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

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ABSTRACT

1. Savanna systems exhibit a high plant functional diversity. While aridity and livestock grazing intensity have 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 vegetation diversity and ecosystem function is widely missing.

2. In this study, we aim at understanding the impact of local heterogeneity in soil conditions 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 livestock 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.

3. Comparisons between homogeneous and heterogeneous landscapes revealed that landscape soil heterogeneity allowed for a higher functional diversity of vegetation under conditions of high competition, i.e. scenarios of low grazing stress. However, landscape heterogeneity did not have this effect under low grazing stress in combination with high mean annual precipitation. Further, landscape heterogeneity led to a higher community biomass, especially for lower rainfall conditions, but also dependent on grazing stress. Total transpiration of the plant community decreased in heterogeneous landscapes under arid conditions.

4. 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.

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). Savanna are characterized by a matrix of abundant perennial grasses and scattered woody plants (Scholes and Archer, 1997). Locally, plant coverage and species composition vary strongly (Asner et al., 1998; Augustine, 2003). 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

Abbreviations: PFT, plant functional type; MAP, mean annual precipitation; LSU, large stock units

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will shift towards more woody plant cover (Sankaran et al., 2005). Livestock 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 intensity of livestock grazing and browsing 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 of different soil properties leading to different pattern in soil water content which is the main limiting resource for plant growth in savanna systems (Walker et al., 1981). 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).

Empirical studies and remote sensing data reveal that savanna landscapes show a high spatial variability in topography (Wu and Archer, 2005) and soil conditions (Williams et al., 1996; Fuhlendorf and Smeins, 1998; Bestelmeyer et al., 2009, 2011; Zhou et al., 2017), such as soil texture and soil depth. However, the impacts of this spatial heterogeneity on vegetation cover and composition have so far received very little attention in the savanna ecology literature in general and in modeling studies in particular, although differences in soil conditions can have multiple effects on vegetation. *Soil texture* results from the fraction of soil particle sizes and determines major physical properties of the soil that control 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). Landscape *topography* mainly influences lateral water fluxes by runoff and soil erosion (Tietjen, 2016) but also influences spatial evapotranspiration patterns through local differences in radiation (Liu et al., 2012). 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 water availability in the soil and thus the abundance and distribution of plant species. Therefore, it will ultimately change the vegetation functional diversity.

Changes in plant functional diversity will clearly entail changes in ecosystem functioning, which is defined as the magnitude and dynamics of ecosystem processes determining plant productivity and resource cycling (Naeem et al., 1999). Thus, unraveling the impact of landscape soil heterogeneity on plant functional diversity can improve our understanding of system level changes. For example, different soil conditions in the landscape have been found to affect biomass production (Tamme et al., 2016). In addition, 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 grazing 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 in combination with 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 herbivores in the Serengeti savanna (Anderson et al., 2006). Increased precipitation shifted the effect of grazing on soil organic carbon from negative to positive on 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 accounts for its interaction with precipitation and grazing intensity.

Simulation models are a suitable 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 the emergence of heterogeneous vegetation patterns in drylands (Rietkerk et al., 2004; Meron, 2011; Ursino and Callegaro, 2016). 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 savanna model EcoHyD (Tietjen et al., 2009, 2010; Lohmann et al., 2012; Guo et al., 2016; Lohmann et al., 2017) to assess the impact of landscape heterogeneity in terms of soil properties under different precipitation and livestock 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?

2. Methods

We used an ecohydrological savanna model to simulate the impact of spatial heterogeneity of soils in terms of their depth and texture on savanna vegetation. We evaluated plant functional type (PFT) diversity and composition as well as the resulting ecosystem functioning (here approximated by vegetation biomass and transpiration) that emerged in artificial heterogeneous and homogeneous landscapes for different domestic livestock 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 (see Fig. 1).

2.1. Model overview

We used the process-based savanna model EcoHyD (Tietjen et al., 2009, 2010; Lohmann et al., 2012; Guo et al., 2016; Lohmann et al., 2017), which calculates soil moisture in two layers and the dynamics of vegetation cover and biomass. This model has basic hydrological and vegetation processes, which are dynamically linked (Fig. 1 and conceptual overview in Fig. A.1 in Appendix A in Supplementary material). The model has been validated for various sites (soil moisture: Tietjen et al., 2009; grass cover: Tietjen et al., 2010; grass biomass and shrub cover: Lohmann et al., 2012). All processes are simulated on a grid cell level with a resolution of 5 by 5 m. In this study, the landscape