



Drivers of forage provision and erosion control in West African savannas—A macroecological perspective



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ABSTRACT

Rangelands' ability to provide ecosystem services (ESs) depends on ecosystem properties and functions, which are interactively driven by biophysical and land-use drivers. In West Africa's savanna rangelands, the relative importance of these drivers for ES supply is still poorly understood, hampering the identification of appropriate management strategies. In this context, trade-offs between the ES of forage provision and the regulating ES of erosion control are of particular importance. Taking a macroecological perspective, we aimed at detecting consistent patterns in ES drivers and identifying good predictors. The study area comprises a steep gradient of climatic aridity across West Africa's Sudanian savannas from northern Ghana to central Burkina Faso, in combination with local gradients of land-use intensity and topo-edaphic conditions. We used aboveground biomass, metabolisable energy and metabolisable energy yield as proxies for forage provision, and the cover of perennials in the grass layer as a proxy for erosion control. Linear mixed-effect models and model selection were used to test relationships between multiple environmental variables and ES proxies. We found differential responses of ES proxies to environmental drivers. Vegetation properties were important for all ESs. Antecedent rainfall was the most important predictor of aboveground biomass, while plants' phenology and land-use were most important for metabolisable energy. Environmental variables (such as aridity, soil properties and grazing intensity) mediated via vegetation properties were the most important predictors of erosion control followed by the direct effect of climatic aridity. Our finding that antecedent rainfall was more important for forage provision than climatic aridity implies that the effects of long-term climatic aridity may in a given year be overridden by current season's precipitation particularly in case of a good rain year. The observed importance of land-use and vegetation properties implies that well-conceived adaptation strategies could mitigate potential negative effects of climate change.

1. Introduction

Ecosystem services (ESs) are the benefits that society derives from nature (MEA, 2005). Ecosystems used as rangelands deliver multiple ESs (Sala and Paruelo, 1997; Sala et al., 2017). Among them, forage supply is the most prominent provisioning ES; it supports approximately 50% of global livestock production (MEA, 2005). Rangeland ecosystems also deliver various supporting, regulating and cultural ESs, with erosion control being of major importance (Orwin et al., 2015;

Sala et al., 2017). Accelerated soil erosion is accompanied by the loss of soil-mediated ESs such as nutrient and greenhouse gas regulation (Delgado-Baquerizo et al., 2013; Orwin et al., 2015). Rangelands' ability to provide essential ESs is mostly determined by biophysical factors such as climate and topo-edaphic conditions, and by land-use (Sala et al., 2017). These factors are also the major determinants of vegetation structure in savanna and grassland rangelands (McNaughton, 1983; Oesterheld et al., 1999; Augustine, 2003). Hence, rangelands' ability to provide essential ESs is intimately linked to

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vegetation structure, and ES delivery can be quantified by ecosystem properties that are commonly measured in ecological studies (Díaz et al., 2007a). However, the relative importance of these drivers for ES supply is still poorly understood, hampering the identification or design of appropriate land management strategies (van Oudenhoven et al., 2012).

Unfortunately, it is not possible to manage ecosystems to simultaneously maximise all ESs; trade-offs exist (López-Ridaura et al., 2002; Polasky et al., 2008; Smith et al., 2012) and are particularly common between provisioning and regulating ESs (Raudsepp-Hearne et al., 2010; Castro et al., 2014). In dryland rangelands, one of the most problematic trade-offs is that between forage supply, which is of immediate importance for livestock production, and erosion control, which if reduced has detrimental feedbacks on forage supply in the long-term due to rangeland degradation (Milton et al., 1994; Kimiti et al., 2016; Linstädter et al., 2016). Since environmental drivers may benefit immediate ES provision while negatively affecting ES provision in the long-term, trade-offs need to be detected and considered in management decisions. However, most studies on rangeland ESs do not address these trade-offs.

Several challenges are pertinent in this context. First, the quantification of ES supply is challenging since many aspects cannot be directly measured (Burkhard et al., 2012). To overcome the methodological obstacles of a direct ES measurement, several sets of ES indicators (or ‘proxies’) have been proposed on local, regional and global scales (MEA, 2005; Kandziora et al., 2013; Albert et al., 2016). Forage quantity is seen as the main factor constraining livestock carrying capacity (Yahdjian and Sala, 2006); it is estimated as aboveground net primary production (ANPP) (Scurlock et al., 2002; Yahdjian and Sala, 2006; Swemmer et al., 2007; Ruppert and Linstädter, 2014) or as aboveground biomass (AGB) (Oomen et al., 2016). Forage quality is assessed with various indices, such as crude protein, in-vitro digestibility or a combination of both into metabolisable energy (ME) (Changwony et al., 2015). It is also desirable to integrate forage quantity and quality into a single proxy, such as metabolisable energy yield (MEY), which quantifies forage nutritive energy per area (Niemeläinen et al., 2001). Vegetation cover can serve as a proxy for erosion control (Kandziora et al., 2013). In dryland ecosystems, a high perennial plant cover (PPC) is particularly important to prevent accelerated wind and water erosion (Rietkerk et al., 2000; Munson et al., 2011). PPC is also a good indicator of an ecosystem’s capacity to capture and retain resources such as water and nutrients (Soliveres et al., 2014).

However, forage services related to forage quality are rarely included in ES studies (e.g. Sawadogo et al., 2005; Palmer et al., 2010; Oomen et al., 2016) probably because measurements are labour- and cost-intensive. To overcome this challenge, suitable ES proxies are required for a fast and cost-efficient estimation of both quantitative and qualitative components of forage provision (Ferner et al., 2015). Such indirect methods are important since the high costs and logistical requirements for direct ES measurements usually constrain their assessment. These constraints are further exacerbated when studies involve large and remote study areas as in our case. Consequently, field studies on rangeland ESs are still often restricted to small study areas and/or tend to focus on ESs that are relatively easy to (directly) measure.

The second challenge is to identify key ES drivers (Díaz et al., 2007a), and to quantify their relative importance for vegetation structure and hence ES supply. As stated above, the structure of grasslands and savanna rangelands is simultaneously influenced by multiple biophysical and land-use drivers. Among them, the frequency and intensity of grazing disturbances is of particular importance, as it determines the extent of biomass removal and destruction (Milchunas et al., 1989; Altesor et al., 2005). The simultaneous influence of multiple drivers makes it difficult to disentangle their independent effects, especially in regions that face high environmental variability (Archer, 1995). Consequently, empirical savanna studies assessing the effects of

environmental drivers on vegetation-mediated ESs mostly have a local scale (e.g. Nacoulma et al., 2011; Schmidt et al., 2011), which hampers detecting consistent patterns of ES drivers at the regional level.

The third challenge relates to the fact that biophysical and land-use drivers do not only have direct effects on ES supply, but also exert indirect effects via their imprint on ecosystem structure and function (de Bello et al., 2010; Gaitán et al., 2014). Although these indirect effects are often subtler than direct effects (Cardinale et al., 2012), they remain useful in predicting effects of ecosystem properties on ES supply (Díaz et al., 2007a; Kandziora et al., 2013). To incorporate indirect effects, studies from dryland rangelands often rely on key vegetation properties such as plant diversity (Gaitán et al., 2014) and/or relative abundances of plant functional types (PFTs; see Linstädter et al., 2014; Ruppert et al., 2015). Although the use of PFTs has widely been accepted in plant ecology, the challenge remains to select trait sets that capture plant responses to environmental drivers of interest (Fry et al., 2013). Due to convergent effects of grazing and climatic aridity on vegetation (Gaitán et al., 2017), this task is particularly challenging in dryland environments (Linstädter et al., 2014). Here, plant traits related to life history, growth form and plant height have been found to be responsive (Díaz et al., 2007b).

In West Africa’s Sudanian savannas, a steep regional gradient of climatic aridity shapes vegetation patterns (White, 1983). ES studies along such gradients may allow extrapolating climate change effects via a space-for-time substitution, if spatial trends reflect projected temporal trends (Dunne et al., 2004). Moreover, steep local gradients of land-use intensity are observable (Ouédraogo et al., 2015). West Africa’s savannas are thus an ideal study area for improving our understanding of ES delivery from savanna rangelands under contemporary and future conditions. However, this opportunity has remained rather unharnessed due to logistical challenges.

Taking a macroecological perspective, our study thus aims at (i) identifying predictors of important ESs (forage supply and erosion control) from West Africa’s savanna rangelands over a broad geographical scale, (ii) quantifying the relative importance of biophysical and land-use drivers for ES supply, with the ultimate goal to identify significant and potentially universal predictors. We use a conceptual model for drivers’ single and interactive effects on ES proxies (Fig. 1), based on current knowledge (e.g. Díaz et al., 2007a). We specifically hypothesise that climate is the major driver of ES supply over and above the effects of more local drivers such as topo-edaphic factors and land-use intensity.

2. Methods

2.1. Study area

The study area (~106 000 km²) reaches from Northern Ghana to Central Burkina Faso in the West African Sudanian savanna zone (Fig. 2). Climate is seasonal; in the southern Sudanian zone, it is humid to dry sub-humid, and in the northern Sudanian zone it is semi-arid (UNEP, 1997). Mean annual precipitation (MAP) and mean annual temperature (MAT) range from 1200 to 600 mm/a, and from 26 °C to 28 °C, respectively.

The grass layer is co-dominated by annual and perennial grasses such as *Brachiaria* spp. and *Andropogon* spp., intermixed with annual forbs. The tree layer consists of species with high resprouting ability (Ouédraogo et al., 2015). Soils develop on acidic metamorphic rocks and have coarse texture (> 80% sand) with low water holding capacity (Callo-Concha et al., 2012). They are highly susceptible to erosion and compaction and, depending on the cultivation history, exhibit low levels of organic matter, nitrogen and phosphorus (Callo-Concha et al., 2012). Besides subsistence agriculture, grazing by domestic herbivores is the most widespread type of land-use in the area (Naah et al., 2017).

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