified by key plant traits.

Simulation results of this thesis indicate that grazing leads to a shift in the composition of perennial grasses (chapter 1). Specifically, fast-growing and short-lived sub-type dominates the perennial grass community under high grazing intensity, while low grazing intensity leads to a dominance of highly palatable and fast-growing perennial grass sub-type. Fast-growing plants might be dominant under grazing since they are able to rapidly recover their organs after grazing disturbances. This result suggests that a stronger resistance to grazing (in terms of palatability) is needed for plants in a highly grazed environment, while maintenance of plant coverage (in terms of longevity) is important under low grazing disturbance.

Increased mean annual precipitation (MAP) reduces the magnitude of grazing-induced shifts in perennial grass sub-types. Under higher precipitation, perennial grass sub-types can compensate biomass losses due to grazing, which may therefore dampen the negative effect of grazing on the perennial grass community.

In chapter 1, I used the meta-PFT perennial grass as a starting point to assess the compositional change within the PFT level along environmental gradients. The results demonstrate that different environmental conditions not only affect the abundance of each perennial grass sub-type in the community, but cause a shift in the composition by eliminating poorly performing perennial grass sub-types and allowing the dominance of well adapted ones. This proves filtering effects of the environment on plant traits (Diaz et al., 1998; Venn et al., 2011).

Besides the trait variability within perennial grasses, two additional important meta-PFTs, i.e. shrubs and annual grasses, also occur in a high functional variability in semi-arid savannas. Therefore, it was important to assess the functional trait composition of all three meta-PFTs for different environmental conditions. I therefore simulated the trait variability within three meta-PFTs, namely shrub, perennial and annual grasses, to evaluate variations of functional composition along the gradients of MAP and grazing intensity (chapter 2). I accounted for the variability of key plant traits such as growth rate, mortality rate, water uptake rate, seed dispersal, establishment, and grazing defense, all of which can be attributed to specific vegetation functions for given meta-PFTs such as resource utilization, recolonization and resistance to disturbance. The simulated results indicate that the importance of these selected traits differs among the meta-PFTs. Perennial plants gain higher competitiveness through balancing several plant traits, while the competitiveness of annual plants is determined by the performance of a single trait, i.e. the "growth rate". This result is consistent with empirical findings which are showing that there are large functional differences between annual and perennial plant species in terms of leaf, root and water use efficiencies (Callaway et al., 2003; Roumet et al., 2006). Specifically, I found that a large growth rate leads to a disproportionately positive effect on dominant annual grasses compared to other selected traits. That is, dominant annual plants foster their opportunistic life-history strategy by maximizing their growth rate. In addition, this plant strategy is even more pronounced under dry and heavily grazed conditions. Under these conditions, dominant perennial grasses invest in the growth and the water uptake rate, but do not invest much energy into seed dispersal and into the non-edible biomass fraction. The harsh environmental conditions lead to a high rate of defoliation, which drives plants to increase the biomass production through a faster growth rate and a more efficient water-use to guarantee their survival. In contrast, seed establishment is mostly limited by aridity, even though increased grazing animals could facilitate the dispersal of plant seeds (Bakker et al., 1996). In addition, the conservative strategy, such as a

stronger grazing defense, seems not important to strengthen the competitiveness of perennial grasses under the harsh environmental conditions. The environmental impacts on the functional composition of woody plants differ from that of grasses. For shrubs, a higher seed establishment rate is important under moist conditions to overcome their recruitment bottleneck (Joubert et al., 2008). Under arid conditions, however, the recruitment success is mostly constrained by soil moisture. Since the overall vegetation cover is relatively low under highly grazed conditions, and therefore grazing animals also have to feed on woody plants to survive, dominant shrubs are characterized by higher non-edible biomass under these conditions. In addition, woody plants were found to obtain the water in deeper soil layers and not to invest much energy to use less available water in the top soil layers in a very arid environment, which matches the expectations of the woody plant strategy in terms of coping with water stress (Eagleson and Segarra, 1985). These differences in functional composition for the respective meta-PFTs indicate altered plant strategies in different environmental conditions. Plant species in savannas were found to resist the risk of environmental stress in different ways, due to e.g., tussocks or a decumbent canopy (to resist grazing disturbances); smaller leaves (to decrease transpiration); longer roots (to better compete for water), less branches (to decrease respiration) (Yakubu, 2011). To sum it up, the functional composition of savanna vegetation is driven by environmental conditions.

Most traits of the dominant meta-PFTs are more sensitive to MAP than grazing intensity (chapter 2). That is, the functional trait composition tends to show a shift along the gradient of MAP. Moreover, this shift is stronger when MAP is more than 500 mm. This might be attributed to a greater abundance of woody plants that are highly defensive to grazing disturbance under moist conditions. In contrast, under drier conditions (MAP < 500 mm), grazing leads to a shift in the functional trait composition of dominant meta-PFTs. This result is consistent with findings from the literature that emphasize convergent effects of aridity and grazing on the vegetation functional composition (Milchunas et al., 1988; Quiroga et al., 2010). However, I found that the response of vegetation composition to precipitation and grazing differs at the trait and the community level (chapter 2). Grazing causes a compositional change at the community level between grass- and woody-dominated communities. This grazing-induced change is often irreversible without external forces on savanna systems (Brown and Archer, 1999). The contrasting effect between precipitation and grazing helps to quantify vegetation compositional changes at different ecological levels.

**4.2 Functional diversity in heterogeneous environment**

Variability of annual precipitation and different grazing intensities alter the trait composition and the community composition of savanna vegetation (see chapter 1 and 2). The functional composition of the plant community is closely associated with functional diversity (Lavorel and Garnier, 2002). The trait variability implemented in chapter 1 and 2 is a solid basis towards a sound representation of functional diversity in the plant community. I thus simulated a functionally diverse plant community in chapter 3 and investigated its response to landscape soil heterogeneity.

One main result is that landscape soil heterogeneity in comparison to homogeneous landscapes allows for a higher plant coexistence (as a form of functional diversity) at low grazing intensities but this effect is not present under high grazing stress (chapter 3). High grazing intensity decreases the total vegetation cover and thereby promotes plant colonization success due to less competition. This intensive grazing effect may suppress the effect of soil heterogeneity on vegetation diversity. In addition, for highly grazed plant communities there is usually a high shrub cover which in turn tends to decrease plant diversity (Price and Morgan, 2008). However, under low grazing intensity and lower MAP of 400 mm, landscape heterogeneity only slightly increases plant diversity, whereas under low grazing and higher MAP of 600 mm there is even no positive effect of landscape heterogeneity on diversity. If I assume the MAP of 500 mm as an intermediate condition, the simulated results might satisfy the expectations of the intermediate disturbance theory (Shea et al., 2004). In contrast, empirical studies discussed the relationship between plant species diversity and environmental heterogeneity in fields less disturbed by grazing livestock (Lundholm, 2009). This might lead to a biased prediction towards a generally positive effect of environmental heterogeneity. In addition, several empirical studies reported that there was no effect of soil resource heterogeneity on plant species diversity (Wijesinghe et al., 2005; Reynolds et al., 2007a). The simulated results help to understand how landscape soil heterogeneity impacts functional diversity across a broad range of disturbance and stress. In addition, the effects of landscape heterogeneity on functional diversity are often dependent on the spatial scale (Stein et al., 2014).

Landscape soil heterogeneity leads to a higher functional diversity in larger areas compared to homogeneous landscapes (in chapter 3). Diverse habitats increase the number of ecological niches and thus larger landscape areas can contain a higher number of plant species (Stein et

al., 2014). In contrast, this positive feedback was not observed at small spatial scales, where sampling effect largely influenced the community composition (chapter 3), as less abundant plant types have a lower probability to be present in smaller plant communities. In addition, not only a mixture of different soil properties leads to variations of functional diversity, but differences of individual soil parameters cause diversity changes. In particular, soil texture, rather than soil depth, significantly affects plant coexistence in semi-arid savannas (chapter 3). Soil texture determines the particle size within soils and various soil hydraulic parameters such as porosity, hydraulic conductivity and soil matric potential, and thus affects plant behaviors in many ways (Maidment, 1993). Sandy loam textured landscapes are consistently characterized by a low functional diversity compared to sandy and loamy sand textured landscapes (chapter 3). For sandy loam textured soils, the smaller particle size leads to a condensed soil porosity and water is mostly stored in the shallow soils (Fernandez-Illescas et al., 2001). The reason for the weak impact of soil depth might be that I exclusively changed the soil depth in the lower layer throughout the simulations. In the lower layer, the relative soil moisture was generally lower than in the upper layer. In addition, the root density of plants was also lower. Thus, changing soil depth did not affect the plant access to soil water.

To sum it up, heterogeneous soil properties drive the vegetation functional diversity in semi-arid savannas. This effect is modulated by different precipitation and grazing regimes. Knowledge of environmental conditions is thus critical to predict the vegetation diversity. Functional diversity, as an emergent property of an ecosystem, is crucial in determining ecosystem functioning (Diaz and Cabido, 2001; Hooper et al., 2005).

## 4.3 The role of functional diversity and environmental conditions for ecosystem functioning

Changes in vegetation functional diversity can alter the manners in which ecosystems work, as these changes may lead to occurrences or losses of some key plant types (Naeem et al., 1999). Ecosystem functioning can be measured by the processes such as plant productivity and water flux rate (Hooper et al., 2005). The relationship between functional diversity and ecosystem functioning has been mostly investigated in grasslands across a broad range of disturbances and stress (Tilman et al., 1997; Loreau et al., 2001; Hooper et al., 2005). These studies consistently found that increased functional diversity increases plant biomass. However, this relationship was less reported in semi-arid savannas. I therefore gave a simple

case for analyzing the effects of increased perennial grass diversity on the functioning of the plant community in savanna ecosystems (chapter 1). The simulated results indicate that increased trait heterogeneity within the meta-PFT perennial grass increases total vegetation cover of the plant community (in particular of perennial grasses). This therefore facilitates the food provision to grazers as an important ecosystem service in the savanna biome, as perennial grasses are a main source of forage for grazing animals (Sarmiento, 1992). Further, the diversification of perennial grasses generally increases the total water use efficiency of the plant community. To sum it up, the relationship between functional diversity and ecosystem functioning in the semi-arid savanna found in my study is in accordance with the findings from grassland ecosystems.

The leading mechanism promoting ecosystem functioning is that higher functional diversity is often linked to a larger probability that the ecosystem will include key plant types maintaining essential functions (Hooper et al., 2005). In addition, key plant types are typically the most abundant plants which in their functioning are characteristic for a given plant community (Grime, 1998). I found that the perennial grass community is always dominated by one perennial grass sub-type (chapter 1). Inclusion of those dominant perennial grass sub-types may lead to an increased total vegetation cover. This strengthens the community level transpiration and thus the water use efficiency.

Another mechanism is that complementary effects between plant types are thought to buffer the environmental stress or disturbance on ecosystem functioning (Hooper et al., 2005). The simulated fast-growing perennial grass sub-type is assumed to rapidly utilize available soil water, while the simulated less palatable perennial grass sub-type is assumed to strongly resist grazing disturbance (chapter 1). These complementary plant strategies in coping with drought stress and land use might promote the ecosystem functioning, in particular in a temporally and spatially variable environment.

Precipitation and grazing intensity, however, modulate the driving effect of trait heterogeneity of perennial grasses on ecosystem functioning in savannas (chapter 1). Under arid and highly grazed conditions, the positive effect of perennial grass diversity on ecosystem functioning is more clear. This might be attributed to a strong selection effect of aridity and grazing on the specific perennial grass sub-types. This strengthens the proportion of dominant perennial grass sub-types in the plant community and thus the role of those dominant sub-types for the community functioning. However, increasing annual precipitation and decreased grazing

intensity dampen this effect. Since vegetation cover of respective perennial grass sub-PFT is relatively high under moist and less grazing-disturbed conditions. To a certain extent this weakens the filtering effect of environmental conditions on the perennial grass community.

I also found that under high grazing intensities, shrub PFTs tend to become more dominant in the plant community (chapter 1 and 2), owing to a considerable reduction of perennial grass biomass induced by grazing animals. In addition, high grazing intensity causes a loss of total vegetation cover under lower precipitation (chapter 1). This will lead to an increased risk of soil erosion due to the generation of low cover patches and changes in plant productivity and water fluxes (Eldridge et al., 2011). Moreover, I observed that the diversification of perennial grasses slightly decreases the cover of shrubs because of an increased perennial grass cover (chapter 1). However, this effect of diverse perennial grasses does not change the shrub dominated state in the community under high grazing intensity. That is, the abundance or the biomass of perennial grasses is not resilient through increased functional diversity.

The effects of environmental conditions on ecosystem functioning are further demonstrated by the patterns of functional trait composition for the respective meta-PFTs (chapter 2). Plant functional traits can reflect vegetation functions in the community and ultimately indicate variations of ecosystem functioning (Diaz and Cabido, 2001; Violle et al., 2007). For example, growth rate is directly linked to plant production; water uptake rate can determine how much water is transpired by plants. Thus, assessing which values of plant functional traits are present in a given environment is important to better understand the changes in ecosystem functions. I found that growth rate is extremely important for the competitiveness of annual grasses. Traits like growth rate and water uptake rate have a strong effect on dominant perennial grasses in a very arid and highly grazed environment. Those both traits are also important for the competitiveness of shrubs when MAP is less than 500 mm (chapter 2). These simulated results suggest that a rapid and efficient growth in biomass is an insurance for plant survival in a highly stressed environment.

In addition to the effects of precipitation and grazing intensity, the savanna ecosystem functioning is also driven by landscape soil heterogeneity (chapter 3). I even found that the effects of landscape heterogeneity on the community biomass and transpiration are modulated by mean annual precipitation and grazing intensity. Under a MAP of 400 mm and low grazing, landscape heterogeneity leads to a higher community biomass. Landscapes with lower precipitation are often characterized by strong plant facilitations (Synodinos et al.,

2015). This leads to heterogeneous vegetation patterns with mosaics of bare patches and vegetated patches differing in their resource availability (Rietkerk et al., 2004). This has been found to increase plant production owing to a more efficient water use by plants (Ludwig et al., 1999). In contrast, under arid environments (400 mm), plant transpiration of the community was found to decrease in heterogeneous landscapes. The reason might be drought-resistant plant types have a higher possibility to be present in heterogeneous landscapes compared to homogeneous landscapes. For higher rainfall, I did not observe significantly heterogeneity-induced changes in community biomass and transpiration.

In summary, variations of vegetation functional diversity lead to changes in the functioning of semi-arid savannas. The changes in ecosystem functions can be furthered quantified by the patterns of functional trait composition. In addition, assessing environmental impacts allows for a profound understanding of plant level response and system-level response. This helps to understand mechanisms of vegetation functional diversity. Until now, I made a thorough analysis of the simulated results throughout three chapters. An assessment of model implementations for realizing these results is very helpful for future simulation studies on functional diversity.

## 4.4 Assessment of simulations on trait variability and future studies

Generally, a model diagnosis is a helpful step towards a better understanding of the underlying simulation aim. Here, I will focus on the analysis of simulations on trait variability in the vegetation module of the model EcoHyD. The methodology of incorporating trait variability within PFT level into the model indicates that constructing new sub-PFTs with trait trade-offs allows us to reproduce a relatively realistic functional diversity of plant communities. However, less dynamic vegetation models explicitly describe the functional diversity using the concept of trade-offs between traits (Pavlick et al., 2013; Sakschewski et al., 2016). I thus incorporated two trade-offs to diversify the meta-PFT perennial grass: i.e. (1) growth versus mortality; (2) grazing resistance versus regrowth (chapter 1). I used a relatively unstressed environmental scenario with a MAP of 500 mm and a grazing intensity of 5 LSU/100 ha to calibrate the trade-offs as drought or high grazing intensity might lead to an overexpression of the selected traits. For instance, the growth and the mortality rate are dependent on the available soil water. There are other typical trait trade-offs for savanna plants. For example, the trade-off between seed size and seed amount is important to

understand plant dispersal and establishment in drought periods (Veenendaal et al., 1996). However, these related traits are not fully involved in the model. In addition, I calibrated both terms of trade-offs based on comparisons with the original perennial grass type in the model to avoid the occurrence of super plant types (chapter 1). I did not use field data to implement the trade-offs within the new sub-PFTs but generated the trait variability of those sub-PFTs through the model itself (chapter 1, 2 and 3). The advantage of simulating trait variability in this way helps to simulate the single trait independently without explicitly considering dependent relationships among traits. Vegetation functional diversity is not only characterized by the trait variability, but is also determined by interactive effects between newly-constructed sub-PFTs. The simulated number of sub-PFTs is an important factor determining the plant interactions. I only simulated a moderate amount of plants in each 5 m by 5 m grid cell to present a functionally diverse but still – in terms of plant quantity – realistic plant community (see chapter 1, 2 and 3). Overall, the simulated trait variability in its current state is very useful to address diversity-related questions. It is helpful to strengthen the simulations of trait variability to improve predictions of vegetation diversity and ecosystem functioning in savanna ecosystems.

In future, simulating trait diversity through single trait plasticity may be a promising extension of the vegetation module of the model EcoHyD. For instance, seasonality might be an important factor influencing the trait plasticity in water-limited ecosystems. For example, root biomass showed a higher plasticity between wet and dry seasons as "buffer against water crisis" (Couso and Fernandez, 2012). However, the plasticity is usually not so important if plant traits are strongly filtered by environmental variables under less-stressed conditions (Siefert, 2012). It could also be important to answer at which spatial or temporal scales trait plasticity occurs to better quantify trait diversity in vegetation models. In addition, not all functional traits are very plastic to environmental stress or disturbance in arid and semi-arid regions (Couso and Fernandez, 2012). Therefore, it would be helpful to only simulate the plasticity of key plant functional traits. Besides generating the trait variability from the current model processes, an extension by new modules into the model can lead to a generation of more functional traits and help to simulate trait trade-offs in a more diverse way. For example, cycling processes of nutrients such as carbon and nitrogen, are not yet considered in the model. Although the present model can be deemed as a useful tool to simulate vegetation functional diversity and its effects, I am looking forward to further improvements and extensions for the model.

**4.5 Conclusion**

In this thesis, I assessed via a modelling approach the effects of vegetation functional diversity on ecosystem functioning, as well as the effects of precipitation, land use and landscape heterogeneity on vegetation diversity and ecosystem functioning in semi-arid savannas.

The functional diversity was presented by simulating the trait variability within broad plant functional types (woody and herbaceous plants) in savannas and was implemented by trade-offs among specific traits. In addition, I simulated different environmental conditions and evaluated independent or interactive effects of different drivers. Through this, the vegetation composition and the ecosystem functioning can be better assessed. Key results of this thesis can be summarized as follows:

- Simulations of trait variability in dynamic vegetation models help to quantify the vegetation composition and ecosystem processes. The diversification within the broad plant functional types promotes ecosystem functioning and leads to a more precise prediction of shifts in vegetation composition. Approaches to quantify trait variability within PFTs deserve further attention.

- Precipitation in interaction with grazing affects the vegetation composition in semi-arid savannas. Precipitation causes compositional changes at the trait level, while grazing leads to a transition of vegetation state at the community level. Accounting for trait variability allows a multitude of responses that ecosystems show in response to multi-dimensional environmental gradients.

- Landscape soil heterogeneity drives vegetation functional diversity. However, this effect is modulated by grazing and annual precipitation. Those two drivers also modulate the impact of landscape heterogeneity on ecosystem functioning. Current threats to vegetation diversity and the provision of ecosystem service in savannas, such as extreme drought through climate change, overgrazing or landscape fragmentation will leave some regions more vulnerable than others. Thus it needs more efforts to optimize landscape management for conserving the biodiversity in these regions.

# Summary

Savanna ecosystems cover approximately 20% of the global land surface and account for 30% of the terrestrial net primary production. Thus, they form integral parts of global cycles such as those for water and carbon. The savanna biome comprises a heterogeneous suite of local soil conditions, as well as a diverse vegetation composition, both of which are key determinants of savanna ecosystem functioning. Its vegetation is characterized by a mixture of woody and herbaceous plants. The relative share of each functional type in the total vegetation cover is thereby determined by a set of environmental and land use factors such as precipitation or grazing. Due to global change, savanna ecosystems are faced with increasing levels of drought and heavy degradation, both of which can alter vegetation composition and biodiversity and ultimately ecosystem functioning. The so-called shrub encroachment represents a particular form of degradation which is common to many savanna ecosystems and manifests in a gradual replacement of the grass components by shrubs and woody plants in general. To which degree the drivers of change such as precipitation regime and grazing intensity affect a given savanna ecosystem, however, depends on local soil conditions as well. Hence, a holistic understanding of savanna ecosystems is required to qualify and quantify the causes and consequences of biodiversity and environmental variations. This will ultimately help to assess variations of ecosystem functioning in semi-arid savannas.

In my thesis, I aim at enhancing this understanding by using a spatially explicit savanna simulation model. I extended an ecohydrological savanna model to simulate vegetation diversity and its response to different precipitation and grazing scenarios, as well as its effect on ecosystem functioning. The model uses the plant functional type (PFT) concept instead of discrete plant species to represent plant assemblies. Each PFT is characterized by its unique combination of functional traits. Thus, vegetation diversity is explicitly modelled as functional diversity of the broad herbaceous and woody plant types. Hence, the aim of this work is to find relationships between functional diversity and ecosystem functioning in semi-arid savannas. Environmental conditions are simulated by different scenarios of mean annual precipitation, grazing intensity, and soil properties. I assess the effects of simulated environmental conditions on the functional composition of savanna vegetation and ecosystem functioning, as well as their interrelations. Based on the simulation results, I identify the response of savanna vegetation to environmental drivers at the community and the trait level, as well as the hierarchical levels of the environmental effects in semi-arid savannas.

In the general introduction to this thesis, environmental conditions and vegetation functional diversity in savanna ecosystems are introduced. With a focus on simulating vegetation diversity, I address the role of plant functional traits in describing the vegetation response to different environmental conditions. In particular, I introduce concepts by which the functional composition and diversity of the plant community can be used as a means for assessing environmental effects on ecosystem functioning.

The simulations in chapter 1 reveal that trait diversity within the broad PFT level strongly affects vegetation composition and ecosystem functioning. As a starting point, I analyzed the community level effects of trait variability within the broad PFT perennial grass on ecosystem functioning. The results show that the functional composition of perennial grasses is strongly affected by grazing intensity while mean annual precipitation moderates those effects. Increasing the functional diversity of perennial grasses generally increases total vegetation cover and water use efficiency of the plant community. This result underlines the positive effect of functional diversity on ecosystem functioning, which is in line with observations of empirical studies. Increasing the perennial grass diversity proves to have a negative effect on shrub cover, nevertheless, the patterns of land degradation associated with encroachment of woody plants still remain observable.

To gain deeper insights into the functional response of savanna vegetation to changes in mean annual precipitation and grazing intensity at the trait level, in chapter 2 each single broad PFT (perennial grasses, annual grasses and shrubs) was subdivided into sub-PFTs, each of which was characterized by its suit of traits. The relative importance of the traits for granting the competitiveness for the respective broad PFT differ largely. The effect of most plant traits on the fate of a given broad PFT is more strongly affected by changes in precipitation than by changes in grazing intensity. In contrast, grazing intensity rather than precipitation causes a compositional change at the community level between grass- and woody-dominated communities. Such findings underline the differential importance of environmental conditions on the trait as well as on the community level.

Apart from their heterogeneous functional vegetation composition, savanna landscapes are characterized by spatially heterogeneous soil conditions, which are addressed by chapter 3. I found that heterogeneous soil landscapes can have positive effects on the functional diversity of their respective plant communities. This result is in line with empirical studies which show that landscape heterogeneity can promote vegetation functional diversity. However, I found

that this positive effect of landscape heterogeneity on functional diversity is inconsistent in different scenarios of mean annual precipitation and grazing intensity. Landscape heterogeneity allows for a higher functional diversity under low grazing stress, while the positive effect induced by heterogeneous landscapes could not be found at high grazing intensity. Furthermore, the effects of landscape heterogeneity on community level biomass and transpiration are also modulated by mean annual precipitation and grazing intensity.

From the overall results of the simulation experiments, the importance of functional trait variability as well as environmental heterogeneity for vegetation simulation models becomes evident. The differential effects of functional diversity under different environmental conditions which were found in this thesis further underline this importance. This is particularly true given a predicted change both in land use and climatic conditions for the upcoming decades. Moreover, spatially heterogeneous soil conditions are found to have different effects on vegetation functional diversity depending on the underlying environmental scenario. Hence, I recommend a strengthening of research efforts into developing ecosystem models which are capable of accounting for changes in environmental conditions as well as functional diversity.

# Zusammenfassung

Savannenökosysteme bedecken ca. 20% der Landoberfläche der Erde und machen 30% der weltweiten terrestrischen Nettoprimärproduktion aus. Sie sind damit ein wesentlicher Bestandteil verschiedener globaler Stoffkreisläufe wie beispielsweise jenen von Wasser und Kohlenstoff. Das Savannenbiom zeichnet sich durch eine heterogene Verteilung lokaler Bodenbedingungen sowie Vegetationszusammensetzung aus, was beides Schlüsselkomponenten für die Funktionsweise dieser Ökosysteme sind. Die charakteristische Vegetation ist aus holzigen und krautigen Pflanzen zusammengesetzt. Das relative Verhältnis dieser jeweiligen funktionellen Pflanzengruppen bezogen auf die gesamte Vegetationsbedeckung wird dabei von verschiedenen Umwelt- und Landnutzungsfaktoren wie z.B. Niederschlag und Beweidung bestimmt. Aufgrund des globalen Wandels sind Savannenökosysteme einer zunehmenden Trockenheit sowie starker Degradierung ausgesetzt. Dies beeinflusst die Vegetationszusammensetzung und Biodiversität und kann in der Konsequenz die Funktionsweise des Ökosystems verändern. Die sogenannte Verbuschung ist dabei eine in Savannen weit verbreitete Form der Degradierung und zeigt sich in einem sukzessiven Austausch der Grasvegetation durch Büsche und andere holzige Gewächse. Die Einflüsse von Faktoren wie beispielsweise des Niederschlagsregimes oder der Beweidungsintensität auf ein gegebenes Savannenökosystem wird außerdem von den vorherrschenden Bodenbedingungen beeinflusst. Darum ist ein holistisches Verständnis dieser Ökosysteme erforderlich, um eine qualitative und quantitative Einschätzung der Ursachen und Folgen von Änderungen der Biodiversität sowie der Umwelt zu ermöglichen. Dadurch wird schließlich die Bewertung funktioneller Verschiebungen innerhalb des Ökosystems semiarider Savannen unterstützt.

Ziel der Thesis ist es, dieses Verständnis durch die Erweiterung eines ökohydrologischen, räumlich expliziten Savannenmodells zu verbessern. Durch Simulationen wurden die Auswirkungen verschiedener Niederschlags- und Beweidungsszenarien auf die Diversität der Vegetation untersucht, sowie deren Rückwirkung auf die Funktionsweise des Ökosystems analysiert. Anstelle der Verwendung diskreter Arten wird die Vegetation im Modell durch das Konzept verschiedener funktionellen Pflanzentypen repräsentiert. Somit wird Biodiversität explizit als funktionelle Diversität innerhalb der allgemeinen Pflanzentypen der krautigen und holzigen Gewächse modelliert. Ziel dieser Arbeit ist es demzufolge Zusammenhänge zwischen der funktionellen Diversität und der Funktionsweise des Ökosystems semiarider

Savannen zu finden. Die vorherrschenden Umweltbedingungen werden dabei durch unterschiedliche Szenarien des mittleren Jahresniederschlags, der Beweidungsintensität und der Bodentypen simuliert. Auf Basis der Simulationsergebnisse werden deren Auswirkungen auf die funktionelle Zusammensetzung der Savannenvegetation, die Funktionsweise des Ökosystems, sowie deren wechselseitige Beziehung bewertet. Dies wird sowohl auf Ebene der Artengemeinschaft als auch der Pflanzeneigenschaften evaluiert. Des Weiteren wird eine Hierarchie der Einflüsse verschiedener Umweltbedingungen in semiariden Savannen ermittelt.

In der allgemeinen Einleitung zu dieser Thesis werden die vorherrschenden Umweltbedingungen sowie die funktionelle Diversität in Savannenökosystemen eingeführt. Ein Fokus liegt dabei auf der Simulation der Vegetationsdiversität und der Rolle funktioneller Pflanzengruppen bezüglich der Reaktion von Pflanzen auf verschiedene Umweltbedingungen. Es werden Konzepte eingeführt, welche die funktionelle Zusammensetzung und Vielfalt der Pflanzengesellschaft als Methode für die Bewertung von Umwelteinflüssen auf die Funktionsweise von Ökosystemen ermöglichen.

Die Simulationsergebnisse aus Kapitel 1 zeigen, dass die Vielfalt der Eigenschaften innerhalb der übergeordneten funktionellen Pflanzengruppe die Vegetationszusammensetzung und die Funktionsweise des Ökosystems stark beeinflussen. Zunächst wurde die Auswirkung der Variabilität von Eigenschaften innerhalb der mehrjährigen Gräser als funktionelle Pflanzengruppe auf die Funktionsweise des Ökosystems analysiert. Die Ergebnisse zeigen, dass die funktionelle Zusammensetzung der mehrjährigen Gräser stark von der Beweidungsintensität abhängt, während der mittlere Jahresniederschlag diese Einflüsse abmildern kann. Allgemein führt dabei eine höhere funktionelle Vielfalt zu einer erhöhten Vegetationsbedeckung und effizienteren Wassernutzung der Pflanzengemeinschaft. Dieses Ergebnis hebt den positiven Effekt funktioneller Diversität auf die Funktionsweise von Ökosystemen hervor, ein Ergebnis welches sich auch in empirischen Studien zeigt. Obwohl eine erhöhte Diversität innerhalb der mehrjährigen Gräser einen abmildernden Effekt auf die Verbuschung hat, bleiben die Degradationsmuster welche mit der Verbreitung holziger Arten zusammenhängen weiterhin erkennbar.

In Kapitel 2 wurde jede übergeordnete funktionelle Pflanzengruppe (mehrjährige Gräser, einjährige Gräser und Büsche) in weitere Untergruppen eingeteilt, welche wiederum durch eine Reihe bestimmter Eigenschaften charakterisiert ist. Motivation hierfür war es, ein

vertieftes Verständnis davon zu erlangen, wie Savannenvegetation auf funktioneller Ebene auf Änderungen des mittleren Jahresniederschlags sowie der Beweidungsintensität reagiert. Dabei unterscheidet sich die relative Bedeutung der verschiedenen Eigenschaften für die Gewährleistung der Wettbewerbsfähigkeit der jeweiligen übergeordneten Pflanzengruppe stark. Des Weiteren werden die Effekte der meisten Pflanzeneigenschaften auf den jeweiligen funktionellen Pflanzentypen stärker durch Änderungen des Niederschlagsregimes als der Beweidungsintensität beeinflusst. Diese ist dagegen entscheidender bei Änderungen der Artzusammensetzung auf Pflanzengesellschaftsebene und beeinflusst die relative Dominanz von Gräsern bzw. holzigen Arten in der Vegetation. Die Ergebnisse des Kapitels betonen die Bedeutsamkeit der Umweltbedingungen sowohl auf Ebene der Pflanzeneigenschaften, als auch der Pflanzengesellschaften.

In Kapitel 3 wird die räumliche Variabilität der Bodenbedingungen angesprochen, welche neben einer heterogenen funktionellen Vegetationszusammensetzung ein weiteres Charakteristikum der Savannenlandschaften ist. Die Ergebnisse zeigen in Übereinstimmung mit empirischen Studien, dass eine heterogene Bodenlandschaft positive Effekte auf die funktionelle Diversität der jeweiligen Pflanzengesellschaften haben kann. Diese positiven Effekte zeigen sich jedoch nicht konsistent in allen Szenarien unterschiedlichen mittleren Jahresniederschlags und unterschiedlicher Beweidungsintensität. Unter geringem Beweidungsdruck führt eine heterogene Landschaft zu erhöhter funktioneller Diversität, während dieser Effekt unter hohem Beweidungsdruck nicht nachgewiesen werden konnte. Zudem beeinflussen sowohl die Beweidungsintensität als auch der mittlere Jahresniederschlag die Auswirkungen einer heterogenen Landschaft auf die Biomasse und Transpiration auf Ebene der Pflanzengesellschaft.

Aus den Gesamtergebnissen der Arbeit wird deutlich, wie wichtig es ist, die funktionelle Variabilität der Pflanzeneigenschaften und die Heterogenität der Umweltbedingungen in Vegetationsmodellen zu berücksichtigen. Die Ergebnisse, welche die unterschiedlichen Effekte funktioneller Diversität in Abhängigkeit von den jeweils vorherrschenden Umweltbedingungen zeigen, betonen diese Bedeutsamkeit weiter. Sie sind vor allem im Hinblick auf den vorhergesagten Landnutzungs- und Klimawandel der kommenden Jahrzehnte von Bedeutung. Darüber hinaus wurde gezeigt, dass räumlich heterogene Bodenbedingungen unterschiedliche Effekte auf die funktionelle Diversität der Vegetation haben können abhängig vom zugrundeliegenden Umweltszenario. Somit empfehle ich eine verstärkte Forschung im Bereich der Entwicklung von Ökosystemmodellen welche sowohl

Veränderungen der Umweltbedingungen als auch der funktionellen Diversität berücksichtigen können.

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# Contribution to the publications

1. **Guo, T.**, Lohmann, D., Ratzmann, G., Tietjen, B., 2016. Response of semi-arid savanna vegetation composition towards grazing along a precipitation gradient – the effect of including plant heterogeneity into an ecohydrological savanna model. *Ecol model* 325, 47-56. doi: 10.1016/j.ecolmodel.2016.01.004

Own contributions: I adjusted various processes of the model EcoHyD and included these adjustments into the model code. I parameterized the model and performed all simulations. I analyzed and plotted all figures. I wrote the first draft of the manuscript and the appendix.

2. Lohmann, D., **Guo, T.**, Tietjen, B.. Zooming in on coarse plant functional types – simulated response of functional savanna vegetation composition in response to aridity and grazing. *Submitted to Theoretical Ecology on 23$^{rd}$ of February 2017.*

Own contributions: I parameterized the model and performed all simulations. I analyzed the simulated results and plotted all figures. I discussed the content of the manuscript and revised drafted versions. I wrote the appendix.

3. **Guo, T.**, Weise, H., Fiedler, S., Lohmann, D., Tietjen, B.. The role of landscape heterogeneity in regulating plant functional diversity under different precipitation and grazing regimes in semi-arid savannas. *To be submitted soon.*

Own contributions: I parameterized the model and conducted all simulations. I analyzed the simulated results and plotted all figures. I wrote the first draft of the manuscript and the appendix.