Global change effects on ecosystem species composition, functions and services of West Africa's Sudanian savannas

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"There is a time for everything, and a season for every activity under the heavens" (Ecclesiastes 3:1)

Goals give you a reason to work hard but determination powers the hard work into success (Author's own motivation)

Dedication

I dedicate this work, with love, to my wife (Alice) and sons (Jesse and Anthony) who made great sacrifices thus paving the way for me to go down this path. Especially to Alice; I could not have achieved this success without your constant understanding, unflinching support and unfailing love. When, at times, it felt so hard to keep my focus, you always provided the motivation and encouragement I required.

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Summary

Savanna ecosystems cover an eighth of the world's land surface and are of immense ecological and economic importance. Ecologically, they help regulate climate, air quality, water quality, and soil erosion. Economically, savannas provide food, medicines and fiber to humans and animals; e.g. they support approximately 50% of global livestock production.

Global environmental change has led to major impacts on savannas worldwide. Key determinants of species distribution, biodiversity and ecosystem functioning in rangelands include grazing and climate. In Africa’s savannas, rangelands provide important ecosystem services and contribute considerably to local livelihoods. Here, grazing by domestic herbivores is an important type of land-use. It is usually done on extensive basis thus highlighting the importance of rangelands. Despite drastic increases in land-use pressure and considerable climatic changes affecting Africa's savannas, there is still limited information about the importance of these global change agents for spatio-temporal patterns in ecosystem functions and services, a situation which hinders the development and implementation of effective land management strategies. In this context, understanding the underlying environmental drivers of herbaceous species composition, diversity, ecosystem functioning and ecosystem service provision is a crucial step. This thesis aimed at filling these critical research gaps by investigating the impacts of multiple environmental factors on savanna ecosystems. In section 2, this study aimed at determining the drivers of herbaceous plant species composition and distribution. In section 3, the study aimed at determining the drivers of plant species and functional diversity of the herbaceous layer while section 4 aimed at determining the drivers of major ecosystem services, namely forage provision and erosion control.

This study was conducted within the framework of the West African Science Service Center on Climate Change and Adapted Land Use (WASCAL) project at the University of Bonn which was funded by the German Federal Ministry of Education and Research (BMBF). Field work was conducted in the Sudanian savannas of Ghana and Burkina Faso. Due to the existence of a steep regional gradient of climatic aridity, a space-time substitution approach was used in this study aiming to understand future climatic impacts on herbaceous vegetation. The sampling was stratified into three rainfall zones oriented along a south-north gradient of increasing climatic aridity. Within strata, sampling was designed to capture as much as possible of the variations in geology, grazing intensity and topography by choosing sites that maximise the range of these gradients. A nested plot

design was used where three 1 m^2 circular subplots were randomly placed in each plot of 10 m x 10 m.

For section 2, I collected data at two spatial scales; a regional scale comprised of long-term climatic data (averaged over a 50-year period) and a local scale comprised of plot characteristics, namely land-use intensity (related to grazing pressure), topo-edaphic conditions (topography, soil physical and chemical properties) and vegetation data (species' name, species' cover and species' height). For section 3, I collected data on long-term climatic conditions, topo-edaphic conditions, disturbance (grazing pressure and fire frequency) and vegetation. The vegetation data comprised of species' name, species' cover and six plant traits, namely life history, height, life form, photosynthetic pathway, growth habit and nitrogen fixation. Vegetation data was used for the calculation of species and functional diversity indices. For section 4, I collected data on long-term climatic conditions, season's antecedent precipitation, topo-edaphic conditions, land-use intensity and vegetation. The vegetation data comprised of species' name, species' cover and three plant traits, namely height, growth form and life form. These traits were used to form plant functional types. Additionally, I derived three proxies of the provisioning ecosystem service of forage provision, namely aboveground biomass, metabolisable energy, metabolisable energy yield and one proxy of the regulating ecosystem service of erosion control, namely perennial plant cover. Aboveground biomass was derived via allometric functions based on biomass measurements from representative sample plots across the study area. A portable field spectro-radiometer was used to measure plant reflectances and I then used a regression model, calibrated in the same area, to estimate the metaboblisable energy. Metabolisable energy yield was obtained as a product of aboveground biomass and metabolisable energy.

In section 2, this study used; (1) Mantel tests and variance partitioning to identify the drivers of vegetation composition, (2) isometric feature mapping and partitioning around medoids (Isomap) to perform agglomerative cluster analysis and (3) non-metric multidimensional scaling (NMDS) to perform ordination. In sections 3 and 4, linear mixed-effect models with model selection procedures were applied to obtain the best set of predictors for each measure of diversity (section 3) and ecosystem service (section 4).

In section 2, the results from variance partitioning showed that the regional scale drivers (long-term climate at a given site) were more important for determining vegetation composition than local scale drivers (topo-edaphic conditions and land-use intensity) and plot's geographic location. The Mantel tests showed that long-term precipitation (averaged over a 50-year period) had the highest correlation with herbaceous vegetation composition.

Ten herbaceous vegetation clusters were found, arranged along three NMDS axes, that mainly represent climatic and land-use (grazing) variations which have been found as major drivers of the spatial differentiation of species composition and vegetation clusters in the area. In section 3, the study found that taxonomic diversity and functional diversity mostly varied independently and were not strongly correlated to each other. Precipitation seasonality and grazing intensity were significantly related to all functional diversity indices but not to any of the taxonomic diversity indices except species richness. Taxonomic diversity indices were significantly related to soil texture and topography. In section 4, the importance of long-term climate regime (averaged over a 50-year period) varied with ecosystem services: it was less important than antecedent precipitation for aboveground biomass, and metabolisable energy yield but was more important for perennial plant cover than antecedent precipitation. Land-use intensity (grazing pressure) was an important predictor for forage provision but not for perennial plant cover. Vegetation attributes (plant functional types, phenological stage and species diversity) were important predictors for all ecosystem services while topo-edaphic conditions were of secondary importance.

In summary, long-term climate was found to mainly drive floristic composition and diversity on a regional scale. It also exerted (indirect) effects on ecosystem service provision via its effects on vegetation attributes and hence on ecosystem structure and function. Land-use (grazing) and topo-edaphic conditions acted mostly as modifiers of ecosystem structure and function at the local scale. These findings have two major implications for understanding climate change effects on ecosystem services provided by West Africa’s Sudanian savannas. First, local site conditions (in soil, topography, land-use etc) could determine to which extent climate change effects on plant communities are actually translated into changes in ecosystem structure and function and second, short-term (seasonal) variation in rainfall may mask effects of changing climate and land-use on forage provision. The findings of this study are useful and can serve as a decision-making support tool for policy makers, rangeland managers and conservationist within the context of ongoing climate change.

Zusammenfassung

Savannenökosysteme bedecken ein Achtel der Landoberfläche der Erde und sind von immenser ökologischer und wirtschaftlicher Bedeutung. Ökologisch betrachtet helfen sie bei der Regulation von Klima, Luft- und Wasserqualität sowie Bodenerosion. Wirtschaftlich betrachtet liefern Savannen Lebensmittel, Medikamente und Textilfasern für den Menschen und ernähren beispielsweise etwa 50% des weltweiten Viehbestandes.

Globale Umweltveränderungen haben weltweit zu starken Veränderungen in Savannen geführt. Beweidung und Klima zählen zu den Schlüsselfaktoren für die Verbreitung von Arten, die biologische Vielfalt und damit die Funktion des Ökosystems „Weideland“. In Afrikas Savannen stellt Weideland wichtige Ökosystemdienstleistungen bereit und trägt wesentlich zum Lebensunterhalt der lokalen Bevölkerung bei. Hierbei stellt die Beweidung mit domestizierten Herbivoren eine wichtige Form der Landnutzung dar. Normalerweise wird extensive Viehhaltung betrieben, was die Bedeutung des Weidelandes unterstreicht. Trotz eines dramatisch ansteigenden Druckes auf die Landnutzung sowie erheblicher klimatischer Veränderungen in den Savannen Afrikas sind noch immer nur unzureichende Informationen über die Bedeutung dieser Veränderungen für raum-zeitliche Muster von Ökosystemfunktionen und -dienstleistungen vorhanden, wodurch die Entwicklung und Implementierung von effektiven Landmanagementstrategien verhindert wird. Ein entscheidender Schritt ist hier das Verständnis der Umweltfaktoren, welche die Verteilung krautiger Pflanzenarten und ihrer Diversität, sowie der Ökosystemfunktionen und -dienstleistungen bestimmen. Die vorliegende Dissertation soll diese kritischen Forschungslücken schließen, indem sie die Auswirkungen von diversen Umweltfaktoren auf die Savannenökosysteme untersucht. Der Abschnitt 2 dieser Studie zielt darauf ab, die Umweltfaktoren zu bestimmen, welche die Zusammensetzung und Verteilung krautiger Pflanzenarten bestimmen. Der Abschnitt 3 beschäftigt sich mit der Untersuchung von Faktoren, welche die Diversität von Pflanzen sowie die funktionelle Diversität beeinflussen, während sich Abschnitt 4 mit der Bestimmung der Faktoren beschäftigt, welche wichtige Ökosystemleistungen, nämlich die Bereitstellung von Viehfutter sowie den Erosionsschutz, beeinflussen.

Diese Dissertation wurde an der Universität Bonn im Rahmen des Projektes WASCAL (West African Science Service Center on Climate Change and Adapted Land Use) erstellt, welches vom Bundesministerium für Bildung und Forschung gefördert wird. Die Datenerhebung (Feldarbeit) fand in der Sudan-Savanne in Ghana und Burkina Faso statt. Mithilfe eines steilen regionalen Ariditätsgradienten wurde in dieser Studie eine Raum-Zeit-

Substitution verwendet, um künftige Klimaauswirkungen auf die krautige Vegetation zu verstehen. Das Untersuchungsgebiet wurde in drei Niederschlagszonen stratifiziert, welche entlang eines Süd-Nord-Gradienten mit zunehmender klimatischer Aridität lagen. Innerhalb der Zonen wurde die Datenerhebung auf den untersuchten Flächen so gestaltet, dass die Variationen in Geologie, Beweidungsstärke und Topographie ein größtmögliches Spektrum abdeckten. Es wurde ein genestetes Untersuchungsdesign verwendet, wobei drei kreisförmige, 1 m^2 große Teilflächen zufällig innerhalb einer Beprobungsfläche von 10 m x 10 m verteilt wurden.

Für die Studie in Abschnitt 2 wurden Daten auf zwei räumlichen Ebenen gesammelt; ein regionaler Datensatz beinhaltet langjährige Klimadaten (gemittelt über einen Zeitraum von 50 Jahren) und ein lokaler Datensatz deckt örtliche Flächeneigenschaften, wie Landnutzungsintensität (bezogen auf Beweidungsdruck), topo-edaphische Bedingungen (Topographie, physische und chemische Bodeneigenschaften) und Vegetationsparameter (Artname, Bedeckungsgrad und Pflanzenhöhe) ab. Für die Studie in Abschnitt 3 wurden Daten über die langjährigen klimatischen Bedingungen, über topo-edaphische Eigenschaften, Störungen (Beweidungsdruck und Feuerhäufigkeit) und Vegetation akquiriert. Die Vegetationsdaten beinhalteten den Artnamen und den Bedeckungsgrad sowie sechs Pflanzenmerkmale, und zwar Lebensdauer, Wuchshöhe, Lebensform, Photosynthesetyp, Wuchsform und Stickstofffixierung. Die Vegetationsdaten wurden für die Berechnung von Indizes der Artendiversität und der funktionellen Diversität verwendet. Für die Studie in Abschnitt 4 wurden Daten über die langjährigen klimatischen Bedingungen, die vorherigen Niederschläge der aktuellen Vegetationsphase, die topo-edaphische Bedingungen, die Landnutzungsintensität und die Vegetation berücksichtigt. Die Vegetationsdaten beinhalteten den Artnamen, den Bedeckungsgrad und drei Pflanzenmerkmale, und zwar Wuchshöhe, Wuchsform und Lebensform. Diese Merkmale wurden verwendet um funktionelle Pflanzengruppen zu bilden. Zusätzlich wurden drei stellvertretende Messgrößen für die liefernde Ökosystemdienstleistung „Bereitstellung von Viehfutter“ bestimmt, und zwar oberirdische Biomasse, metabolisierbare Energie und metabolisierbarer Energieertrag. Außerdem wurde eine stellvertretende Messgröße für die regulierende Ökosystemdienstleistung „Erosionsschutz“ bestimmt, uns zwar die Pflanzenbedeckung mit mehrjährigen Arten. Die oberirdische Biomasse wurde über allometrische Funktionen geschätzt, welche wiederum von Biomasseproben von repräsentativen Probeflächen im Untersuchungsgebiet abgeleitet wurden. Ein tragbares Spektralradiometer wurde verwendet, um die reflektierte Strahlung der Pflanzendecke zu messen. Mit einem Regressionsmodell, welches im Untersuchungsgebiet kalibriert wurde, konnte daraus die metabolisierbare Energie der Pflanzen abgeschätzt werden. Der metabolisierbare Energieertrag wurde aus dem Produkt aus der oberirdischen Biomasse und der metabolisierbaren Energie errechnet.

Im Abschnitt 2 verwendet diese Studie: (1) Manteltests und Partitionierung der Stichprobenvarianz, um die beeinflussenden Faktoren der Vegetationskomposition zu identifizieren, (2) isometrisches Feature Mapping und Partitionierung um Medoite (Isomap), um eine agglomerative Clusteranalyse durchzuführen und (3) nicht-metrische multidimensionale Skalierung (NMDS) zum Zwecke einer Ordination. In den Abschnitten 3 und 4 wurden lineare gemischte Modelle mit Modellauswahl angewendet, um die beste Zusammenstellung von Prädiktoren für jedes Diversitätsmaß (Abschnitt 3) bzw. jede Ökosystemdienstleistung (Abschnitt 4) zu erhalten.

Die Ergebnisse der Partitionierung der Stichprobenvarianz in Abschnitt 2 zeigen, dass regionale Faktoren (langjährige Klimabedingungen eines Ortes) eine größere Rolle für die Vegetationskomposition spielten als lokale Faktoren (topo-edaphische Bedingungen und Landnutzungsintensität) sowie die geographische Lage der Untersuchungsflächen. Der Manteltest zeigte, dass der langjährige Niederschlag (gemittelt über 50 Jahre) am stärksten mit der Komposition der krautigen Vegetation korrelierte. Es wurden zehn krautige Vegetationscluster entlang von drei NMDS-Achsen gefunden. Die Achsen repräsentieren hauptsächlich Variationen in Klima und Landnutzung (Beweidung) und somit die Hauptfaktoren für die räumliche Differenzierung der Artenkomposition und der Vegetationscluster im Gebiet. Abschnitt 3 behandelt das Ergebnis, dass die Artendiversität und die funktionelle Diversität größtenteils unabhängig voneinander variierten und dabei nur schwach miteinander korrelierten. Die Saisonalität der Niederschläge sowie der Beweidungsdruck standen in signifikantem Zusammenhang mit allen Indizes der funktionellen Diversität, jedoch nicht mit den Indizes der Artendiversität mit Ausnahme von Artenreichtum. Die Indizes der Artendiversität standen in signifikantem Zusammenhang mit Bodentextur und Topographie. Im Abschnitt 4 wird erörtert, dass der Einfluss langjähriger Klimabedingungen (gemittelt über 50 Jahre) auf verschiedene Ökosystemdienstleistungen variierte: Er war weniger wichtig für die oberirdische Biomasse und den metabolisierbaren Energieertrag als die vorherigen Niederschläge der aktuellen Vegetationsphase, wohingegen er für die Pflanzenbedeckung mit mehrjährigen Arten wichtiger war als der vorherige Niederschlag. Die Landnutzungsintensität (Beweidungsdruck) war ein wichtiger Prädiktor für die Bereitstellung von Viehfutter, jedoch nicht für die Pflanzenbedeckung mit mehrjährigen Arten. Vegetationseigenschaften (wie funktionelle Pflanzengruppen, Phänologie und

Artendiversität) waren wichtige Prädiktoren für alle Ökosystemdienstleistungen, während topo-edaphische Bedingungen von untergeordneter Bedeutung waren.

Zusammenfassend wurde festgestellt, dass das langjährige Klima hauptsächlich die floristische Zusammensetzung und Diversität auf regionaler Ebene bestimmt. Es hat außerdem (indirekte) Auswirkungen auf die Ökosystemdienstleistung durch seine Effekte auf die Vegetationseigenschaften und damit auf die Ökosystemstruktur und -funktion. Die Landnutzung (Beweidung) und die topo-edaphischen Bedingungen wirken meist modifizierend auf Ökosystemstruktur und -funktion auf lokaler Ebene. Diese Ergebnisse haben zwei wichtige Implikationen für das Verständnis der Auswirkungen des Klimawandels auf die Ökosystemdienstleistungen der westafrikanischen Sudan-Savanne. Einerseits könnten lokalen Standortbedingungen (hinsichtlich Boden, Topographie, Landnutzung usw.) bestimmen, in welchem Ausmaß die durch den Klimawandel hervorgerufenen Effekte auf die Pflanzengesellschaften tatsächlich zu Veränderungen der Ökosystemstruktur und -funktion führen. Andererseits könnten kurzfristige (saisonale) Veränderung der Niederschläge die Auswirkungen von Klimaveränderungen und Landnutzungswandel auf die Bereitstellung von Viehfutter maskieren. Die Ergebnisse dieser Studie sind sehr hilfreich und können sowohl politische Entscheidungsträger, als auch Weidemanager und Umweltschützer im Kontext des anhaltenden Klimawandels bei der Entscheidungsfindung unterstützen.

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List of Abbreviations

AGB	Aboveground biomass
AI	Aridity index
AIC	Akaike information criteria
ANOVA	Analysis of variance
ANPP	Aboveground net primary production
BIC	Bayesian information criteria
BSC	Bare soil cover
CA	Climatic aridity
CAL	Calcium-acetate-lactate
Clay	Soil clay content
CS	Coarse gravel cover
CWM	Community-weighted mean
DEM	Dynamic equilibrium model
ES	Ecosystem service
ES	Ecosystem services
FAO	Food and agriculture organization
FDiv	Functional divergence
FEve	Functional evenness
FG	Fine gravel cover (%)
Fire	Fire frequency
FIRM	Fire Information for Resource Management System
FRao	Rao’s quadratic entropy
FRic	Functional richness
GP	Grazing pressure
IDH	Intermediate disturbance hypothesis
Lat	Latitude
LC	Litter cover
LMM	Linear mixed-effect models
Lon	Longitude
MAT	Mean annual temperature
Max.	Maximum
ME	Metabolisable energy
MEY	Metabolisable energy yield
mg kg^{-1}	Milligrams per killogram
Min.	Minimum
mm/a	Millimetres per annum
MMC	Moribund material cover
MSL	Milchunas, Sala and Lauenroth’s generalised model
N	Soil nitrogen content

NA	Not available
NASA	National Aeronautics and Space Administration
NMDS	Non-metric multidimensional scaling
P	Plant-available phosphorus content
PC	Principal component
PCA	Principal component analyses
pH	Soil acidity
Phen	Phenophase
PPC	Perennial plant cover
PS	Precipitation seasonality
PWM	Precipitation of the wettest month
r	Correlation (Mantel or Pearson)
REML	Restricted maximum likelihood estimation
SAF	Small annual forbs
SAG	Small annual graminoids
SAP	Season’s accumulated precipitation before sampling
SD	Standard deviation
SDI	Simpson's diversity index
SEve	Species evenness
SP	Slope position
SPG	Small perennial graminoids
SRic	Species richness
SS	Stone cover
Sand	Soil sand content (%)
Silt	Soil silt content (%)
TAF	Tall annual forbs
T_{Min}	Minimum temperature of coldest month
TPG	Tall perennial graminoids
UNEP	United nations environment programme

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1 General introduction

1.1 Overview

Savanna ecosystems cover an eighth of the world's land surface (Figure 1-1) and support a large proportion of human population (Schumann, 2011). They are characterised by a continuous grass layer (also called ‘herbaceous layer’ in this study) and a discontinuous tree layer (Figure 1-2; Scholes & Archer, 1997).

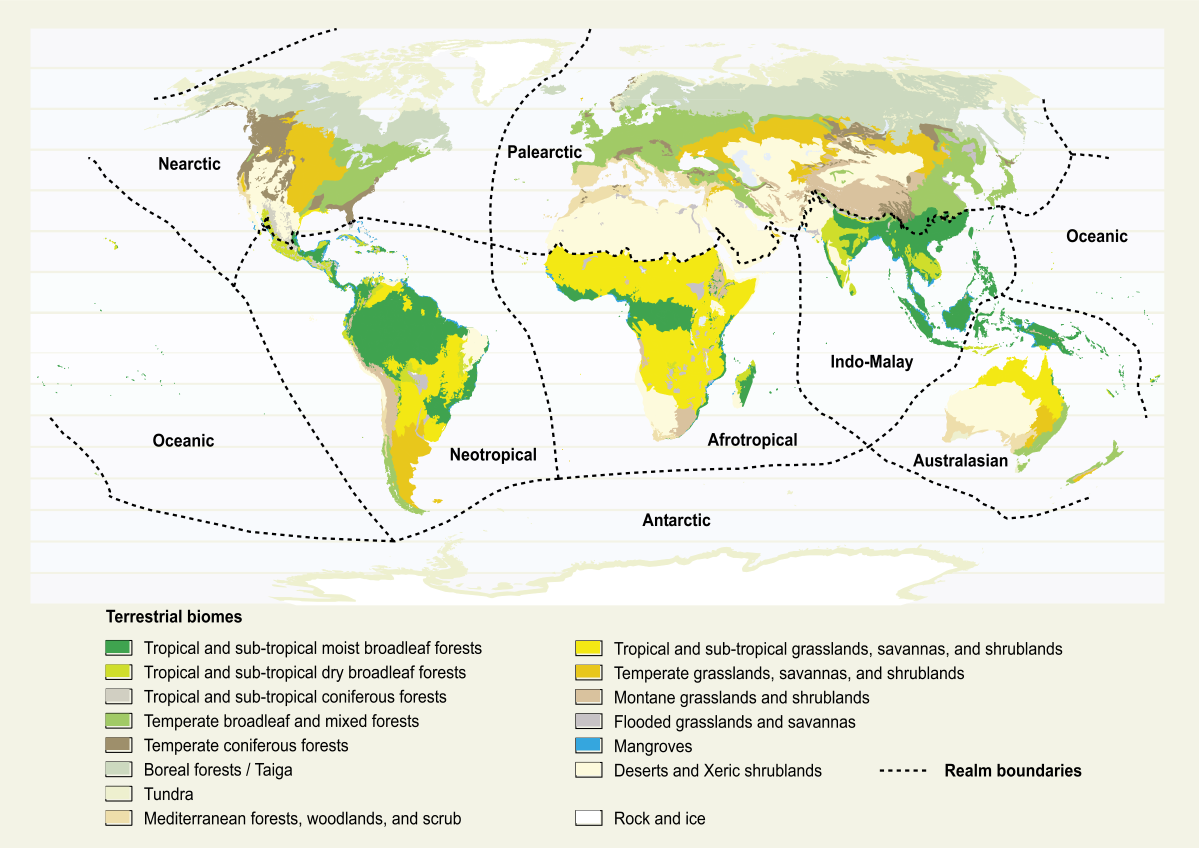


Figure 1-1: The biomes of the world also showing the global extent and coverage of savannas. Map is taken from the Millennium Ecosystem Assessment (2005a).

The distribution, structure, and composition of savanna ecosystems are mainly influenced by climate, soils, geomorphology, herbivores, topography, and fire (Figure 1-2; Scholes & Archer, 1997). Besides these cardinal factors, human land-use activities have also affected savannas over millennia (Figure 1-2; Wittig *et al.*, 2007). Thus land-use and its effects on savanna vegetation should be taken into consideration when trying to understand the current status of savannas or predict their future development (Heubes *et al.*, 2011). In West African savannas, land is mostly used as common property (Cotula *et al.*, 2006) and the most common land uses are agriculture, livestock rearing, and harvesting of natural products (Schumann, 2011).

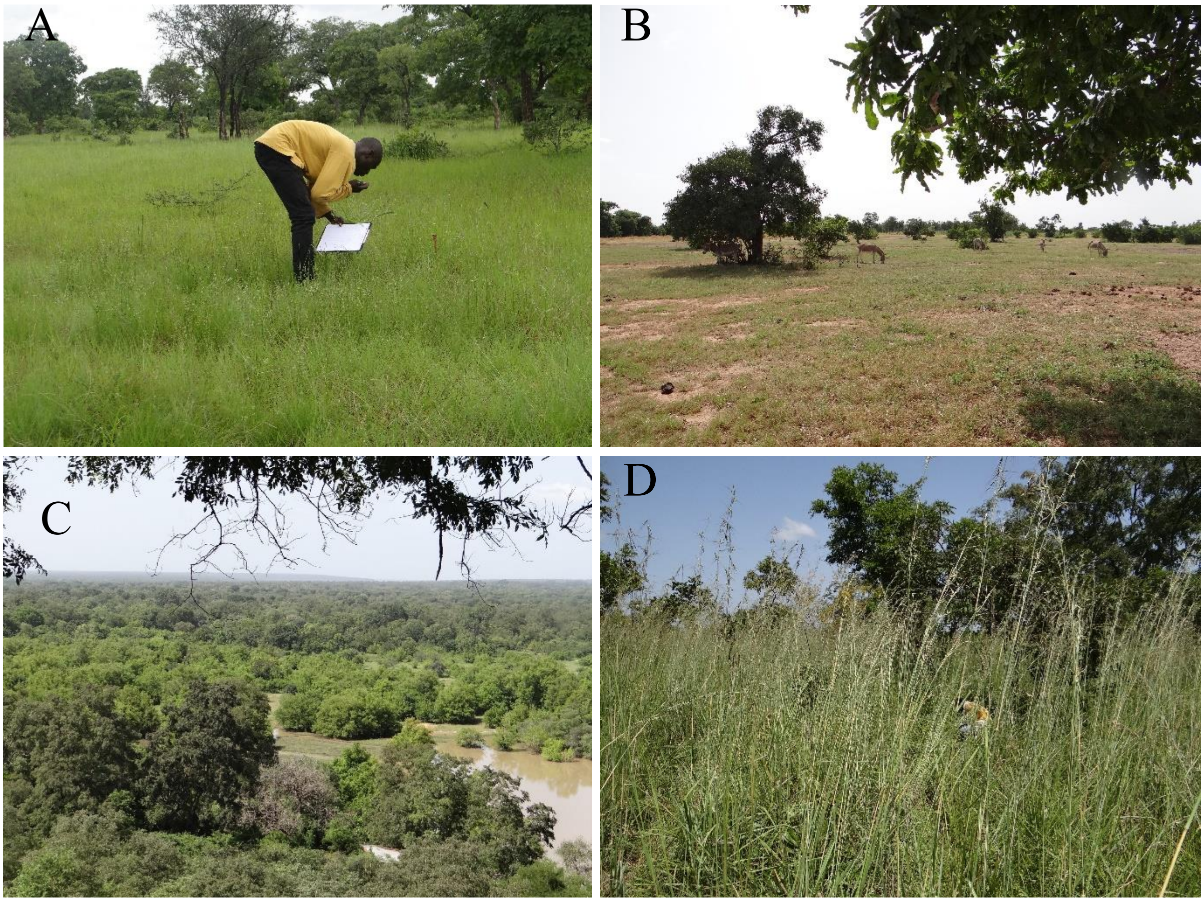


Figure 1-2: Examples of savanna vegetation in the study area under different climate and grazing conditions. (A) Savanna vegetation in the relatively high rainfall zone (humid to dry sub-humid) of the study area with low grazing pressure. (B) Savanna vegetation in the relatively low rainfall zone (semi-arid) of the study area with high grazing pressure. (C) and (D) Near natural savanna vegetation under light to no grazing pressure in protected parks of the study area. Picture (C) was taken in the Mole national park of Ghana and picture (D) was taken in the Nazinga protected area in Burkina Faso. Source: Author's own photo, 2013.

Grazing systems are characterised by continuous and close interactions between the social and the ecological subsystem of coupled social-ecological systems (SES: Anderies *et al.*, 2004). These interactions are difficult to understand because they are highly complex (Blench & Sommer, 1999). The impact of climate change (such as increasing frequency and intensity of meteorological drought events) on the social subsystem of West African SES has attracted increasing attention in the past years (Mertz *et al.*, 2010; Mertz *et al.*, 2011). In contrast, we still know surprisingly little about the impacts of climate change on the ecological subsystem. More importantly, the combined effects of changing land-use and climate on vegetation composition and ecosystem functioning need to be better understood.

1.2 Floristic composition and functional diversity in rangelands

Key determinants of species distribution and biodiversity in rangelands include grazing and climate (Blench & Sommer, 1999). Heavy grazing has the tendency to cause a decline in palatable species and to result in a dominance of other, less palatable species (Zhang *et al.*, 2004). Grazing effects on vegetation and hence on rangeland state mainly depend on the intensity and frequency of grazing (Díaz *et al.*, 2007c). Vegetation dynamics in semi-arid rangelands can also be related to variable climatic conditions (Blench & Sommer, 1999). However, the extent of vegetation change that is attributed to grazing impact versus climatic variability is still debatable (Gillson & Hoffman, 2007) and thus need to be fully understood.

Although many biodiversity studies commonly base on species richness, and other measures of taxonomic diversity (Peco *et al.*, 2012; Li *et al.*, 2015), the concept of functional diversity has gained prominence in recent decades (Díaz *et al.*, 2007a; Zhang, 2011). A multiplicity of species in a community does not necessarily imply a better ecosystem functioning as they could be functionally redundant. In contrast, it is the functional diversity, i.e. the functional multiplicity within a community that is closely related to ecosystem functioning (Weithoff, 2003). However, a high functional redundancy provides resilience against the loss of functions and services provided by that species group. Hence, the concept of functional diversity links species to ecosystem functioning (Weithoff, 2003; Petchey & Gaston, 2006). A higher functional diversity and redundancy among functional groups helps to buffer environmental fluctuations such as variable rainfall, and thus leads to more resilient ecosystems and to a more reliable provision of ecosystem services over time (Linstädter *et al.*, 2013).

To quantify the functional diversity of an ecosystem, plant functional traits need to be measured. These are a well-known approach for describing plant responses to plant-available resources (such as nutrients and moisture), climatic conditions and to disturbances such as grazing (McIntyre *et al.*, 1995; Díaz *et al.*, 2007c). Functional traits have the advantage that they can be aggregated on different levels of biological organization (Schellberg & Pontes, 2012). Plants possessing similar combinations of traits (‘trait syndromes’) may be classified into plant functional types (PFTs). The use of PFTs is based on the assumption that plants with similar ecological trait attributes will respond to environmental changes in similar ways (McIntyre *et al.*, 1995). To analyse trait responses on any environmental gradient, a classification of traits into the fundamental stages in the life-cycle of plant species is helpful (Bernhardt-Römermann *et al.*, 2008). Different classification systems have been developed including life forms (Raunkiaer, 1937), plant strategies (Grime, 2001) and functional types (McIntyre *et al.*, 1999). A plant trait may be called functional if it impacts plant fitness through its effects on growth, reproduction and survival (Bernhardt-Römermann *et al.*, 2008). Using plant traits to study plant responses to changes is an important part of plant ecological studies. Although functional traits and PFTs have widely been accepted in plant ecology, the challenge still remains to select trait sets that capture plant responses to major environmental drivers. This is particularly true for trait responses to grazing in semi-arid environments (Díaz *et al.*, 2007c). For example, there is still no consensus if an optimum type of trait aggregation exists for detecting grazing effects against the background of a high environmental variability which is typical for semi-arid environments. Moreover, it appears problematic to transfer grazing responses to sites with different climatic and/or edaphic aridity, and to scale up from the plant community to the biome level and beyond (Linstädter *et al.*, 2014).

Major issues to note in the calculation of functional diversity include; which functional traits are chosen, how they are assessed (Lavorel *et al.*, 2008), and which index or indices of functional diversity are used (Chillo *et al.*, 2011). Various indices have been proposed for this purpose (Petchey & Gaston, 2006), and there is still no consensus on which index should be used (Schleuter *et al.*, 2010). Mason *et al.* (2005) suggested three main components of functional diversity, i.e. functional richness, functional evenness, and functional divergence (see section 3). Functional diversity is high when species with many differing functional traits are present in the same community (Weithoff, 2003) and vice versa.

1.3 Ecosystem services from savannas

Ecosystem services (ESs) are the link between ecosystems and human society (Millennium Ecosystem Assessment, 2005b). Ecosystems used as rangelands deliver a number of ESs, with forage services being the most prominent (see Figure 1-3); supporting approximately 50% of global livestock production (Millennium Ecosystem Assessment, 2005b). Savanna ecosystems also deliver numerous supporting and regulating ESs of which erosion control via vegetation cover (Figure 1-3) is of major importances (Millennium Ecosystem Assessment, 2005b). In West Africa, livestock serves as a major income source for about 45% of households (Mertz *et al.*, 2010), underlining the importance of forage services for local livelihoods.

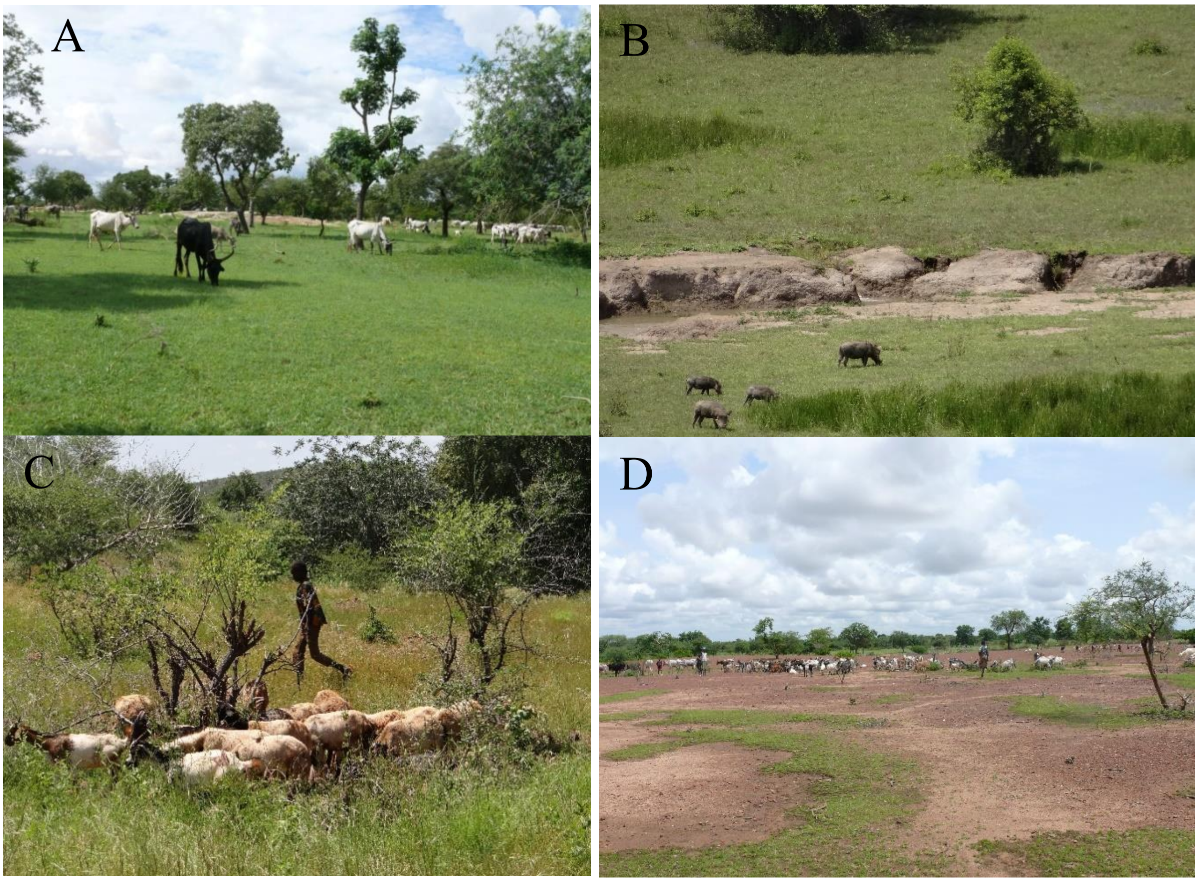


Figure 1-3: Effect of grazing on savanna vegetation and ecosystem services of forage provision and vegetation cover. (A) Cattle grazing on the open savanna in relatively high rainfall area. (B) Warthogs grazing in the Mole national park (protected area). (C) Sheep grazing on the open savanna in relatively high rainfall area (humid to dry sub-humid). (D) Overgrazed area in the relatively low rainfall area (semi-arid) showing signs of erosion and land degradation. Source: Author's own photo, 2012

Aforementioned factors which affect species distribution patterns and diversity also greatly influence ESs that are delivered by these ecosystems. Environmental factors (e.g. grazing and climatic aridity) cause changes in taxonomic and functional diversity which inturn affects ecosystem structure and functioning (Díaz *et al.*, 2007b). These changes have a potential to influence vital ESs such as forage provision in the long term (Díaz *et al.*, 2007b). Plant functional traits and types are also linked to service provision since different plant types are better suited for providing different types of services. Research in plant functional traits uses two different approaches to address ecosystem functioning (Lienin & Kleyer, 2012): either trait responses to environmental drivers or to ecosystem properties are evaluated, including the forage provision of rangelands and how these depend on functional traits.

Ecological studies commonly assess trait-mediated ecosystem functioning along environmental gradients (Bernard-Verdier *et al.*, 2012). In a quite rigorous way, (Shipley, 2010: 48) defines an environmental gradient as "*a mathematical function, g(e), which maps values of a set of environmental variables onto some property of plants and (preferably) reflects the causal relationships between the environmental variables and the plant property*."

1.4 Research objectives

In the Sudanian savannas of West Africa, rangelands provide important ecosystem services. Livestock remain an important aspect of livelihoods for most farmers in the region providing nutrition, food and economic support for some of the poorest people in the world. Additionally, some species (e.g. *Echinochloa* spp., *Panicum laetum* and *Cenchrus biflorus*) are commonly collected as wild cereals (Pedersen & Benjaminsen, 2008). To meet conservation/management needs, it is necessary to assess the current vegetation status and to initiate measures towards the monitoring of vegetation changes over time. Using a space-time substitution approach, the overall aim of this study was to enhance current knowledge and understanding of vegetation scientists and conservationists on the Sudanian savanna ecosystem of West Africa. The study is relevant because it adds new dimensions to existing knowledge within the broad field of plant ecology and particularly in the West African region. The wide spatial coverage of the study (~106 000 km²), large number of vegetation relevés (450 plots) and simultaneous consideration of climatic and land-use gradients provide a new approach to vegetation studies in the region. It is envisaged that the study would thus contribute to an improvement in land management so as to enhance ecosystem integrity and the provision of ecosystem services. The three main objectives (papers) addressed in this thesis are;

1. to determine the drivers of herbaceous species composition and distribution in the Sudanian savannas of West Africa.
2. to determine the drivers of taxonomic and functional diversity in the Sudanian savannas of West Africa
3. to determine the drivers of ecosystem service provision (forage services and erosion control) in the Sudanian savannas of West Africa

1.5 Thesis outline

The thesis is composed of five interrelated sections. The first section is a general introduction to the research after which sections 2 to 4 address the three main objectives of this study. Section 2 investigates the determinants of vegetation composition and distribution patterns, section 3 investigates the effects of different environmental factors on biodiversity and section 4 investigates the drivers of ecosystem service provision in the Sudanian savannas of West Africa. Finally, section 5 provides a general conclusion of the study. The sections 2 - 4 are presented in the form of scientific articles and therefore all possess separate introduction, methodology, results, discussion and conclusion sections.

2 Drivers of herbaceous species composition and distribution in the Sudanian Savannas of West Africa

2.1 Abstract

What are the drivers of herbaceous plant species composition and distribution in West Africa's savannas? Despite dramatic increases in land-use pressure and considerable climatic changes in West Africa's savannas, we still have a limited understanding of how these agents affect herbaceous vegetation composition and distribution in this region. 450 plots were located along a climate gradient of 530 km x 200 km, reaching from northern Ghana to central Burkina Faso. In these plots, we assessed herbaceous plant species composition and environmental variables related to topography, soil and land-use (grazing pressure). Other variables that entered the analyses were related to climate and geographic location. We used Mantel tests to explore vegetation-environment relationships and to partition variance explained by groups of variables. We also used non-metric multidimensional scaling (NMDS) ordination and hierarchical cluster analysis to visualise and describe the patterns of species composition. We found that 22.8% of variation in the species composition and abundance matrix was explained by the considered variables including geographic location. Over half of the variance explained by climate was related to broad-scale geographic location. Ca. one-fourth of the variance explained by plot characteristics was related to broad-scale pattern. Our expectation of climate as a dominant driver of herbaceous vegetation differentiation was confirmed. Climatic drivers (mainly precipitation) were more important for species composition (62.5% of the total explained variance) than plot characteristics (19.9% of the total explained variance). We distinguished ten vegetation clusters arranged along three NMDS axes explaining 52% of variation in species composition. All three axes were related to climate and grazing pressure. This highlights the importance of climate change for vegetation composition and species distribution in the region. Our findings are important for supporting land management conservation planning in the region.

2.2 Introduction

In contemporary ecological research, the quantification of ecosystem responses to global environmental change and the description of species' composition and distribution patterns are major goals (Reed *et al.*, 2012). African ecosystems are biologically and ecologically unique, and provide important ecosystem services at local, regional and global levels (Midgley & Bond, 2015). During the past decades, Africa has been and is projected to be subject to substantial changes in land-use pressure and climate. These changes are particularly dramatic in West Africa (Knippertz *et al.*, 2015). However, we still have a limited understanding of how these agents of global environmental change interactively affect herbaceous vegetation composition in this region (Midgley & Bond, 2015), which hampers the design of appropriate land management strategies. In this context, there has been growing interest in understanding plant distribution patterns along climate gradients in West Africa (Wittig *et al.*, 2007; Schmidt *et al.*, 2010). The main reason for this approach is that it has the potential to improve our understanding of climate change impacts via a space-time substitution (Malanson *et al.*, 1992; Rutherford *et al.*, 1995).

Previous research outlined the importance of climatic variables for the distribution of vegetation types across the continent (Adejuwon, 1971; Swaine *et al.*, 1992), with precipitation as the most important climate predictor (Sankaran *et al.*, 2005; Bucini & Hanan, 2007). In West Africa, vegetation species composition changes from south to north in response to a strong south-north rainfall gradient from the coastal to the Sahelian zone (Van Rompaey, 1993; Bongers *et al.*, 1999). However, some research findings have suggested that rainfall alone cannot be used as a good indicator of vegetation distribution patterns and that other factors should be considered (Bongers *et al.*, 1999; Gautier & Spichiger, 2004).

One of these factors is certainly land-use, and livestock grazing in particular (Linstädter & Baumann, 2013), which is a common practice in West Africa (Schumann, 2011). Many studies have investigated effects of grazing gradients on vegetation distribution (Pickup & Chewings, 1994; Sasaki *et al.*, 2008). Previous studies hold that grazing effects on plants are positive or negative depending on the position on the intensity gradient (Noy-Meir *et al.*, 1989; Cingolani *et al.*, 2005). Therefore, to adequately capture grazing impacts, it is important to sample the full range of grazing intensities from ungrazed to heavily grazed sites (Shipley, 2010). Besides climate and grazing, rangelands in this region exhibit a wide range of heterogeneity in response to topography and edaphic conditions, so their effect on plants also need to be considered to better understand vegetation distribution patterns. Soils are important for plant growth and different properties of soil (e.g. fertility and texture) affect plant species composition and distribution (Sylvain & Wall, 2011). Due to its influence on local resources such as soil moisture, light incidence, and soil fertility among others, topography also affects plant species distribution to varying degrees (Grant & Scholes, 2006). At landscape and regional scales, topography is known as one of the most important determinants of plant species composition because it provides a variety of different habitats (Augustine, 2003; Moeslund *et al.*, 2013). In this study, 'regional scale drivers' refer to all the climate-related variables including phenology and 'local scale drivers' refer to all the topo-edaphic plus management variables (also called ‘plot characteristics’) while ‘environmental variables’ refer to the whole range of drivers except spatial influence (i.e. geographic location).

Spatial variation (based on geographic location) has over the years received increasing importance in ecological theory and since most ecological data are spatially autocorrelated, it becomes necessary to consider spatial variation (Wiens, 1989; Borcard *et al.*, 1992). As has been shown by Legendre and Troussellier (1988), if the species and the environmental data sets share a spatial structure, the result could be an overestimation of the interactions between the species and the measured environmental variables.

The factors discussed above among others interact in a complex way in nature (Davies *et al.,* 2007) to shape patterns of vegetation composition. Climate and grazing for example are considered to have the most influential effects on the evolution of grasses (Milchunas *et al.*, 1988). An important concept in this context is the convergence model of aridity and grazing which states that aridity and grazing are convergent selective forces each one selecting simultaneously for higher drought and grazing resistances (Quiroga *et al.*, 2010). To disentangle the effects of different factors on vegetation, a promising approach is the simultaneous study of gradients or a combined gradient approach (Fukami & Wardle, 2005; Ren *et al.*, 2012). Despite the importance of combining gradients, many studies in West Africa focus on a single gradient (e.g. Schmidt *et al.*, 2010; Nacoulma *et al.*, 2011). There have been studies of gradient effects on economically relevant trees (Swaine *et al.*, 1992; Van Rompaey, 1993) and the few relating to herbaceous plant species composition have a local focus (Schmidt *et al.*, 2005; Schmidt *et al.*, 2011), which makes it difficult to upscale to broader geographical scales.

Using samples from a broad geographical area (47 sites and 450 plots across 106 000 km^2 in the West African Sudanian rangelands) and simultaneously analysing climate, topo-edaphic and land-use gradients, our study aims to identify the major plant communities, to determine their geographical distribution, and to assess their ecological relationships with hypothesised environmental factors. We specifically hypothesised that climate would be most important due to the steep south-north climatic gradient we studied.

2.3 Materials and methods

2.3.1 Study area

The study sites are located along a south-north climate gradient of increasing aridity reaching from northern Ghana to central Burkina Faso and covered an area of ~106 000 km^2 (Figure 2-1), enabling us to place our results within a macroecological context. The area is characterised by a unimodal rainy season from April to November in the south and May to September in the north with average annual rainfall sums between 1200 mm/a in the south and 600 mm/a in the north. The herbaceous layer is dominated by grasses and forbs: the most common species include *Brachiaria lata*, *Brachiaria jubata*, *Eragrostis turgida*, *Digitaria horizontalis*, *Spermacoce stachydea*, *Tephrosia pedicellata*, *Pandiaka angustifolia*, *Zornia glochidiata* and *Waltheria indica.*

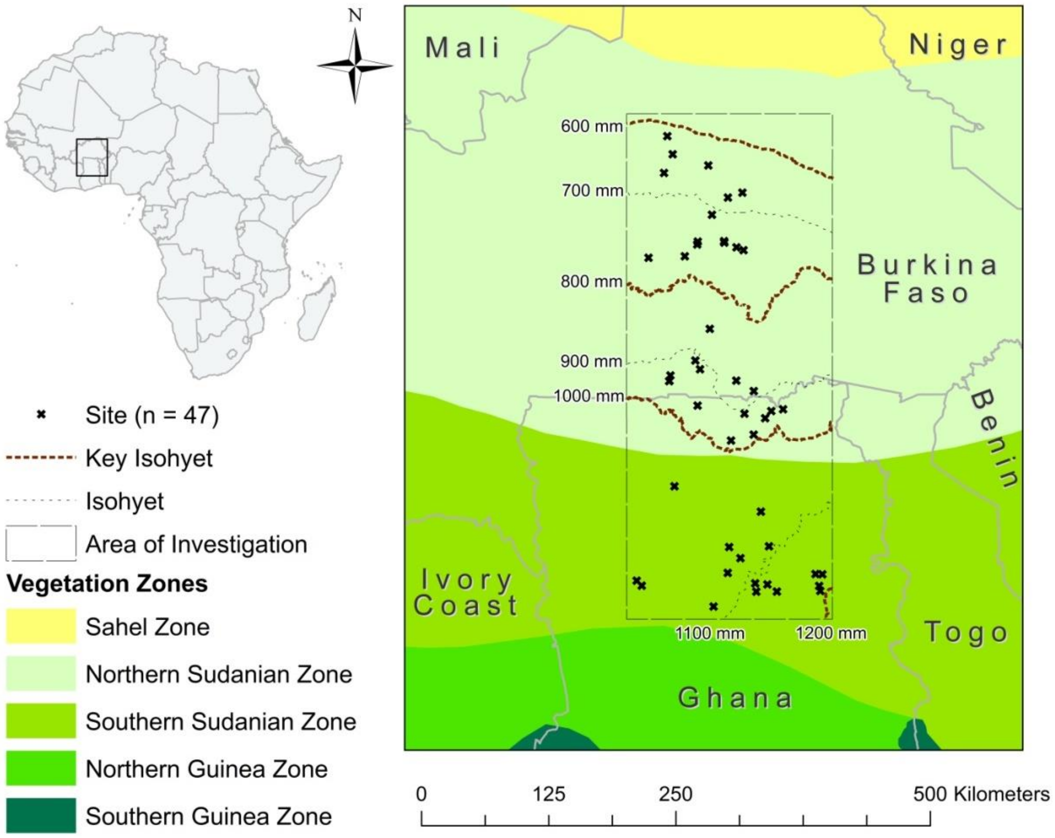


Figure 2-1: Study area and location of 47 sampled sites. The area covers the southern and northern Sudanian savanna vegetation zones following (White, 1983). Sampling is stratified into three zones of decreasing climatic aridity (hereafter called 'rainfall zones'), as indicated by isohyets (low rainfall: mean annual precipitation 600 – 800 mm/a; intermediate rainfall: 800 – 1000 mm/a; high rainfall: 1000 – 1200 mm/a).

The geology in the south of the climatic gradient is dominated by Voltain, Tarkwaian and Birimian systems (Carrier *et al.*, 2008) while the north is dominated by Precambrian crystalline rocks consisting of meta-igneous and intrusive granitic rocks (British

Geological Survey, 2002) with landforms dominated by rocky elevations within sedimentary basins (Butt & Bristow, 2013). The dominant soils are luvisols in the south (Wood, 2013) and lixisols in the north (Savadogo *et al.*, 2007). These soils have coarse texture (> 80% sand), low water holding capacity, and depending on the cultivation history, 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; its importance increases with climatic aridity (Blench, 1999; Mertz *et al.*, 2010). During the past decades, transhumant pastoralism has partly been replaced by more sedentary forms of herd management (Turner & Hiernaux, 2008; Brottem *et al.*, 2014), with livestock kept year-round in close proximity to settlements. Apart from few protected areas, grazing by wild animals is not considered an important driver of species composition in this area.

2.3.2 Sampling design

To address our research questions, we applied a preferential sampling within strata. The three principal strata were oriented along a gradient of climatic aridity (Figure 2-1). For site selection within strata, we tried to capture as much as possible of the variation in geology and land-use by choosing rangeland sites that maximised the range of grazing and topo-edaphic gradients. To capture the full range of grazing gradient in the three climate zones, we sampled ranging from heavily utilised sites to protected areas (two per climate zone). To capture regional variation in topo-edaphic conditions, we used a geological map to select rangeland sites in major geological units. Within sites, we preferentially placed nine plots representing three per slope position (upslope, midslope and lowland) to assess local topography and soil characteristics. We avoided the inclusion of distinct ecotones within these plots. To avoid seasonal bias and to capture intraseasonal dynamics of species distribution, we sampled during two growth periods (June to October 2012 and 2013) and varied the time of sampling independent of the above-mentioned sources of variation. The number of sites amounted to 47 with a 3 km minimum distance between sites to reduce effects of spatial autocorrelation. The size of each square plot was 10 m x 10 m and three 1 m² circular subplots were randomly placed within each square plot for the assessment of vegetation attributes. In total, 450 plots and 1350 subplots were sampled. For each plot, we recorded the geographical positioning system coordinates; obtaining the latitude and longitude as indicators of spatial variation.

2.3.3 Data collection

Regional scale drivers (climate)

For each site, climatic data for the period 1950 – 2000 was obtained from the WorldClim (http://www.worldclim.org/; (Hijmans *et al.*, 2005)) database. Eleven variables related to plant growth were used (see Table 2-1). We calculated the UNEP aridity index (AI) as the ratio of MAP to potential evapotranspiration (UNEP, 1997).

Table 2-1: Worldclim bioclimatic variables used in this study. NA = not applicable

Variable	Acronym	Unit
Mean annual temperature	MAT	°C
Isothermality	ISO	NA
Temperature seasonality	TS	NA
Maximum temperature of the warmest month	T_{Max}	°C
Minimum temperature of the coldest month	T_{Min}	°C
Mean temperature of wettest quarter	MTWeQ	°C
Mean annual precipitation	MAP	mm
Precipitation of wettest month	PWM	mm
Precipitation seasonality	PS	NA
Precipitation of the wettest quarter	PWeQ	mm
Aridity index (UNEP)	AI	NA

Local scale drivers (plot characteristics)

The local scale drivers were grouped into topo-edaphic variables (topography and soil), land-use related variables and vegetation data.

Topo-edaphic variables

Besides slope position and bare soil cover, we recorded a suite of variables related to a plot's soil characteristics (see Appendix 1 for details). Following FAO (2006), we estimated the cover of soil surface fragments. To quantify physical and chemical soil properties, a composite sample from five soil cores (0–4 cm depth) per plot was collected. Samples were homogenised, air-dried for more than 21 days, and shipped to the Soil Laboratory at the Department of Geography, University of Bonn, Germany. Here, soil fractions < 2 mm were analysed. Particle size distribution was determined by laser diffraction method, using a Laser Particle Size Analyser (Horiba LA–960). Soil acidity was determined in a 1:2.5 water suspension. Plant-available phosphorus was measured via calcium-acetate-lactate (CAL) extraction (mg kg^{-1}), following standard protocols (VDLUFA, 2008). Soil N and C content was analysed by dry combustion with a CN analyser (Vario EL cube).

Land-use intensity

As main proxies for land-use intensity, we recorded six biotic surface characteristics with a known positive (+) or negative (-) response to increasing grazing pressure in (sub-) tropical savannas (Zimmermann *et al.*, 2010; Linstädter *et al.*, 2014). We estimated the cover of cattle and donkey dung (+), smallstock droppings (+), litter (-), biological soil crusts (-), earthworm excrements (-), and moribund material (-). We also combined physical evidence of grazing (trampling, dung, and the removal of standing biomass) in an expert assessment of recent grazing pressure (following Linstädter *et al.*, 2014).

Vegetation data

Phytosociological relevés were conducted during the rainy seasons of 2012 and 2013. We visually estimated the ground cover of all vascular plants (identified to the species level) within subplots, and measured species' vegetative height to the nearest centimeter. We included seedlings and saplings (≤2 m) of woody species, following Le Roux *et al.* (1995). To sort out sampling biases due to season we also recorded species' phenological stage, using a simplified BBCH scale (Hess *et al.*, 1997). We distinguished between germinating (0), sprouting (1), shooting (2), flowering (3), fruiting (4), and senescent (5). We calculated species' biovolume per quadrat as cover x height (Jauffret & Visser, 2003) and obtained plot-level cover and biovolume as average of the three subplot values. The species biovolume data was then used to create a plots-vs-species matrix.

2.3.4 Data Analyses

The analyses involved three steps. First, we reduced the number of explanatory environmental variables to avoid multicollinearity. Second we estimated the relationships between environmental variables and species composition. Finally, we applied cluster analysis and ordination to ease description of the found pattern.

Step 1: Selection of explanatory environmental variables

We performed separate principal component analyses (PCAs) to select potential drivers of vegetation composition from eleven variables available on site level (regional scale variables) and twenty variables recorded on plot level (local scale variables). We then identified variables highly loading ($\geq|0.8|$) on principal components (PC) with eigenvalues > 1 to reduce collinearity within variable sets. In case of competing variables (several terms highly loading on the same PC), we chose the variable with the highest proportion of explained variance in single-variable models. In addition, we chose grazing pressure (GP), slope position (SP) and phenophase (Phen) as potential drivers. Given their ordinal nature, GP and SP could not be included in the PCA-based selection routine and were included in further analyses due to their prevalent importance (Augustine, 2003; Ouédraogo *et al.*, 2015). Phenophase was selected to account for intraseasonal variability (Brüser *et al.*, 2014). Spearman's rank correlation was used to check multicollinearity.

Step 2: Testing the correlation between environmental variables and species abundance

We used Mantel tests to obtain the correlations (based on Pearson correlation coefficients) between selected explanatory variables and species abundance. The Mantel test is used to test the correlation between two square symmetrical (distance) matrices and is an alternative to regressing one matrix against the other but circumvents the problem of partial dependences within each matrix (McCune & Grace, 2002). We avoided the use of Mantel's significance estimates (p values) because the cells of our distance matrices are not independent of each other. To obtain an idea of spatial influence on environmental variables, we also tested the strength of relationship (correlation coefficient) between each environmental variable and space (i.e. geographic location). Geographic location was taken as the composite of latitude and longitude. Additionally, we used multiple linear regressions (based on distance matrices) to partition explained variation (in species data) into environmental and spatial components (Legendre *et al.*, 2005).

Step 3: Vegetation classification and ordination

We used hierarchical divisive clustering to classify species into plant communities. The default settings of Isopam – isometric feature mapping and partitioning around medoids – (Schmidtlein *et al.*, 2010) were used for the cluster analysis with Bray-Curtis as the dissimilarity coefficient. The plots-vs-species data were log transformed in order to reduce skewness and kurtosis. Isopam is a useful tool when groups with many good indicator species and high overall fidelities of species to clusters are desired and it often results in high quantity and quality of indicator species per group (Schmidtlein *et al.,* 2010). Each of the resulting clusters was summarised and described using species relative abundance and field notes. Diagnostic species for clusters were determined using the G statistic fidelity coefficient (Sokal & Rohlf, 1995). Statistical significance was obtained by a simultaneous calculation of Fisher's exact test. Species with phi values higher than 0.26 and Fisher's exact test significance lower than 0.05 were deemed to be diagnostic. To support results of the Mantel tests and hierarchical classification and to analyse relationships between environmental variables and the distribution pattern of herbaceous vegetation clusters, non-metric multidimensional scaling (NMDS) was performed. The NMDS was done using Bray-Curtis dissimilarity measure and a three-dimensional solution was chosen for the analysis with 50 random starts in search of the stable solution. To visualise relationships between the distribution of vegetation types and environmental variables, we fitted environmental vectors onto the ordination using variables with relatively high Mantel correlation (i.e. > 0.2). All analyses were conducted using the statistical software R in version 3.2.2 (R Core Team, 2015).

2.4 Results

2.4.1 Selected potential explanatory environmental variables

From the two PCAs, we selected nine variables (see Appendix 2 for PCA results) for further analyses. In total, fourteen variables were selected as potential drivers of vegetation composition (Table 2-2).

Table 2-2: Selected explanatory environmental variables. Local scale and regional scale drivers were selected via principal component analysis except phenophase, slope position and grazing pressure.

Variable set	Variable	Acronym	Mean	Standard deviation	Min.	Max.
Geographic location	Longitude	Lon	-1.07	0.41	-1.88	-0.22
	Latitude	Lat	10.96	1.32	9.13	13.32
Regional scale	Precipitation seasonality	PS	77.16	13.83	52.58	100
	Precipitation of the wettest month	PWM	230.7	19.82	196.0	271
	Mean annual temperature	MAT	27.93	0.341	26.92	28.38
	Phenophase	Phen	2.54	0.673	1.02	4.96
Local scale	Soil nitrogen content	N	0.089	0.064	0.030	0.670
	Soil acidity	pH	5.325	0.505	3.900	6.900
	Soil silt content	Silt	38.60	15.07	11.71	87.85
	Fine gravel cover	FG	11.53	9.17	0.000	50.00
	Coarse gravel cover	CS	13.04	16.88	0.000	91.50
	Stone cover	SS	9.21	15.44	0.000	75.80
	Slope position [a]	SP	-	-	1	3
	Grazing pressure [b]	GP	-	-	1	5

[a] Categorical variable (1-3) – lowland (1), midslope (2), upslope (3)

[b] Ordinal scale (0-4) – 0 (very light GP), 1 (light GP), 2 (moderate GP), 3 (heavy GP), 4 (very heavy GP)

2.4.2 Total explained variance by all explanatory variables

We found that 22.8% of variation in species data was related to all the explanatory variables (geographic location, climate and plot characteristics) while 77.2% remained unexplained (Figure 2-2a; in the following we use the term "explained" even though there is not necessarily a causal relation). Of the explained variance, environmental variables (i.e. plot characteristics plus climate variables) were more important than geographic location (explained 12.2% and 1.3% of variance respectively; Figure 2-2a). The amount of variance jointly explained by environmental variables and geographic location (9.3%) was also higher than variation due to geographic location alone (Figure 2-2a).

Table 2-3: Mantel test results showing the correlation; (1) between species composition and measured environmental variables and (2) between geographic location (space) and environmental variables.

Variable set	Variable	Mantel correlation (r) – variables and vegetation	Mantel correlation (r) – environment and location
Geographic location	Location (Lat/Lon)	**0.3264**	
Regional scale	Mean annual temperature	0.1387	0.1281
	Precipitation seasonality	**0.2691**	**0.9442**
	Precipitation of the wettest month	**0.3126**	**0.2883**
	Phenophase	**0.2024**	0.1222
Local scale	Total nitrogen	0.0586	0.0206
	Soil acidity	0.0902	0.0115
	Soil silt content	0.0504	0.0101
	Fine gravel cover	0.0291	-0.0006
	Coarse gravel cover	0.1038	0.0107
	Stone cover	0.0560	0.1348
	Slope position	0.0574	-0.0024
	Grazing pressure	**0.2184**	0.0427

2.4.3 Relationship between species composition and geographic location

Our results showed that geographic location had the highest correlation with species composition (Table 2-2). However, only 3.1% of the total explained variation in species composition was independently related to geographic location (Figure 2-3). A relatively high amount of explained variance (9.3%) was shared by environment (climate and plot characteristics) and geographic location (Figure 2-2a). As expected, the amount of shared explained variance between geographic location and climate was much higher than that between geographic location and plot characteristics (Figure 2-3). This was also corroborated by higher correlations between geographic location and climate variables than between geographic location and plot characteristics (Table 2-3).

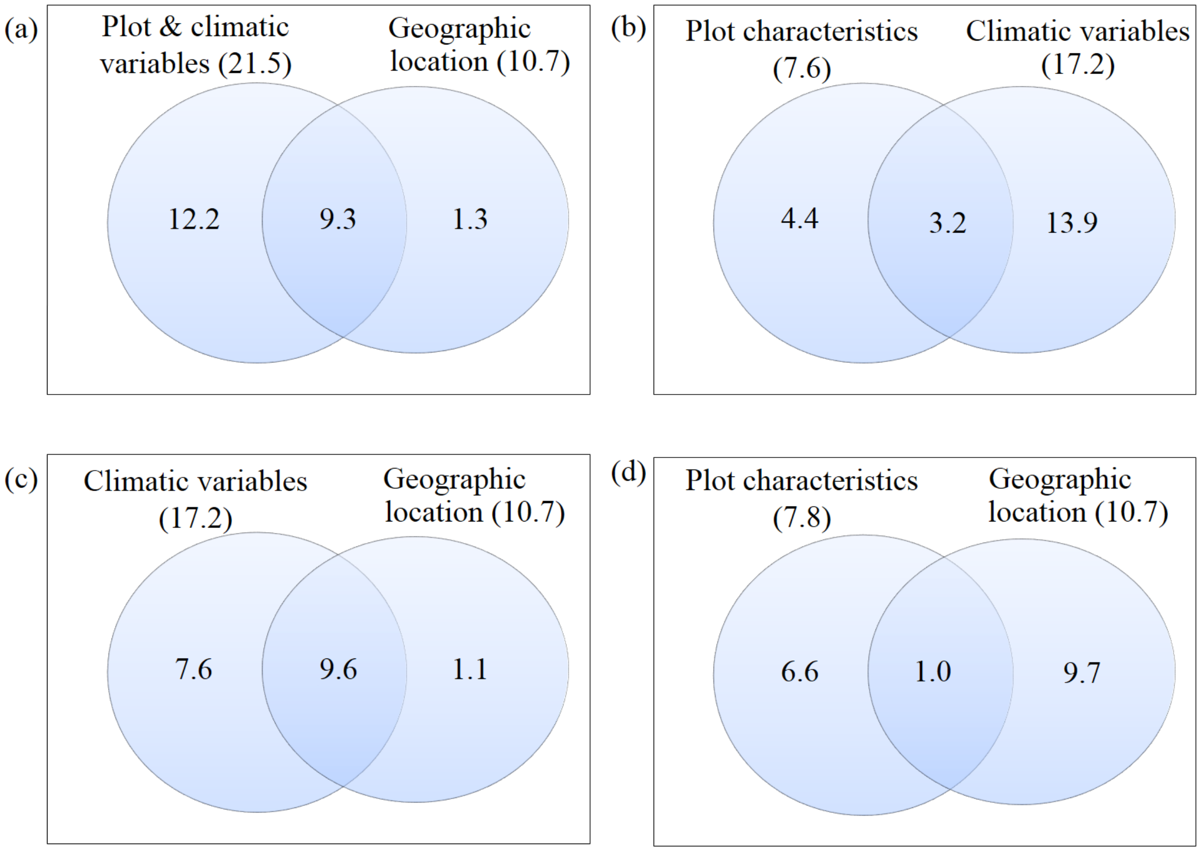


Figure 2-2: Two-set Venn diagrams showing variance explained by variable sets; (a) environment and geographic location (space), (b) plot characteristics (local scale drivers) and climate (regional drivers), (c) climate and geographic location, (d) plot characteristics and geographic location. All numbers represent percentages of explained variance.

2.4.4 Relationship between species composition and climate

Among the environmental variables, climate variables had higher correlation with species composition (Table 2-3) and explained more variance than plot characteristics (Figure 2-2b) and geographic location (Figure 2-2c) both independently and in totality. Precipitation seasonality and precipitation of the wettest month were the most important climate variables (Table 2-3).

2.4.5 Relationship between species composition and plot characteristics

The variable set, plot characteristics was less important than climate (Figure 2-2b) and geographic location (Figure 2-2d) when compared separately. However, when all three variable sets were considered together, plot characteristics were more important than geographic location but less important than climate (Figure 2-3). Plot characteristics accounted for 17.9% of the total explained variance in species composition (Figure 2-3). Among plot characteristics, grazing pressure was the most important variable: it had the highest correlation with species composition (Table 2-3).

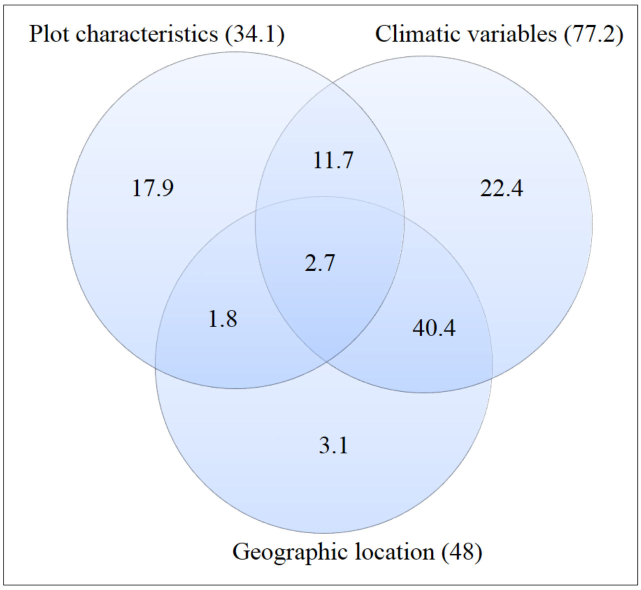


Figure 2-3: Three-set venn diagram showing the percentage of total explained variance accounted for independently by variable sets; plot characteristics (local scale drivers), climate (regional scale drivers), geographic location (space) and the shared variance. All numbers represent percentages.

2.4.6 Distributional patterns of vegetation clusters

The cluster analyses and non-metric multidimentional scaling (NMDS) ordination were used to derive vegetation clusters and to visualise the major gradients underlying vegetation composition, respectively. From the cluster analysis result, the second level of grouping gave the maximum of insights into the ecology of the plots, resulting in ten clusters (Table 2-5). NMDS ordination result showed that a three-dimensional solution (stress = 0.21) appeared useful with our data and the three axes together accounted for 52% of total variation in species data (Table 2-4).

Table 2-4: Variance explained by NMDS ordination axes.

NMDS axes	Explained variance
Axes 1	23%
Axes 2	18%
Axes 3	11%
Cumulative variance	52%

The NMDS stress = 0.21

The resulting ordination showed clumps representing the arrangement of clusters along gradients of grazing pressure and precipitation or latitude (Figures 2-4 and 2-5). This arrangement, of clusters, represents the correlations between species composition and environmental variables and or gradients. Clusters arranged close to each other represent similarity in ecological requirements (i.e. short distances between them). Axes 1 and 2 were more important (related to 23% and 18% of total variation respectively) and better delineated than axis 3 (related to 11% of total variation). Overlaid environmental variables on NMDS diagrams suggests that axis 1 better correlated with grazing pressure (Figure 2-4a and Appendix 3) while axes 2 and 3 were better correlated with precipitation (i.e. precipitation seasonality in Figure 2-4b and precipitation of the wettest month in Figure 2-4c, d). Due to the strong correlation between precipitation and latitude (*cf.* Table 2-3), axes 2 is also correlated with latitude (Figure 2-5a). The results of the cluster analysis also generally reflect the most important trends in the species data (i.e. related to precipitation and grazing pressure) as indicated by the overlay of generated vegetation clusters and important environmental variables on NMDS ordination diagrams (Figures 2-4 and 2-5). Clusters 4 and 9 which are at opposite ends of axis 1 are mainly indicated by annual herbaceous plants and perennial plants respectively (*cf.* Table 2-5). Also, the opposite ends of axes 2 are occupied by clusters 10 and 3 which are composed of plant species that differ in their ecological requirements (discussed later).

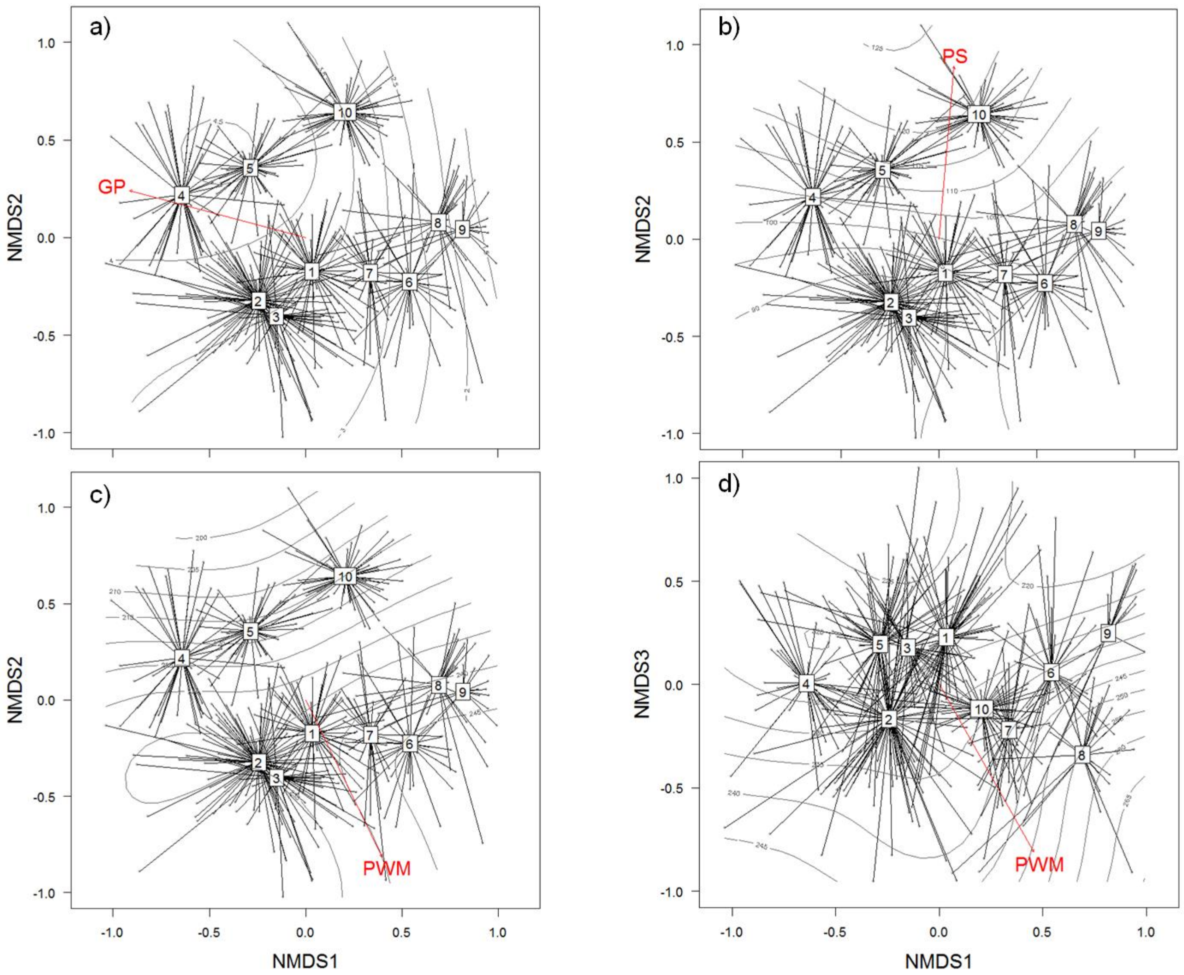


Figure 2-4: NMDS ordination of herbaceous vegetation data showing the distribution of 10 vegetation clusters and isoline trends in environmental variables; (a) grazing pressure (b) precipitation seasonality (c) precipitation of the wettest month along axes 1, 2 and (d) precipitation of the wettest month along axes 1, 3. Vectors indicate direction and relative strength of trends in relation to the plotted axes.

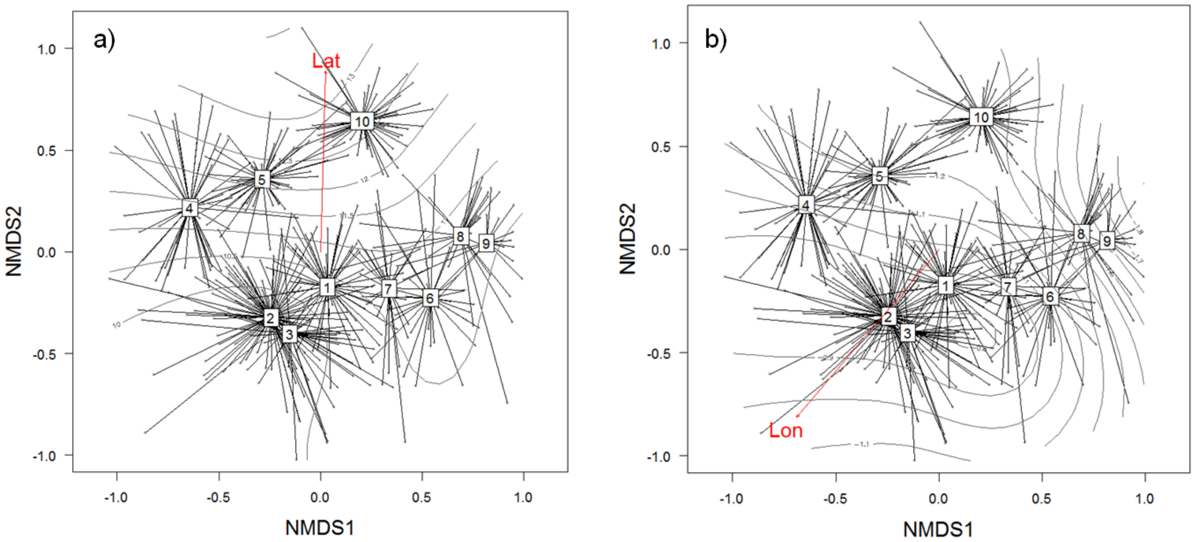


Figure 2-5: NMDS ordination of herbaceous vegetation data showing the distribution of 10 vegetation clusters and isoline trends in (a) latitude and (b) longitude.

Table 2-5: Synoptic table showing percentages of diagnostic species occurrences (bold values) identified by cluster analysis. The diagnostic species have phi values > 0.26 and Fisher's exact test significance < 0.05 and are presented in descending order of indicator value.

Cluster No. and No. of plots	1 (59)	2 (93)	3 (38)	4 (43)	5 (56)	6 (34)	7 (30)	8 (25)	9 (15)	10 (57)
Cluster name	Brac.stig	Sper.fili	Spor.pyra	Brac.lata	Zorn.gloc	Andr.gaya	Indi.brac	Andr.chin	Hypa.smit	Penn.seta
Brachiaria stigmatisata	**39**	6	5	16	7	3	0	0	0	2
Indigofera dendroides	**29**	1	0	0	7	6	0	4	7	7
Cynodon dactylon	**15**	1	0	0	4	0	0	0	0	0
Digitaria nuda	**12**	0	0	0	0	0	0	0	0	0
Indigofera aspera	**10**	0	0	0	0	0	0	0	0	0
Spermacoce filifolia	49	**68**	11	19	38	26	10	24	20	7
Commelina nigritana	3	**38**	16	33	2	3	3	4	0	0
Acroceras amplectens	3	**24**	0	9	2	0	0	0	0	0
Indigofera congolensis	0	**10**	0	0	0	0	0	0	0	0
Sporobolus pyramidalis	73	49	**84**	7	25	21	47	8	0	0
Stylochaeton hypogaeus	19	54	**76**	28	2	21	13	8	0	4
Phyllanthus amarus	24	23	**63**	21	4	24	10	16	0	0
Indigofera paniculata	3	4	**55**	0	0	12	3	12	20	2
Cyperus iria	2	1	**50**	26	0	12	0	0	0	2
Tephrosia nana	14	1	**42**	2	0	32	0	24	7	4
Digitaria ciliaris	2	4	**34**	5	4	21	10	0	0	0
Cissus cornifolia	0	1	**26**	9	0	9	0	0	0	0
Amorphophallus aphyllus	0	3	**21**	0	0	0	0	0	0	0
Triumfetta pentandra	2	0	**18**	7	0	0	3	0	0	0
Flueggea virosa	0	0	**13**	0	0	0	3	0	0	2
Brachiaria lata	22	59	74	**84**	54	0	3	0	0	9
Digitaria horizontalis	5	25	32	**79**	30	0	0	8	0	4
Senna obtusifolia	36	14	8	**63**	61	3	10	0	0	39
Dactyloctenium aegyptium	37	5	24	**60**	7	0	0	0	0	14
Chloris pilosa	3	3	5	**28**	5	0	3	0	0	2
Pycreus lanceolatus	0	3	0	**16**	0	3	0	0	0	0
Synedrella nodiflora	0	0	0	**12**	0	0	0	0	0	0

Table 2-5 continued

Zornia glochidiata	24	2	3	51	**82**	3	3	0	0	58
Alysicarpus ovalifolius	14	16	0	33	**66**	6	3	0	7	7
Brachiaria jubata	22	10	29	26	**59**	9	3	0	0	5
Microchloa indica	0	4	11	16	**55**	3	3	12	13	32
Eragrostis amabilis	7	1	3	5	**54**	0	0	0	0	0
Eleusine indica	2	1	0	30	**46**	0	0	0	0	0
Chrysanthemum americanum	2	4	0	14	**36**	0	7	0	0	12
Tripogon minimus	5	0	0	0	**34**	0	3	0	0	2
Portulaca oleracea	0	0	0	0	**14**	0	0	0	0	0
Andropogon gayanus	2	10	16	5	4	**85**	20	44	0	11
Striga dalzielii	2	1	3	0	0	**18**	0	0	0	2
Indigofera bracteolata	39	25	45	5	7	71	**77**	60	20	14
Heteropogon contortus	0	26	0	7	0	6	**70**	0	0	7
Aneilema setiferum	0	5	0	5	0	24	**57**	8	0	2
Striga hermonthica	8	11	11	7	5	0	**43**	20	0	25
Indigofera leprieurii	12	5	8	9	0	12	**40**	4	27	5
Aspilia paludosa	2	6	3	2	2	12	**37**	0	20	2
Andropogon chinensis	2	3	0	0	0	9	10	**72**	0	2
Aspilia bussei	0	3	0	0	0	3	0	**48**	20	23
Andropogon pseudapricus	0	0	0	0	0	3	0	**32**	0	4
Ctenium elegans	0	1	0	0	0	12	0	**32**	0	2
Buchnera hispida	0	0	0	0	0	0	0	**28**	0	11
Hyparrhenia glabriuscula	0	0	0	0	0	0	0	**28**	0	4
Chasmopodium caudatum	0	0	0	0	0	0	0	**20**	0	2
Schizachyrium brevifolium	0	0	0	0	2	6	0	**20**	0	2
Schizachyrium sanguineum	0	0	0	0	0	0	0	**20**	0	0
Polycarpaea eriantha	2	0	0	0	2	0	0	**12**	0	0
Hyparrhenia smithiana	0	0	0	0	0	0	0	8	**93**	2
Hyparrhenia cyanescens	0	0	0	0	0	0	0	0	**87**	0
Monechma ciliatum	14	12	18	2	2	12	3	32	**87**	0

Table 2-5 continued

Scoparia dulcis	0	0	13	7	0	0	3	8	**60**	0
Lepidagathis anobrya	3	1	0	0	0	0	0	20	**47**	0
Tephrosia elegans	0	5	11	0	0	21	13	0	**47**	0
Aspilia rudis	0	0	0	0	0	0	3	4	**40**	0
Cochlospermum planchonii	2	3	3	0	2	21	7	16	**33**	0
Tinnea barteri	2	0	0	0	0	6	0	0	**33**	2
Andropogon schirensis	0	2	3	0	0	18	7	0	**27**	0
Cochlospermum tinctorium	5	2	3	0	0	24	7	4	**27**	0
Crotalaria hyssopifolia	0	0	0	0	0	0	0	8	**27**	0
Euclasta condylotricha	0	0	0	0	0	0	0	0	**27**	0
Loudetia simplex	0	1	0	0	0	0	0	24	**27**	0
Gladiolus gregarius	0	0	0	0	0	3	3	4	**20**	0
Panicum anabaptistum	0	3	0	0	0	0	0	0	**20**	0
Pennisetum setaceum	0	0	0	7	2	0	0	28	0	**89**
Hyparrhenia involucrata	0	0	0	2	0	3	7	84	0	**84**
Loudetia togoensis	0	1	0	5	11	0	7	4	0	**79**
Elionurus elegans	0	1	0	2	0	3	3	28	0	**72**
Waltheria indica	51	29	26	40	39	15	23	0	7	**72**
Hackelochloa granularis	2	2	18	7	0	0	37	4	0	**53**
Polygala arenaria	8	12	0	16	32	6	17	16	13	**53**
Evolvulus alsinoides	2	3	0	5	30	0	7	0	0	**46**
Spermacoce chaetocephala	0	2	0	19	0	0	3	12	0	**39**
Cymbopogon schoenanthus	2	0	0	0	4	0	13	0	0	**37**
Schoenefeldia gracilis	0	4	0	19	0	0	13	0	7	**35**
Ipomoea coscinosperma	0	0	0	0	2	3	0	0	0	**23**
Tephrosia gracilipes	0	0	3	0	0	0	3	0	0	**18**
Eragrostis tremula	0	0	0	2	0	0	0	0	0	**12**
Wissadula amplissima	0	0	0	0	0	0	0	0	0	**9**

2.5 Discussion

Examining the relationships between species composition and environmental variables helps us to understand species composition and distributional patterns in space. This study investigates the effects of local scale drivers (plot characteristics), regional scale drivers (climate variables) and space (geographic location) on herbaceous species composition along gradients of climatic aridity, topo-edaphic conditions and land-use intensity (grazing pressure). The findings support the view that climate is the most important driver of vegetation at large spatial scales and that land-use plays a modifying role on the effects of climate at local (small) scales (Bucini & Hanan, 2007). The floristic composition recorded in this study is consistent with findings by other researchers (e.g. Lebrun *et al.*, 1991; Schmidt *et al.*, 2011) who reported from their study in Burkina Faso, that Poaceae is the most species-rich family of vascular plants followed by Fabaceae and Cyperaceae.

2.5.1 Total explained variance by all explanatory variables

The high unexplained variation (77.2%) is probably due to high heterogeneity in our data and wide coverage of sampling, resulting in high beta diversity; these same reasons might also explain the high stress value from the ordination (McCune & Grace, 2002). The unexplained variance is most likely related to local processes (biotic or abiotic and their interactions) considering the fact that the total variation accounted for by geographic location (space) alone was small (1.3% or 3.1% of the total explained variance in species data) indicating that no (or little) fundamental spatial-structuring processes have been missed during data collection (Borcard *et al.*, 1992).

The relatively high amount of explained variance shared by environment and geographic location (9.3%) shows that the species and environmental data have a fairly similar spatial structuring, which may be due to common underlying causes or the direct response of the species data to spatially structured environmental conditions (Borcard *et al.*, 1992). For example, grazing, species composition and precipitation are similarly organised in space. Grazing pressure in our study area tends to increase along the climatic gradient of decreasing precipitation from south to north. The similar trends between grazing and climate might be explained by the influence of climatic conditions (especially rainfall) on land-use choices; livestock is more important in drier sites (Mertz *et al.*, 2010).

2.5.2 Relationship between species composition and geographic location

Although there was a relatively high correlation between species data and geographic location, only a small proportion of the total explained variance in species composition

(3.1%) was related independently to geographic location. This indicates that very little spatial variation has been missed (see above). The amount of explained variance attributable to geographic location (space) alone can be taken as a descriptor of unmeasured underlying processes including external causes and biotic factors (Borcard *et al.*, 1992). The findings of this study are in line with those of Greve *et al.* (2011) who found that rangeland vegetation distribution across Africa was poorly predicted by investigated environmental variables and concluded that hidden factors such as competition may assume a greater role (Scholes & Archer, 1997).

2.5.3 Relationship between species composition and climate

Climatic variables (regional scale drivers) were more important drivers of herbaceous vegetation composition than plot characteristics (i.e. topo-edaphic and land-use variables). Since temperature is not limiting in the tropics, precipitation (during the wettest month and intraseasonal distribution) was the most important climatic driver of herbaceous species composition. The Mantel test results were corroborated by NMDS ordination results as we inferred that two of the axes (i.e. 2 and 3) were related to climate. The clumping of clusters at opposite ends of axis 2 was interpreted with the help of field notes and ecological knowledge revealing that all plots in cluster 10 (with a positive value on axis 2) were sampled in the low rainfall zone (north of the climatic gradient) and was typically represented by species which are adapted to arid sites (Akoegninou *et al.*, 2006). The species were mostly annual plants such as *Hyparrhenia involucrata*, *Loudetia togoensis*, *Elionurus elegans* etc but also some aridity tolerant perennials like *Pennisetum setaceum*. On the other hand all the plots in cluster 3 were sampled in the high rainfall zone (south of the climatic gradient) and were typically dominated by species which are suited to high moisture conditions (Akoegninou *et al.*, 2006). Under arid conditions, the concept of habitat filtering shapes vegetation composition by allowing only species which are tolerant of the arid conditions to survive. Habitat filtering in general imposes ecological filters that select species because they possess a trait syndrome suitable for a given habitat (Keddy, 1992; Díaz *et al.*, 1998). This explains why annual plants were mostly found in cluster 10 as opposed to cluster 3. Considering the strong correlation between geographic location and precipitation, it is not surprising that latitude was also highly correlated with axis 2. Our result that climate (precipitation) was a more important driver of herbaceous vegetation composition than plot characteristics, which is in accordance with our expectations, is well documented for different vegetation types in Africa, such as forests (e.g. Van Rompaey, 1993; Bongers *et al.*, 1999), woody vegetation (e.g. Sankaran *et* *al.*, 2005; Bucini & Hanan, 2007) and herbaceous vegetation (e.g. Bocksberger *et al.*, 2016; Zerbo *et al.*, 2016). Precipitation seasonality may be associated with the magnitude, timing, and duration of the wet and dry seasons (Borchert, 1999). Aspects of precipitation seasonality – such as start of the rainy season and wet season length – play important roles in plant growth (Schwartz, 2003). Changes in rainfall regimes, a possible outcome of climate change, is expected to exert more serious impacts in arid and semiarid regions (Trenberth et al., 2007). More generally, precipitation has been found to be the most important determinant of species distribution for all land cover types across Africa (Adams, 2007; Greve *et al.*, 2011).

As expected, there was a higher overlap between geographic location (i.e. spatially explained variance) and climate (40.4% of the total explained variance) than between geographic location and plot characteristics (1.8%). Independent of plot characteristics, climate accounted for 62.8% of the total explained variation while plot characteristics accounted for 19.7% of total explained variation independent of climate. This result agrees with our hypothesis that, at the selected scale of study, climate is a more important driver of herbaceous vegetation composition than land-use due to the steep climatic gradient present in the study area.

2.5.4 Relationship between species composition and plot characteristics

Our results showed grazing to be the most important local scale driver of species composition. Similarly, NMDS axis 1 (related to 23% of variation in species data) was related to grazing pressure.

The clumping of clusters composed of annual plants (e.g. cluster 4) and perennial plants (e.g. cluster 9) to two opposite ends of axis 1 was interpreted with the help of field data and ecological knowledge revealing that cluster 4 (with a negative value on axis 1) comprised of heavily grazed plots from all rainfall zones and was typically represented by annual species (*Brachiaria lata, Digitaria horizontalis, Senna obtusifolia, Dactyloctenium aegyptium, Chloris pilosa, and Synedrella nodiflora)* which are known to be well adapted to disturbed sites (Akoegninou *et al.*, 2006). Similarly, clusters 6, 8 and 9 (on the positive end of axis 1) were composed of plots from lightly grazed sites with relatively higher moisture (all from high and intermediate rainfall zones). These clusters (6, 8 and 9) were typically dominated by hemicryptophytes (*Andropogon gayanus, Andropogon chinensis* and *Hyparrhenia smithiana*) which are suited to sites with high moisture and low disturbance (Akoegninou *et al.*, 2006). Clusters 8 and 9 with the highest positive values on axis 1 have plots from protected areas in Nazinga Park and Mole Park respectively. Three of the plots in the Mole National Park which were (relatively) heavily grazed by wild herbivores were grouped into cluster 2; composed of annual species. This cluster was typically represented by *Spermacoce filifolia, Commelina nigritana, Acroceras amplectens* and *Indigofera dendroides*. This suggests that land-use (in this case grazing) could modify the effect of climate on vegetation composition at small spatial scales.

Several researchers have investigated the relative importance of land-use and climate on vegetation distribution at different spatial scales. Consistent with our findings, Greve *et al.* (2011) reported a weak effect of anthropogenic impacts on vegetation distribution at a large scale while other researchers (e.g. Nyssen *et al.*, 2004; Kiage & Liu, 2009) have shown that anthropogenic activities affect vegetation on a local scale. From the foregoing, land-use activities or disturbances, such as grazing, can be seen to play a modifying role on the effects of climate at local (small) scales (Bucini & Hanan, 2007). Therefore, under similar climatic conditions, other factors such as grazing become important for distinguishing herbaceous vegetation distribution. Grazing could exert drastic impacts on plant communities as it could lead to complete shifts in species composition from palatable grazing intolerant to unpalable grazing tolerant species (Zhang *et al.*, 2004). Intensive grazing could also lead or contribute to biotic homogenisation (McKinney & Lockwood, 1999; Smart *et al.*, 2006) thus eliminating several species (losers) and replacing them with few species which are able to tolerate prevailing conditions (winners). This could explain the absence of perennial species in highly grazed sites (e.g. in cluster 4). In concordance, Nacoulma *et al.* (2011) found that perennial grasses are usually favoured fodder species during their young stages and are weakened by continuous grazing.

2.6 Conclusion

The study aimed at determining drivers of herbaceous species composition on a regional scale along climatic, topo-edaphic and land-use gradients in West Africa. The approach, using combined gradients and variance partitioning, to disentangle climatic, plot characteristics and spatial effects was successful; the findings support the much-stated hypothesis that climate (particularly precipitation) is the most important driver of species composition in this region. The use of space-time substitution approach allows us to make inferences about how climate change might affect herbaceous vegetation in the region. Our results suggest that land-use factors act as modifiers of climate imposed changes on vegetation. This implies that appropriate management strategies could help mitigate climate change impacts on plants whereas inappropriate strategies could worsen climate change effects. The promising success of combined gradient analysis and variance partitioning could be used in future research to better understand plant diversity across different spatial scales.

3 Drivers of taxonomic and functional diversity in West African Sudanian savannas

3.1 Abstract

Which factors influence the different aspects of species and functional diversity in Sudanian savannas of West Africa? Rangelands' health and functioning is closely related to the diversity of plants and their traits. Plant diversity is interactively driven by biotic and abiotic environmental factors. The importance of these drivers for plant diversity, and particularly for functional diversity, is still poorly understood. Additionally, there is limited knowledge about how different aspects of taxonomic diversity relate to functional diversity measures. This lack of adequate knowledge affects ecosystem management and the provision of services from ecosystems. By sampling a wide area (covering ~106 000 km²), this study investigates the relationship between different biodiversity measures and environmental variables. The study area comprises a steep gradient of climatic aridity across West Africa's Sudanian savannas ranging from northern Ghana to central Burkina Faso, in combination with local gradients of topo-edaphic conditions and land-use intensity. Using three taxonomic diversity indices and three functional diversity indices as response variables, linear mixed-effect models and model selection were applied to test the links between ten environmental variables and the diversity indices. We found that climate and disturbance were more important than topo-edaphic variables; particularly for functional diversity indices. Precipitation seasonality was the most important driver of species richness, functional evenness and functional divergence. Grazing pressure was most important for functional richness while soil clay content and slope position were most important for species evenness and Simpson's diversity index. Our study showed inconsistent diversity-grazing relationships for different diversity indices suggesting that the intermediate disturbance hypothesis cannot be extended to all measures of diversity. There were no strong correlations between any of the taxonomic and functional diversity indices suggesting that single taxonomic diversity measures should not be used to represent functional diversity. These results are useful for land managers and can be used as a guide for conservation planning and rangeland management in general.

3.2 Introduction

The study of biodiversity and its response to changes in environmental conditions is a question of major interest in ecological research (Currie *et al.*, 2004; de Bello *et al.*, 2006). Both taxonomic diversity and functional diversity are important concepts affecting ecosystem functioning and therefore need to be understood for better ecosystem management and conservation (Da, 2010). Taxonomic diversity is mostly represented by two concepts; species richness (SRic) and species evenness (SEve). Species richness refers to the number of individual species in a community, while SEve is a measure of the relative abundance of the different species (homogeneity) making up the richness of an area (Colwell, 2012). Additionally, various diversity indices have been proposed such as the Simpson's diversity index (SDI), which incorporates both SRic and SEve into a single measure of diversity. The SDI measures the probability that two randomly selected individuals from a sample will belong to different species. Over the last few decades, the concept of functional diversity has gained prominence in ecology (Zhang, 2011) because taxonomic diversity per se is inadequate for understanding ecosystem functioning due to the effect of functional redundancy. Functional redundancy implies that two sites with exactly the same number of species may be different in their functional diversity (hence functioning) depending on how similar/dissimilar (trait distance) the species' traits are among the species in the communities (de Bello *et al.*, 2006). A multiplicity of similar species (functional redundancy) in a community does not necessarily imply a better ecosystem functioning; it is rather the functional diversity (i.e. the functional multiplicity) that is closely related to ecosystem functioning (Weithoff, 2003). However, a high functional redundancy provides resilience against the loss of functions and services provided by specific species groups.

Critical points in the estimation of functional diversity are related to which functional traits are chosen, how they are assessed (Lavorel *et al.*, 2008), and how trait information is aggregated into a measure of functional diversity (Chillo *et al.*, 2011). The functional diversity of an ecosystem can vary significantly when different traits as well as different number of traits are used (de Bello *et al.*, 2006; Peco *et al.*, 2012). Similarly, functional diversity-environment relations can be a function of the number of traits and the particular traits used for calculating functional diversity (see de Bello *et al.*, 2006). Various indices have been proposed for the calculation of functional diversity (Mason *et al.*, 2005; Petchey & Gaston, 2006), and there is still no consensus on which index should be used (Schleuter *et al.*, 2010), as none of the existing ones meet all the requirements for general use (Villéger *et al.*, 2008). Three main independent components of functional diversity have been suggested i.e. functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv) (Mason *et al.*, 2005; Schleuter *et al.*, 2010). Functional richness measures the proportion of niche space that is occupied by the species in a plot, FEve measures the extents to which mean species traits are distributed regularly within the occupied trait space and FDiv describes the variance of species traits in the community (Schleuter *et al.*, 2010).

To understand the drivers of rangeland diversity, key biotic and abiotic drivers need to be identified and their relationships with various aspects of diversity need to be assessed. Abiotic drivers like climate, topography and soil seem to be of major importance (Fuhlendorf *et al.*, 2001; Augustine, 2003) and also, biotic drivers like anthropogenic disturbances are known to play an important role (Ouédraogo *et al.*, 2015). Our knowledge on plant diversity is partly limited as many studies focus on taxonomic diversity (e.g. Zerbo *et al.*, 2016) without assessing the functional diversity. Additionally, there is still limited knowledge about the degree to which taxonomic and functional diversity are correlated.

Several hypotheses have been proposed to explain the spatial patterns of plant diversity in response to disturbances such as grazing; prominent among them are the dynamic equilibrium model (DEM: Huston, 1979), the intermediate disturbance hypothesis (IDH: Connell, 1978) and Milchunas, Sala and Lauenroth's (hereafter MSL) generalised model of grazing effects on plant diversity (Milchunas *et al.*, 1988). The IDH (a special case of the DEM) simply predicts a state of maximised species richness at intermediate levels of disturbance (here; grazing pressure) while the DEM predicts that the effect of disturbance depends on the level of productivity. Furthermore, the MSL model postulates that grazing effects on plant diversity are modulated by resource availability (e.g. moisture, soil nutrients) and evolutionary history of grazing. Although Milchunas et al distinguished between short and long evolutionary histories of grazing, we focus here on the predictions for long grazing history which best define our study sites. We consider grazing as a disturbance since it leads both to removal of biomass and trampling on vegetation. Several studies testing the DEM and IDH obtained inconsistent results mostly due to improper statistical testing (e.g. Mackey & Currie, 2000; Fox, 2012). Huston (2014) discussed some critical issues which might obscure the diversity-disturbance relationship and hence cause inconsistent findings. The first issue is that since the diversity-grazing relationship is dependent on productivity (here; moisture), data should be stratified by productivity and the IDH/DEM should never be analysed using a single factor approach (i.e. involving only disturbance). Second, the entire gradients of grazing and moisture need to be covered if the full response of diversity is to be detected. Two opposing ecological mechanisms are often invoked to explain these hypotheses: (1) where productivity is low and disturbance is high, diversity is predicted to be low because species which are intolerant to disturbances are eliminated through habitat filtering and (2) where productivity is high and disturbance is low, diversity is also predicted to be low because dominant (highly competitive) species occupy resources and eliminate weak competitors through high rates of competitive exclusion.

In complex natural environments where several biotic and abiotic factors (varying in space and time) interactively drive diversity differentiation, studies using gradients are useful (Shipley, 2010). Our study area is characterised by a steep south-north gradient of increasing climatic aridity (Mertz *et al.*, 2012), which shapes the spatial patterns of vegetation distribution (White, 1983). This spatial aridity gradient allows a space-time substitution for an increased climatic aridity, as projected for most dryland environments (Stocker *et al.*, 2013). Also, there are local gradients of land-use intensity (disturbance) throughout the region (Ouédraogo *et al.*, 2015), ranging from protected to degraded areas. Land-use is characeterised by disturbances like grazing and fire. The existence of both types of gradients in the region makes it an ideal study area for improving our understanding of how these two factors interactively shape not just taxonomic diversity but also functional diversity. These good opportunities have remained unharnessed thus limiting our knowledge about how changing climate and land-use will jointly shape species and functional diversity in this region.

Using samples from a broad geographical area (see below), our study aims at (i) assessing whether taxonomic diversity indices can be used as good proxies of functional diversity, (ii) quantifying the importance of biotic and abiotic factors as drivers of species and functional diversity, (iii) understanding how grazing pressure and moisture jointly affect taxonomic and functional diversity. We hypothesise that:

1. Taxonomic diversity indices are strongly correlated to functional diversity indices.
2. The steep gradient of climatic aridity is a more important driver of biodiversity in West Africa’s sudanian savannas than topo-edaphic factors and disturbances.
3. The diversity-grazing relationship is influenced by moisture levels (productivity) as predicted by the DEM; a unimodal grazing-diversity relationship exists at intermediate grazing levels (Figure 3-1).

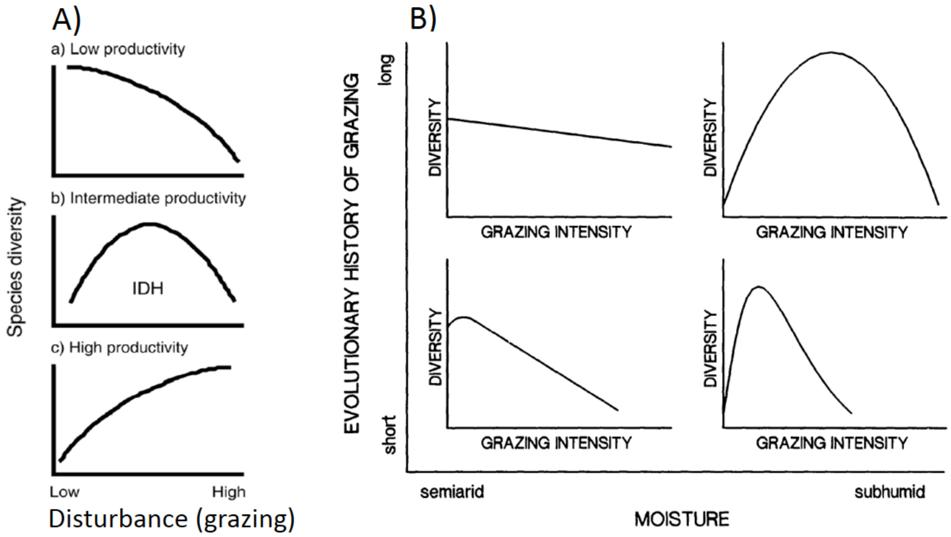


Figure 3-1: Prediction curves showing grazing effects on diversity. (A) Predicted responses of plant diversity along gradients of grazing with moisture held constant in each panel at a specific level (low, intermediate, or high). (B) Plant diversity of rangelands in relation to grazing pressure along gradients of moisture and of evolutionary history of grazing. Figure 1A is adapted from Fig. 1D of Huston (2014) and Fig. 1B is adapted from Fig. 3 of (Milchunas *et al.*, 1988). Productivity in this study is equated to moisture and disturbance is equated to grazing.

3.3 Materials and methods

3.3.1 Study area

The study sites are located along a south-north climate gradient reaching from northern Ghana to central Burkina Faso and covers ~106 000 km² of West Africa's Sudanian savanna zone (Figure 3-2). Climate is seasonal and characterised by a unimodal rainy season; in the southern Sudanian zone the rainy season is from April to November (average of 1200 mm/a), while in the northern Sudanian zone, it is from May to September (average of 600 mm/a). Depending on the land-use intensity, the vegetation ranges from an open to close savanna characterised by grasslands with interspersed trees and shrubs. The herbaceous layer is dominated by grasses and forbs: common species include *Brachiaria lata*, *Brachiaria jubata*, *Eragrostis turgida*, *Digitaria horizontalis*, *Spermacoce stachydea*, *Tephrosia pedicellata*, *Pandiaka angustifolia*, *Zornia glochidiata* and *Waltheria indica*. The tree layer consists of species with a high ability to resprout (Ouédraogo *et al.*, 2015). The geology in the south of the climatic gradient is dominated by Voltain, Tarkwaian and Birimian systems (Carrier *et al.*, 2008) while the north is dominated by Precambrian crystalline rocks consisting of meta-igneous and intrusive granitic rocks (British Geological Survey, 2002). The dominant soils are luvisols in the south (Wood, 2013) and lixisols in the north (Savadogo *et al.*, 2007). These soils have coarse texture (> 80% sand), low water holding capacity and depending on the cultivation history low levels of organic matter, nitrogen and phosphorus (Callo-Concha *et al.*, 2012). Peasant agriculture (rain-fed farming and livestock rearing) is the most common land-use type in the region (Blench & Sommer, 1999). Livestock grazing – mainly by cattle, sheep and goats – is mostly extensive and is concentrated on communal fallow lands. Transhumant pastoralism has partly been replaced by more sedentary forms of herd management over the past decades (Turner & Hiernaux, 2008; Brottem *et al.*, 2014).

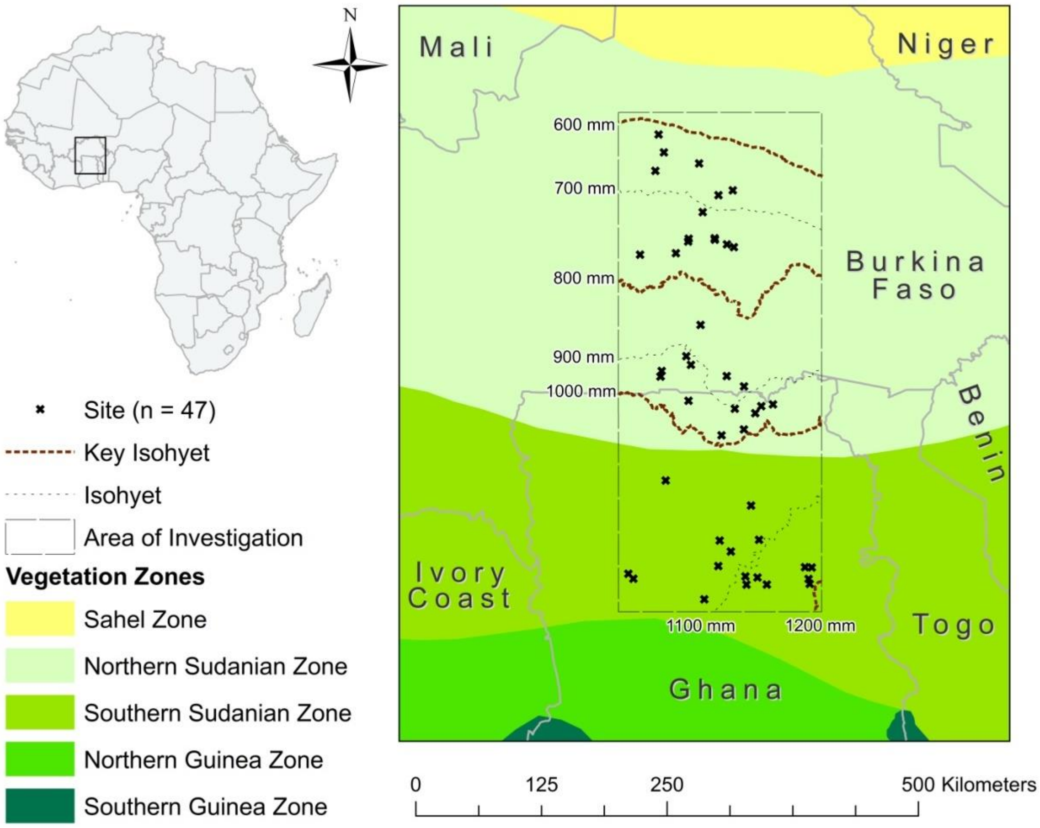


Figure 3-2: Study area and position of 47 sampled sites. The area covers the Southern and Northern Sudanian savanna vegetation zones following White (1983). Sampling is stratified into three zones of decreasing climatic aridity (hereafter called 'rainfall zones'), as indicated by key isohyets (low rainfall: mean annual precipitation 600 – 800 mm/a; intermediate rainfall: 800 – 1000 mm/a; high rainfall: 1000 – 1200 mm/a).

3.3.2 Sampling design

We stratified sampling in three rainfall zones oriented along the south-north gradient of increasing climatic aridity (Figure 3-2). In each zone, our sampling approach was designed to best measure local environmental gradients of interest (i.e. gradients in topo-edaphic factors and grazing pressure), following recommendations of Shipley (2010). This was achieved by choosing sites that maximised the range of grazing and topo-edaphic gradients. For grazing gradients, we explicitly included heavily grazed sites close to settlements and lightly grazed to ungrazed sites in protected areas (two per climate zone). To capture regional variation in topo-edaphic conditions, we used a geological map to select sites (with ≥3 km distance) in major geological units. To capture local variation, we stratified our within-site sampling into slope positions (upslope, midslope and lowland) and placed ≥3 plots per slope position and site in homogeneous vegetation (distance between plots ≥30 m; plot size 10 m x 10 m). Within each plot, we randomly placed three circular subplots of 1 m² for the assessment of vegetation attributes. To avoid seasonal bias and to capture intraseasonal diversity dynamics, sampling was done during two growth periods (June to October 2012 and 2013), and we varied the time of sampling independent of other sources of variation. In total, we sampled 47 sites (17 in the high rainfall zone, 15 in the intermediate rainfall zone, and 15 in the low rainfall zone), and 450 plots (≥9 per site).

3.3.3 Data collection

Climatic variables

For each site, we obtained climatic data from interpolations provided by the WorldClim database (www.worldclim.org/; (Hijmans *et al.*, 2005)). Extracted variables were mean annual precipitation (MAP), mean annual temperature, minimum temperature of the coldest month, maximum temperature of the warmest month, precipitation of the wettest quarter, precipitation of the wettest month (PWM), mean temperature of the wettest quarter, isothermality, temperature seasonality and precipitation seasonality (PS). We calculated aridity index as the ratio of MAP to annual potential evapotranspiration (UNEP, 1997).

Topo-edaphic variables

Apart from slope position and soil depth, we also collected information on soil physical and chemical composition (see Appendix 4). Following FAO (2006), we estimated the cover of soil surface fragments. To quantify physical and chemical soil properties, a composite sample from five soil cores (0-4 cm) per plot was collected. Samples were homogenised, air-dried for > 21 days, and shipped to the Soil Laboratory of the Geography Institute, University of Bonn, Germany. Here, soil fractions < 2 mm were analysed. Particle size distribution was determined by laser diffraction method, using a Laser Particle Size Analyser (Horiba LA-960). Soil acidity was determined in a 1:2.5 water suspension. Plant-available phosphorus was measured via calcium-acetate-lactate (CAL) extraction (mg kg^{-1}), following standard protocols (VDLUFA, 2008). Soil N and C content was analysed by dry combustion with a CN analyser (Vario El cube). Additionally, the soil organic carbon content was determined using the loss-on-ignition method (Schulte & Hopkins, 1996).

Variables were categorised into slow and fast responding (soil) attributes to land-use pressure, based on findings from other African dryland rangelands (Angassa *et al.*, 2012; Linstädter & Baumann, 2013; Sandhage-Hofmann *et al.*, 2015); *cf.* Appendix 4). Fast variables (e.g. soil C and N) are mainly driven by direct inputs via herbivore excreta (Angassa *et al.*, 2012; Sandhage-Hofmann *et al.*, 2015). Slow variables (soil texture, soil acidity, bare soil cover and the cover of coarse surface fragments) are largely driven by underlying geology and local topography (see Vries *et al.*, 2012 for a similar approach).

Disturbance

As proxies for vegetation disturbance, we recorded livestock grazing pressure and downloaded satellite data of fire frequency. To obtain grazing pressure, we combined physical evidence of grazing (trampling, dung, and the removal of standing biomass) in an expert assessment of recent grazing pressure (following Linstädter *et al.*, 2014) described as very light (0), light (1), moderate (2), heavy (3) and very heavy (4) grazing. Fire frequency was obtained from the fire information for resource management system archive of the national aeronautics and space administration. This product is a global moderate resolution imaging spectroradiometer based yearly fire frequency measurement per 10 km^2 covering the period from January 2008 to October 2013 (https://firms.modaps.eosdis.nasa.gov/download/).

Vegetation data

Phytosociological relevés were conducted during the rainy seasons of 2012 and 2013. We visually estimated the ground cover of all vascular plant species within subplots, and measured species’ vegetative height to the nearest centimeter. We focused on the herbaceous layer, but included seedlings and saplings (≤2 m) of woody species, following Le Roux *et al.* (1995). We calculated species’ biovolume per quadrat as cover x height (Jauffret & Visser, 2003) and obtained plot-level cover and biovolume as average of the three subplot values. To quantify diversity, we recorded plant species (351 species in total; Appendix 17) and their traits. We selected six plant traits; life history ('annual', 'perennial'), plant height ('small' - ≤50 cm, 'tall' - > 50 cm), life form ('chamaephytes', 'geophytes', 'hemicryptophytes', 'phanerophytes', 'therophytes'), photosynthetic pathway ('C3', 'C4'), growth habit ('erect', 'prostrate') and nitrogen fixation ('legume', 'non-legume'). These traits were selected because they reflect different plant species strategies and are responsive to environmental changes – such as climate and grazing – on a regional to global level (Díaz *et al.*, 2007c). Plant height data was obtained from heights measured during data collection while the other traits were extracted from literature (e.g. Poilecot, 1999; Clayton *et al.*, 2006; Schmidt *et al.*, 2011).

3.3.4 Data Analyses

The statistical analyses involved four steps. First, we selected environmental variables as potential predictors. Second we calculated taxonomic and functional diversity indices. Third, we assessed the relationship between the diversity indices and potential predictors. Finally, we tested the interactive effects of grazing pressure and moisture on diversity indices.

Step 1: Selection of environmental variables as potential predictors

We predict that climate, disturbances and topo-edaphic variables would affect plant diversity. Inspection of our data indicated that most of the environmental variables show monotone relations with selected diversity indices. For such variables, we performed principal component analyses (PCAs) to select potential predictors of diversity from eleven variables available on site level (climate variables) and fifteen variables recorded on plot level (grazing and topo-edaphic variables). Separate PCAs were performed for three variable sets related to different biotic and abiotic factors: (i) climate, (ii) topo-edaphic variables with slow response or (iii) fast response to land-use. We then identified variables highly loading ($\geq \left| 0.8 \right|$) on principal components (PC) with eigenvalues > 1 to reduce collinearity within predictor sets. In case of competing variables (several terms highly loading on the same PC), we chose the variable with the highest loading. We additionally chose study site, slope position (SP), grazing pressure (GP) and fire frequency. Given their ordinal nature, GP and SP could not be included in the PCAs and were included in modelling due to their prevalent importance (Augustine, 2003; Ouédraogo *et al.*, 2015).

Inspection of our data indicated that grazing pressure has a hump-shaped relationship with (some) diversity indices which could be well modelled with a second order polynomial regression (Soliveres *et al.*, 2014). To model these unimodal relationships, we included a composite variable in our model including both x and x^2, x being the raw predictor (grazing pressure). The use of these composite variables does not alter the underlying model, but collapses the effects of the variables included into a single path coefficient, aiding interpretation of model results (Grace, 2006). Multicollinearity of selected potential predictors was checked using Spearman's rank correlation.

Step 2: Calculation of taxonomic and functional diversity indices

From the vegetation and trait data, three indices were selected to estimate taxonomic diversity (Table 3-1). We calculated three functional diversity indices (functional richness, functional evenness, functional divergence, *cf.* Table 3-1) as recommended by (Schleuter *et al.*, 2010) based on six binary/categorical traits (described above). To obtain the FDiv – using Rao's quadratic entropy (FRao) in this study – we first calculated the trait dissimilarity (i.e. *dij*) among all pairs of species. The FRao has several desirable properties for describing the functional diversity of a community and is thus the most commonly used index (Botta-Dukát, 2005; Ricotta, 2005). We obtained trait dissimilarities for our traits by coding them as binary and factor variables following the method proposed by Laliberté *et al.* (2014). The parameter dij expresses the dissimilarity between each pair of coexisting species i and j and varies between 0 (two species with exactly the same traits) and 1 (two species with completely different traits). We assessed the correlation between taxonomic diversity and functional diversity using Pearson's product-moment correlation coefficient with t-test for significance (at $\alpha = 0.05$).

Step 3: Testing the relationship between environmental variables and diversity indices

We used linear mixed-effect models (LMM) to explore the effect of selected potential predictors on diversity. Initially, full LMMs – including all selected variables as fixed effects – were established for each diversity index in focus (six in total); ‘site’ was included as random-intercept term. Due to the different units and scales of potential predictors, we first standardised all variables before performing LMMs. Statistical assumptions were explored visually as proposed by Zuur and colleagues (2010). The initial, full models were subject to (Akaike information criteria) AIC-based model selection – which allows comparison of multiple, non-nested models of all possible subsets (Bolker *et al.*, 2008), – using restricted maximum likelihood estimation (REML; Zuur *et al.*, 2009). We used REML estimates because they are generally less biased than (unrestricted) maximum likelihood estimates (Bolker *et al.*, 2008). LMMs were calculated using the lme4-package for R (Bates *et al.*, 2015). We selected final models solely based on the principle of parsimony (Vandekerckhove *et al.*, 2014), thus going for the model with the least AIC for each diversity index. To estimate the variance explained by fixed and random effects, we used the method proposed by Nakagawa and Schielzeth (2013) and extended by Johnson (2014). Specifically, we distinguished between marginal and conditional R^2 values. The first is the proportion of explained variance by fixed-effects, and the second the proportion explained by fixed plus random effects (Ruppert *et al.*, 2015). Final models were further explored using ANOVAs (Type III). We estimated the proportion of variance explained by individual predictors via classical eta-squared values. We plotted Moran’s I spatial correlograms for final models to check for spatial autocorrelation (Legendre & Legendre, 1998; Griffith, 2009).

Table 3-1: Taxonomic diversity and functional diversity indices used in this study.

Aspect of Diversity	Index	Acronym	Formula	Meaning of terms	Reference
Taxonomic diversity	Species richness	SRic	$\mathrm{SRic} = \mathrm{N}$	N: number of species	Colwell (2012)
	Species evenness	SEve	$SEve = \frac{H'}{In(S)}$	H': Shannon diversity index S: Species richness	Colwell (2012)
	Simpson's diversity index	SDI	$SDI = 1 - \sum_{i=1}^{S} (pi)^2$	S: Species richness pi: proportion of individuals belonging to the ith species	Colwell (2012)
Functional diversity	Functional richness	FRic	Quickhull algorithm		Villéger *et al.* (2008)
	Functional evenness	FEve	$FEve = \frac{\sum_{i-1}^{S-1} \min(PEWi, A) - A}{1 - A}$	PEW: partial weighted evenness (see reference for details) S: SRic, A: $(S - 1)^{-1}$	Villéger *et al.* (2008)
	Functional divergence	FDiv	$FDiv = \sum_{i-1}^{S-1} \sum_{j=i+1}^{S-1} d_{ij} p_i p_j$	Dij: Euclidean dissimilarity between the traits of each pair of species i and j S: species richness	Mouchet *et al.* (2010)

Step 4: Testing the interactive effects of grazing pressure and moisture on diversity

We used linear regressions to test the effects of grazing pressure and moisture on each of the diversity indices. Box plots were used to visualise the diversity-grazing pressure relationships stratified by moisture conditions. All analyses were conducted using the statistical software R in version 3.2.2 (R Core Team, 2015).

3.4 Results

3.4.1 Selected potential predictors of diversity

From the PCAs, we selected eight variables for further analyses (Appendix 5). Soil silt content was dropped from the potential predictors due to its high correlation with nitrogen content (Appendix 6). In total, eleven variables were selected as potential predictors (Table 3-2).

3.4.2 Correlations of taxonomic diversity indices with functional diversity indices

Species richness (SRic) and functional richness (FRic) showed the strongest positive correlation (Pearson r = 0.62) while SRic had weak but significant correlations with functional evenness and functional divergence (Figure 3-3 and Appendix 7). Both species evenness (SEve) and Simpson’s diversity index (SDI) were quite well correlated with functional divergence (Pearson r = 0.59 and 0.58 respectively). However, none of SEve and SDI were highly correlated with FRic and functional evenness (FEve). Also, FEve was not highly correlated with any taxonomic diversity index (SRic, SEve and SDI).

Table 3-2: Selected variables for linear mixed-effect models with statistical descriptive measures. Fixed effects were grouped into four predictor sets. The random effect ‘study site’ was also considered.

Effect type	Predictor set	Potential predictor	Mean	Standard deviation	Minimum	Maximum
Fixed	Climate variables	Precipitation seasonality	101.0	15.03	79.00	124.0
		Mean annual temperature	27.93	34.08	26.92	28.38
		Precipitation of the wettest month	230.7	19.82	196.0	271.0
	Slow topo-edaphic variables	Slope position[a]	-	-	1	3
		Soil clay content	10.75	7.90	1.13	47.71
		Soil depth	49.59	18.49	10.00	90.00
	Disturbance variables	Grazing pressure[b]	-	-	0	4
		Grazing pressure^2	-	-	-	-
		Fire frequency	1.14	3.78	0	24
	Fast topo-edaphic variables	Soil nitrogen content	0.09	0.06	0.03	0.67
		Plant-available phosphorus	10.75	0.87	1.13	49.71
Random		Study site	-	-	-	-

[a] Categorical variable (1-3) – lowland (1), midslope (2), upslope (3)

[b] Ordinal variable (0-4) – 0 (very light GP), 1 (light GP), 2 (moderate GP), 3 (heavy GP), 4 (very heavy GP)

Table 3-3: Summarised results of linear mixed-effect models testing the effects of climate, disturbance and topo-edaphic variables on taxonomic and functional diversity of the herbaceous layer. + = positive effect of predictor on diversity index; - = negative effect of predictor on diversity index. SRic = species richness, SEve = species evenness, SDI = Simpson's diversity index, FRic = functional richness, FEve = functional evenness, FDiv = functional divergence.

Predictor set	Potential predictor	SRic	SEve	SDI	FRic	FEve	FDiv
Climate variables	Precipitation seasonality	(+) **	(-) ***		(+) *	(-) ***	(-) **
	Mean annual temperature	(-) *					
	Precipitation of wettest month		(+) *			(-) n.s	(+) n.s
Topo-edaphic variables	Slope position		(-) *	(-) *			
	Percent clay	(-) *	(-) *	(-) *	(-) **		
	Soil depth					(-) n.s	
	Total nitrogen	(-) n.s					
	Plant-available phosphorus		(+) n.s			(-) n.s	
Disturbance variables	Grazing pressure	(+) *			(+) ***	(+) **	(+) ***
	(Grazing pressure)^2	(-) *	(+) *		(-) ***		
	Fire frequency		(+) n.s	(+) n.s			

p-values: *** < 0.001; ** < 0.01; * < 0.05, ns = non-significant (but retained in final model)

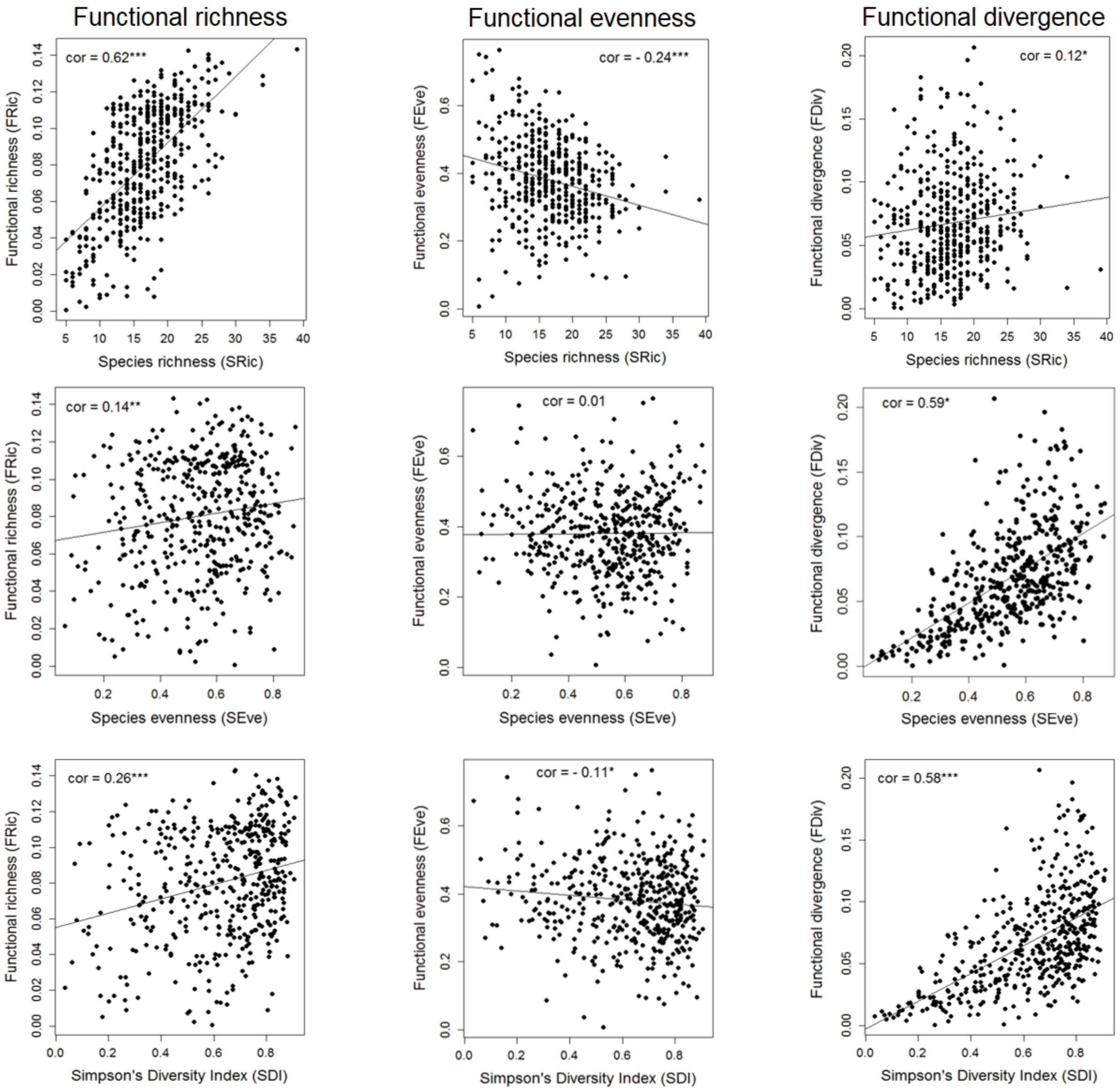


Figure 3-3: Correlations between taxonomic diversity indices and functional diversity indices. SRic = species richness, SEve = species evenness, SDI = Simpson's diversity index, FRic = functional richness, FEve = functional evenness, FDiv = functional divergence.

3.4.3 Relationships between predictors and diversity indices

LMMs were calculated for each diversity index to analyse the influence of climate, topo-edaphic factors and disturbances (Table 3-3). Climate and disturbance had significant relationships with all diversity indices except SDI while topo-edaphic factors were significantly related to all diversity indices except FEve and FDiv (Table 3-3). Precipitation seasonality was the most important climatic variable: it had positive effects on richness measures and negative effects on evenness measures. Grazing pressure was the most important disturbance and had positive effects on all diversity indices except SDI. For topo-edaphic variables, clay content and slope position significantly affected SEve and SDI while SRic and FRic were significantly influenced by only clay content (Table 3-3). Generally, our models performed poorly, as shown by low explained variances (total explained variance < 40%; Table 3-4). The SRic model explained the highest variance (34%) while for all the other diversity indices, our models explained only ca. 20% of variance (Table 3-4).

For all functional diversity indices and species richness, climate (mainly precipitation seasonality) and disturbance (mainly grazing pressure) were more important predictors than topo-edaphic variables (Figure 3-4). In contrast, topo-edaphic variables (mainly clay content and slope position) were more important predictors for species evenness and Simpson's index than climate and disturbance.

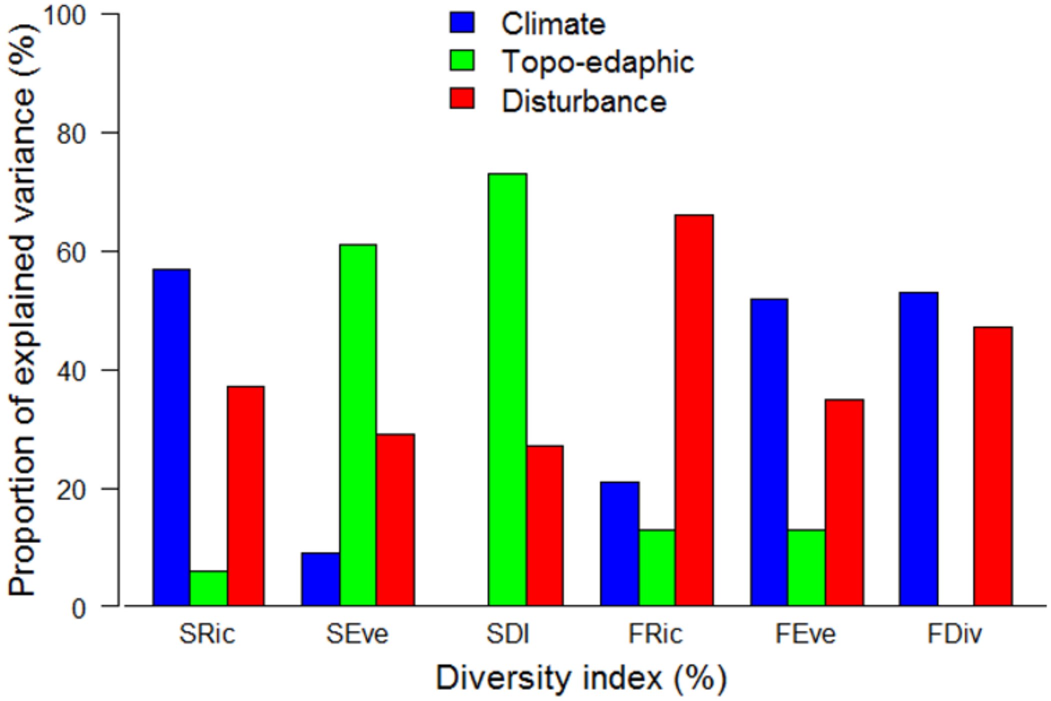


Figure 3-4: Proportion of explained variance (by fixed-effects) that is attributable to climate, disturbances and topo-edaphic variables. SRic = species richness, SEve = species evenness, SDI = Simpson's diversity index, FRic = functional richness, FEve = functional evenness, FDiv = functional divergence.

3.4.4 Interactive effects of grazing pressure and moisture on diversity

Based on linear regression, we found significant interactions between grazing pressure and moisture for all diversity indices except functional- evenness and divergence (Table 3-5). Consistent with the DEM, the clearest hump-shaped species richness-grazing pressure relationship was obtained at intermediate levels of both grazing pressure and moisture (Figure 3-5a). A similar relationship was also observed for functional richness under intermediate moisture (Figure 3-5d). Functional evenness and functional divergence showed positive linear relationships with grazing especially under intermediate and low moisture conditions while for species evenness and Simpson's index, no clear relationships were evident.

Table 3-4: Percentage of explained variance by fixed- and random- effects from the linear mixed-effect model. SRic = species richness, SEve = species evenness, SDI = Simpson's diversity index, FRic = functional richness, FEve = functional evenness, FDiv = functional divergence.

Variance category	SRic	SEve	SDI	FRic	FEve	FDiv
Explained variance by all fixed-effects (%)	9	6	8	10	13	10
Explained variance by random-effect, ‘site’ (%)	25	15	13	11	11	13
Total explained variance; fixed-plus random- effects (%)	34	21	21	21	24	23
Percentage of total explained variance attributable to fixed-effects alone (%)	26	29	38	48	62	43

Table 3-5: Effects of interaction between grazing pressure and moisture on diversity indices.

Predictor	Species richness	Species evenness	Simpson’s index	Functional richness	Functional evenness	Functional divergence
Grazing pressure	(-)***	(-)***	(+)*	(+)**	(+)***	(+)***
Moisture2	(+)***	(-)***	(-)**	(+)***		(-)**
Moisture3						
Grazing pressure x Moisture2	(-)**	(+)***	(+)*	(-)**		
Grazing pressure x Moisture3						

*p-values: *** < 0.001; ** < 0.01; * < 0.05*

Moisture = high moisture, intermediate moisture and low moisture corresponding to high, intermediate and low rainfall zones defined in Figure 3-2.

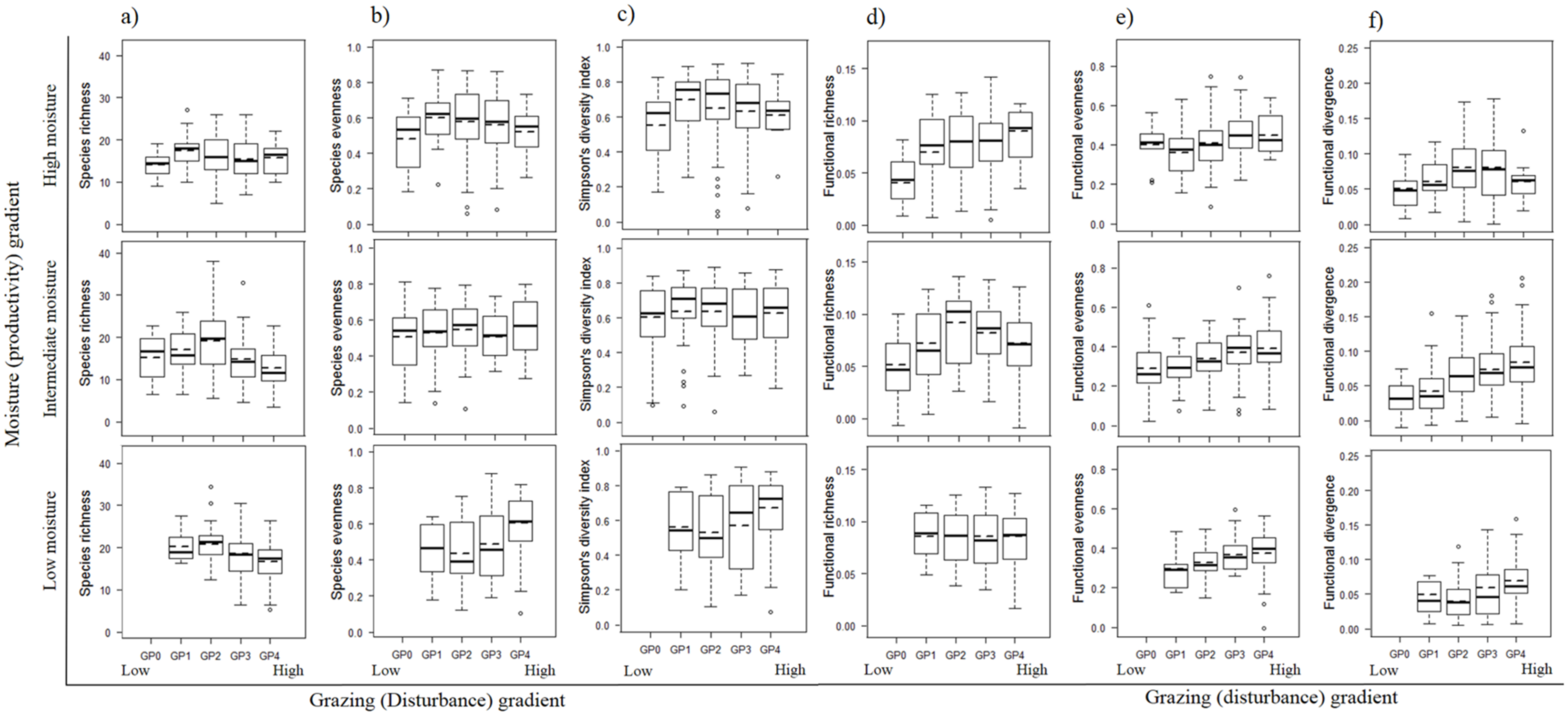


Figure 3-5: Interacting effect of grazing pressure and moisture on herbaceous plant diversity; (a) species richness, (b) species evenness, (c) Simpson's diversity index, (d) functional richness, (e) functional evenness, (f) functional divergence. Grazing pressure (GP) is an expert estimate based on physical evidence of grazing; GP0 = very light, GP1 = light, GP2 = moderate, GP3 = heavy, and GP4 = very heavy grazing pressure. Moisture is analogous to the three rainfall zones defined in Figure 3-2, i.e. high rainfall zone, intermediate rainfall zone, low rainfall zone. The figure shows the response of different diversity indices to grazing under varying rainfall zones (moisture levels). Dashed lines in boxplots represent mean values, and solid lines represent medians.

3.5 Discussion

Despite considerable interest in diversity and ecosystem functioning of dryland rangelands, very few studies have assessed how both climate and grazing affect not just taxonomic diversity but also functional diversity. We investigated the effects of environmental variables on taxonomic and functional diversity of West Africa's Sudanian savannas along gradients of climatic aridity and grazing. We found that the relative importance of predictors and predictor sets differed considerably across diversity indices thus providing evidence that environmental variables exert inconsistent effects and that taxonomic diversity and functional diversity can be independent of each other. These findings support the view that the factors that drive species differentiation in savannas do not necessarily also drive the variations in traits (i.e. functional diversity) among species (Huston, 1994; Fukami *et al.*, 2005). Our results highlight the need to take multiple diversity indices into account when investigating environmental impacts on biodiversity and ecosystem functioning.

3.5.1 Correlations of taxonomic diversity indices with functional diversity indices

Our results show that no taxonomic diversity index is a good proxy for all three components of functional diversity. Species richness (SRic) was quite strongly correlated with functional richness (FRic) while species evenness (SEve) and Simpson's diversity index (SDI) were quite well correlated with functional divergence. Our finding suggests that contrary to the common usage of SRic as an estimate of ecosystem functioning (and hence functional diversity), based on assumptions of strong correlations between them (Balvanera *et al.*, 2006), SRic is not a good proxy for functional diversity in our study area (de Bello *et al.*, 2006). Our results agree in parts with findings by Li *et al.* (2015) who found all the taxonomic and functional diversity indices to be independent of each other. Similarly, other studies (e.g. Mayfield *et al.*, 2010; Rolo *et al.*, 2016) found taxonomic and functional diversity to be decoupled in response to land-use. This independence of taxonomic and functional diversity measures suggest that a consideration of different diversity indices – as opposed to single indicators – would be more informative (Petchey & Gaston, 2002; Mayfield *et al.*, 2010). Since functional divergence (calculated using Rao's quadratic entropy) is gaining acceptance as a good measure of functional diversity (Lepš *et al.*, 2006), our results show that species evenness and Simpson's diversity index are better proxies (although not optimal) of functional diversity than species richness.

3.5.2 Relationships between predictors and diversity indices

Our models performed poorly for explaining variations in diversity. In all cases – except for the species richness model – the total explained variance was less than 25%. The proportion of the total explained variance attributable to fixed-effects alone was higher for functional diversity indices (> 40%) than taxonomic diversity indices: species richness and Simpson's index had the lowest values (ca. 25%). This suggests that variation in diversity is complex and difficult to predict considering the fact that a similar dataset – for the same plots – performed much better (with higher explained variances) for predicting ecosystem service supply (see section 4). This problem might have been aggravated by the wide coverage of our sampling and high heterogeneity in our data (see section 2). Another factor that could account for the low explained variances is related to the complexity of natural processes that shape these ecosystems; hence interactions between predictors might have higher effects on diversity than individual predictors' effects. The low explained variances may also imply that some important drivers of diversity were not taken into account, either because we did not record them in the field, and or because variable selection missed them. For the species richness model, it appears that some site level drivers were missing considering the fact that it had the lowest proportion of fixed-effect explained variance despite having the highest total explained variance. Such missing factors might be related to historical events (e.g. floods and droughts) or land-use activities (e.g. farming) which occur at the site level but which were not captured in our data collection.

Effect of climate on diversity

Our second hypothesis (that climate would be the most important driver of diversity) was confirmed in the case of species richness, functional evenness and functional divergence but was rejected for species evenness, Simpson's index and functional richness. Precipitation seasonality (PS) was the most important climate variable; significantly related to all diversity indices except Simpson's index. PS may be associated with the magnitude, timing, and duration of the wet/dry seasons (Borchert, 1999). Increasing PS has strong positive effects on richness measures (species and functional richness) while having strong negative effects on evenness measures (species evenness, functional evenness) and functional divergence. This result provides evidence that precipitation and its intraseasonal variations are important for determining both taxonomic and functional diversity of a community. Aspects of precipitation seasonality – such as start of the rainy season and wet season length – play important roles in plant growth (Schwartz, 2003). Changes in rainfall regimes – a possible outcome of climate change – is expected to exert more serious impacts in arid and semiarid regions (Trenberth et al., 2007). Since PS has a strong inverse relatationship with precipitation (Pearson r = -0.95), the positive relationship between richness measures (SRic and FRic) and PS is surprising and contrary to what is commonly found for similar studies along climatic gradients (e.g. de Bello *et al.*, 2006; Zerbo *et al.*, 2016). However, we found a positive effect of moisture on both beta and gamma diversity (Appendix 8) suggesting that certain local scale processes – e.g. evolutionary history (Harrison & Grace, 2007) and seed abundance/dispersal limitation (Pärtel & Zobel, 2007; Zobel & Pärtel, 2008) – might be responsible for the alpha diversity (species richness) result. Dispersal limitation may lead to species rarity (Bruno, 2002; Mabry, 2004) or patch occupancy (Matlack, 2005; Helm *et al.*, 2006). The higher alpha diversity in arid areas might also be related to the species-area relationship/sample size effect (Oksanen, 1996; Gotelli & Colwell, 2001). Aridity may decrease plant size; a mechanism which might lead to increased point diversity (alpha diversity) in arid vrs humid conditions if a fixed plot size is used (Oksanen, 1996) as done in this study.

Our finding of a strong negative relationship between PS on one hand and evenness measures (i.e. species and functional evenness) and functional divergence on the other hand might be jointly explained by two deterministic processes; habitat filtering (Keddy, 1992) and niche differentiation (Silvertown, 2004). Habitat filtering imposes ecological filters that select species because they possess a trait syndrome suitable for a given habitat (Keddy, 1992; Díaz *et al.*, 1998) while niche differentiation implies the selection of species based on their functional dissimilarity (Maire *et al.*, 2012). This implies that in the driest parts of the study area (where PS is higher), species are forced to converge towards an optimum trait value (and become functionally similar) thus excluding functionally dissimilar species that cannot cope with the prevailing environmental stress or competition (Mayfield & Levine, 2010). Alternatively, niche differentiation suggests that co-occurring species differ in their resource acquisition traits and hence decrease the intensity of inter-specific competition (Gross *et al.*, 2007). Such a phenomenon results in the co-occurrence of species with divergent traits (higher functional divergence) which promotes the complementarity of resource use in space and time (Silvertown, 2004; Carroll *et al.*, 2011).

Effect of topo-edaphic factors on diversity

Topo-edaphic factors (topography and soil variables) were more important than climate and land-use variables for species evenness and Simpson’s index. Soil texture (percent clay) and topography exerted strong negative effects and were more important drivers of diversity than soil chemistry (soil nitrogen and phosphorus content). The observed effects of topography might be linked to its influence on local resources such as soil moisture, light incidence, and soil fertility (Grant & Scholes, 2006). The higher resource supplies in lowland areas provide more growth niches that could be beneficial for a variety of species and thus allows the co-occurrence of (almost equally favoured) species. The importance of soil texture for plant growth is well documented (e.g. Zemmrich *et al.*, 2010) and it has been found that some texture characteristics can impose drought on plants even in areas with suitable climatic conditions (Fernandez-Illescas *et al.*, 2001).

Effect of disturbance on diversity

Disturbance was the most important driver of functional richness and the second most important driver of all the other diversity indices. Grazing pressure was the most important disturbance predictor: it had significant positive effects on all functional diversity indices and species richness while fire frequency had no significant effects on any of the diversity indices. Our results confirm the importance of herbivores' grazing on plant species composition and diversity (Blench & Sommer, 1999; Hahn-Hadjali *et al.*, 2006; Zerbo *et al.*, 2016). Grazing impacts on diversity in this region should be discussed and interpreted with caution because pastures are mostly also fallows – as part of shifting cultivation practice in the area – which complicates the interpretation of different species composition in response to pasture or fallow succession (Hahn-Hadjali *et al.*, 2006).

3.5.3 Interactive effects of grazing pressure and moisture on diversity

In agreement with findings from grasslands elsewhere (e.g. Mayfield *et al.*, 2010; Rolo *et al.*, 2016), our results show that the different components of diversity followed different trajectories in response to changes in grazing pressure. Additionally, we found inconsistent relationships between diversity indices and grazing pressure under varying moisture conditions. Consistent with the dynamic equilibrium model (Huston, 1994), intermediate disturbance hypothesis (Connell, 1978) and the MSL model for areas with long grazing history (Milchunas *et al.*, 1988), we found a hump-shaped relationship between species richness and grazing under intermediate moisture conditions. However, our results show that these models are not applicable to all diversity indices, at least in our study area. The relationship between grazing pressure and the diversity indices was modulated by moisture except for functional evenness and functional divergence which increased with increasing grazing pressure irrespective of moisture conditions. Consistent with this finding, Hahn-Hadjali *et al.* (2006) found higher evenness in grazed than ungrazed plots probably due to strong dominance of specific species (e.g. perennials) in ungrazed plots.

Our result of higher functional divergence (FDiv) under higher grazing pressure agrees with the hypothesis by Grime (2006) that FDiv is promoted by disturbances in response to stronger competition and niche differentiation between persisting species (Mason *et al.*, 2005; Mouchet *et al.*, 2010). Following similar findings, de Bello *et al.* (2006) suggested that in areas with more patchy vegetation – as exists in arid locations, – grazing might increase heterogeneity in resource distribution to cover a wider niche space (Adler *et al.*, 2001) and therefore promote the coexistence of species with dissimilar traits or resource acquisition strategies (i.e. niche differentiation) through an increase of aggregation patterns (Pugnaire *et al.*, 2004).

Our findings may also be explained by the traits selected for the estimation of functional diversity; different traits might have resulted in different FDiv-grazing relationships (Flynn *et al.*, 2009; Zhang, 2011). For example, from a study of five traits, Peco *et al.* (2012) found that grazing abandonment decreased functional diversity for some traits (growth form and onset of flowering) but not others (plant height, specific leaf area and seed mass). In our study, we further explored the relationships between grazing and FDiv of individual traits (Figure 3-6) as well as between grazing and relative abundance of different trait attributes (Figure 3-7). Photosynthetic pathway, nitrogen fixation and growth habit had significant positive relationships with grazing pressure while the remaining were nonsignificant (Appendix 9).

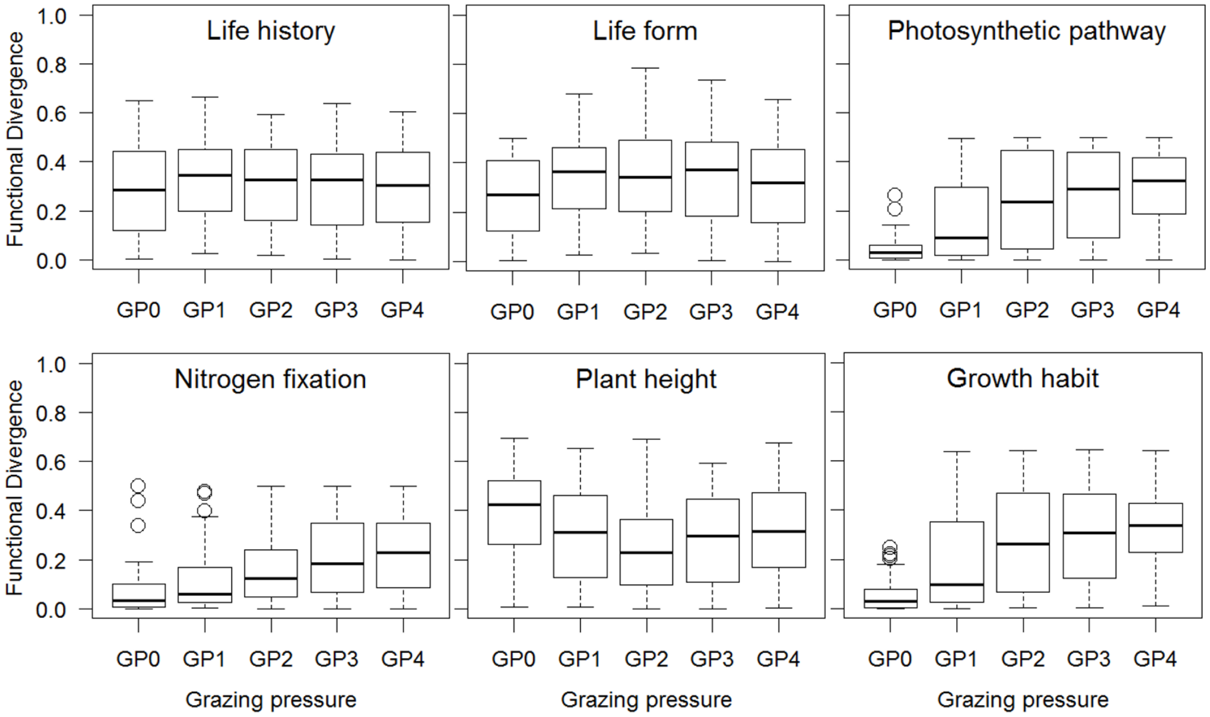


Figure 3-6: Relationship between grazing pressure and the functional divergence of individual traits.

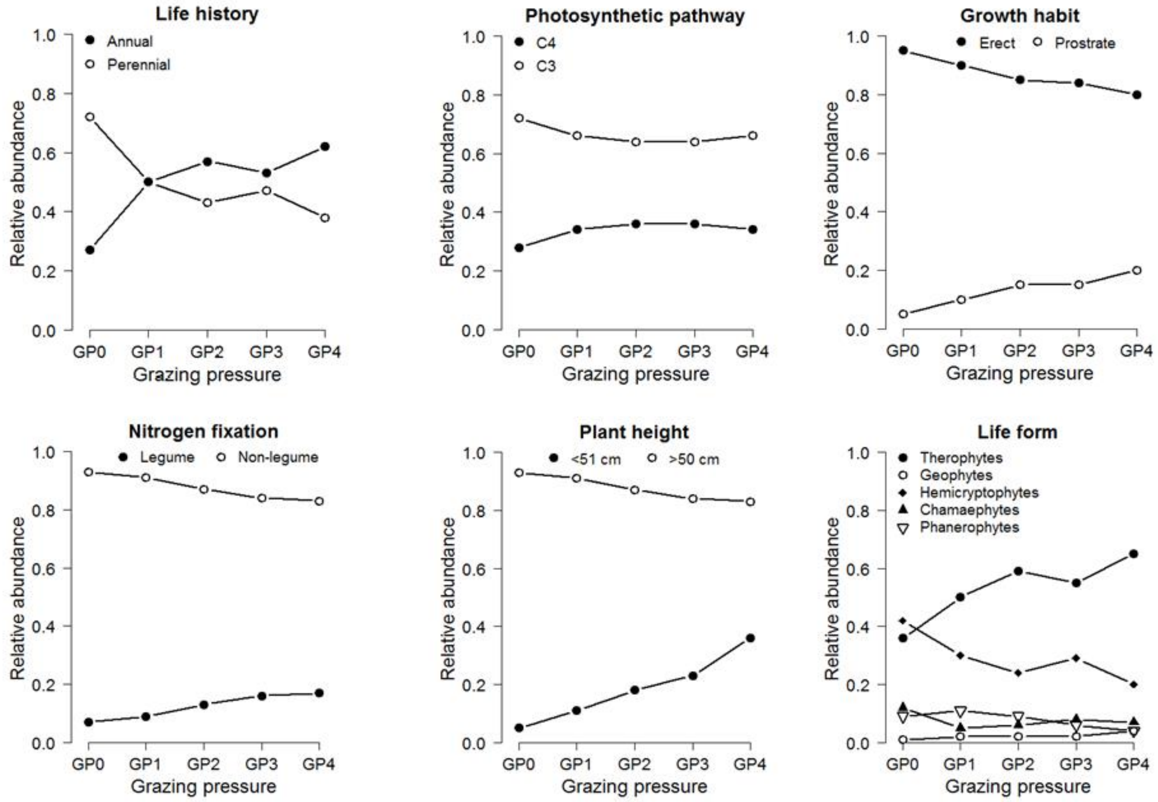


Figure 3-7: Relationships between grazing pressure and the relative abundances of trait attributes.

For photosynthetic pathway, growth habit, nitrogen fixation, and height, grazing benefited one of the trait attributes while negatively affecting the other (Figure 3-7). These results support the view that grazing might be required to facilitate the introduction or elimination of certain species in an ecosystem (Noy-Meir *et al.*, 1989) and are consistent with the predictions by several grazing models (see Díaz *et al.*, 2007c for a review). The ecological mechanisms underpinning these results remain debatable and appear ungeneralizable (for almost all traits) with many researchers concluding that the effects of grazing may be context dependent on factors such as grazing intensity, type of herbivores and the history of herbivory (Milchunas *et al.*, 1988; Díaz *et al.*, 2007c) .

3.6 Conclusion

The objective of this study was to investigate the effects of environmental factors on the taxonomic and functional diversity of West African Sudanian savannas. Our study suggests that taxonomic diversity may not always be a good surrogate for ecosystem functional or ecological quality. Despite its ease of measurement, we do not recommend the use of species richness as a proxy for biodiversity in general as has been commonly done in ecological research. Our results suggest that changes in precipitation and grazing pressure will exert the highest impacts on the diversity and functioning of ecosystems in the area compared with other drivers like soil, fire, and topography. Due to the use of a space-time substitution approach in this study, our findings provide considerable insights into how changing climate and land-use might generally affect diversity and ecosystem functioning. Considering the regulatory role of topography and texture on soil moisture levels, we deduce that moisture – which is a function of several factors e.g. precipitation, temperature, topography, soil texture – is the most important limiting factor in the region. Future research should consider the use of more direct quantitative measurements of plant traits, and tie these traits to specific ecosystem processes of interest. In general, our results are useful for land managers as they provide important insights into the responses of ecosystems to environmental changes. These findings can therefore be used as a guide for conservation planning and rangeland management in general.

4 Drivers of forage provision and erosion control in West African savannas – a macroecological perspective

4.1 Abstract

What drives the capability of West African Sudanian rangelands to provide forage and erosion control? Rangelands' ability to provide vital ecosystem services (ESs) depends on ecosystem properties and functions, which are interactively driven by biotic and abiotic environmental conditions. The relative importance of these drivers for ES supply is still poorly understood, hampering the identification of appropriate management strategies. Taking a macroecological perspective, we aimed at detecting consistent patterns in ES drivers and supply, focusing on the provisioning ES forage provision and on the regulating ES erosion control. 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 topo-edaphic conditions and land-use intensity. We used aboveground biomass, metabolisable energy and metabolisable energy yield as proxies for forage provision, and the cover of perennials in the herbaceous layer as a proxy for erosion control. Linear mixed-effect models and model selection were used to test relationships between twenty biotic and abiotic variables and ES proxies. We found differential responses of ES proxies to environmental drivers. Antecedent rainfall was the most important predictor of aboveground biomass, while phenophase and land-use (grazing) were most important for metabolisable energy. The indirect influence of climatic aridity, topo-edaphic factors and land-use (reflected in the relative abundances of plant functional types) was the most important predictor of erosion control followed by the direct influence 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 be overridden by current season's precipitation. The observed importance of land-use and vegetation attributes implies that well-conceived adaptation strategies could mitigate potential negative effects of climate change. This finding is generally of great value for land management planning.

4.2 Introduction

Ecosystem services (ES) are the link between ecosystems and human society (Millennium Ecosystem Assessment, 2005b). Despite a steady increase in ES-related research, challenges remain in quantifying spatio-temporal patterns of ES supply and in understanding how these are connected to basic ecosystem properties and functions (Kandziora *et al.*, 2013; Villamagna *et al.*, 2013). In this context, it is even more challenging to identify consistent patterns in ES drivers and supply at broad spatial scales due to the complex interactions between drivers. Ecosystems used as rangelands deliver a number of provisioning ESs, with forage services being the most prominent; supporting approximately 50% of global livestock production (Millennium Ecosystem Assessment, 2005b). Rangeland ecosystems also deliver numerous supporting and regulating ESs. Among them, erosion regulation – also called 'erosion control' (Orwin *et al.*, 2015) – is of major importance (Millennium Ecosystem Assessment, 2005b; Kandziora *et al.*, 2013). Accelerated soil erosion is accompanied by the loss of other soil-mediated ESs such as nutrient and greenhouse gas regulation (Orwin *et al.*, 2015). Ca. 25% of Africa's land surface (excluding deserts) is prone to water erosion and about 22% to wind erosion (Reich *et al.*, 2001).

Rangelands' ability to provide essential ESs is interactively driven by biotic and abiotic factors such as climate, topo-edaphic factors and land management (Díaz *et al.*, 2007b; Ruppert *et al.*, 2012). However, the relative importance of these drivers for ES supply is still poorly understood (van Oudenhoven *et al.*, 2012), particularly in savanna rangelands (Heubes, 2012). This hampers the implementation of monitoring systems for ES supply, and ultimately the identification or design of appropriate land management strategies (Trilleras *et al.*, 2015).

A number of challenges are pertinent in this context. First, it is already challenging to quantify ES supply in savanna rangelands, e.g. due to difficult measurement conditions, or a lack of appropriate ES indicators (Ferner *et al.*, 2015). This is particularly true for forage services: although several sets of indicators have been proposed for regional to global assessments, forage services are mostly not included (Millennium Ecosystem Assessment, 2005b; Kandziora *et al.*, 2013). To overcome this challenge, easy-to-measure ES indicators are required that cover both quantitative and qualitative components of forage provision (Ferner *et al.*, 2015). Forage quantity is closely connected to livestock carrying capacity, and is often estimated as aboveground net primary production or standing crop also known as aboveground biomass (Ruppert & Linstädter, 2014). Forage quality is assessed with various indices such as crude protein, in-vitro digestibility (Changwony *et al.*, 2015), or a combination of both into metabolisable energy (ME). It is also desirable to integrate forage quantity and quality in 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 (Millennium Ecosystem Assessment, 2005b; Kandziora *et al.*, 2013). In dryland ecosystems, a high perennial plant cover (PPC) is particularly important to prevent accelerated wind and water erosion (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).

The second challenge is to identify key biotic and abiotic drivers and to quantify their relative importance for ES supply (Díaz *et al.*, 2007b) particularly in savanna rangelands. Abiotic drivers such as climate and topo-edaphic conditions seem to be of major importance for ESs provided by savanna rangelands (Fuhlendorf *et al.*, 2001; Augustine, 2003) but grazing and other biotic drivers also play an important role (Moreno García *et al.*, 2014). However, empirical studies focusing on savannas mostly assess patterns of vegetation distribution (e.g. Schmidt *et al.*, 2011) or address interactions between tree and grass layer (Belay & Moe, 2015), but rarely quantify impacts of biotic and abiotic drivers on vital ESs (Reed *et al.*, 2015). Moreover, most of these studies have a local focus, which makes it impossible to detect consistent patterns of ES drivers at regional scales and hence difficult to upscale to broader geographical scales.

The third challenge relates to the fact that biotic and abiotic 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 (Loreau *et al.*, 2001), they remain useful in predicting effects of ecosystem integrity (or degradation) on ES supply (Díaz *et al.*, 2007b; Kandziora *et al.*, 2013). Again, appropriate approaches are needed to evaluate indirect effects. Studies from dryland rangelands often rely on key vegetation attributes 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). The use of PFTs is based on the assumption that plants with similar ecological trait attributes will exhibit similar responses to environmental changes and perform similar functions (McIntyre *et al.*, 1995). A central hypothesis is that functional traits simultaneously explain individual plant responses to biotic and abiotic changes (Lavorel & Garnier, 2002). Although the use of PFTs has widely been accepted in plant ecology (Gillison, 2013), the challenge remains to select trait sets that capture plant responses to environmental drivers of interest. Due to convergent effects of grazing and climatic aridity, this task is particularly challenging in dryland environments (Quiroga *et al.*, 2010; 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.*, 2007c).

Gradient studies are useful in ecological research (Shipley, 2010) and ES studies along steep climate gradients may allow extrapolating climate change effects on ES supply via a space-time substitution, if spatial trends reflect projected temporal trends (Dunne *et al.*, 2004). For these reasons, West Africa's Sudanian savannas are an ideal study area for improving our understanding of ES delivery from tropical savannas under contemporary and future conditions. In the study area, a steep south-north gradient of increasing climatic aridity has been observed (Mertz *et al.*, 2012), shaping spatial patterns of vegetation attributes (White, 1983). At the same time, local gradients of land-use intensity can be found throughout the region ranging from protected areas over fallows to non-arable land (Ouédraogo *et al.*, 2015). However, these good opportunities have previously remained rather unharnessed due to logistical challenges. Consequently, we still know very little about how changing climate and land-use will jointly shape ecosystem functioning and ES supply in West Africa's Sudanian savannas.

Taking a macroecological perspective, our study thus aims at (i) assessing vital ESs (forage supply and erosion control) from West Africa's savanna rangelands over a broad geographical scale with the aid of appropriate indicators, (ii) quantifying the relative importance of direct and indirect ES drivers, with the ultimate goal to identify significant yet easy to measure and potential universal predictors. We use an *a-priori* conceptual model for direct and indirect effects of biotic and abiotic drivers on ESs (Figure 4-1), based on current knowledge (e.g. Díaz *et al.*, 2007b). We specifically hypothesise that the steep gradient of climatic aridity is a more important driver of ES supply in West Africa's Sudanian savanna rangelands than topo-edaphic factors or land-use intensity.

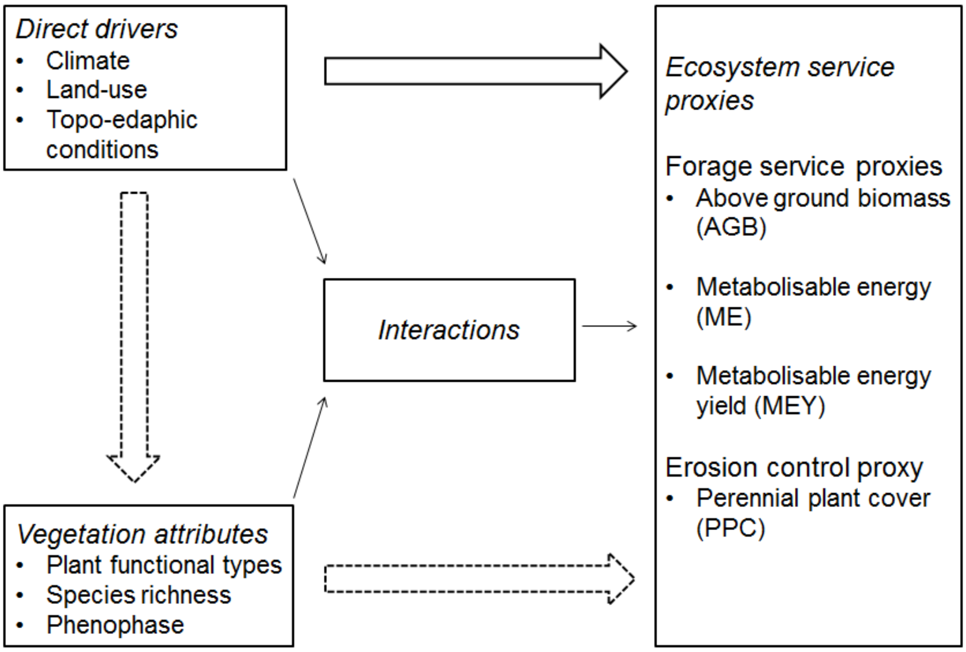


Figure 4-1: Flow chart describing the conceptual approach used in this study for showing the direct and indirect effects of biotic and abiotic drivers on ecosystem services. Double arrows indicate direct drivers, dashed double arrows indicate indirect effects and single line arrows indicate interactions.

4.3 Materials and methods

4.3.1 Study area

The study area reaches from Northern Ghana to Central Burkina Faso and covers ~106 000 km² in the West African Sudanian savanna zone (Figure 4-2). 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). The rainy season is from April to November in the south and May to September in the north. Mean annual precipitation (MAP) and mean annual temperature range from 1200 to 600 mm, and from 26°C to 28°C, respectively. The vegetation is an open to close savanna. The herbaceous layer is dominated by grasses and forbs: common species include *Brachiaria lata*, *Brachiaria jubata*, *Eragrostis turgida*, *Digitaria horizontalis*, *Spermacoce stachydea*, *Tephrosia pedicellata*, *Pandiaka angustifolia*, *Zornia glochidiata* and *Waltheria indica.* The tree layer consists of species with a high ability to resprout (Ouédraogo *et al.*, 2015).

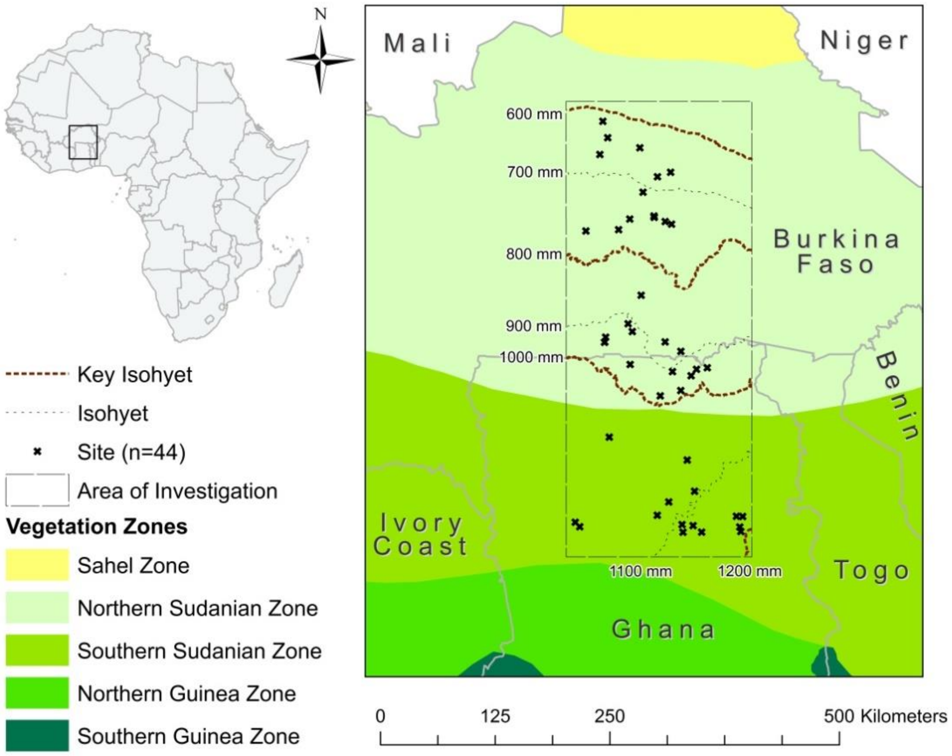


Figure 4-2: Study area and location of 44 sampled sites. The study area covers the southern and northern Sudanian vegetation zones, following White (1983). Sampling is stratified into three rainfall zones of decreasing climatic aridity, as indicated by isohyets (low rainfall: mean annual precipitation 600 – 800 mm/a; intermediate rainfall: 800 – 1000 mm/a; high rainfall: 1000 – 1200 mm/a).

The geology in the south of the climatic gradient is dominated by Voltain, Tarkwaian and Birimian systems (Carrier *et al.*, 2008) while the north is dominated by

Precambrian crystalline rocks consisting of meta-igneous and intrusive granitic rocks (British Geological Survey, 2002) with landforms dominated by rocky elevations within sedimentary basins (Butt & Bristow, 2013). The dominant soils are luvisols in the south (Wood, 2013) and lixisols in the north (Savadogo *et al.,* 2007). These soils have coarse texture (> 80% sand), low water holding capacity, and depending on the cultivation history, 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; its importance increases with climatic aridity (Blench, 1999; Mertz *et al.*, 2010). During the past decades, transhumant pastoralism has partly been replaced by sedentary forms of herd management (Turner & Hiernaux, 2008; Brottem *et al.*, 2014), with livestock kept year-round in close proximity to settlements. In West Africa, livestock serves as a major income source for about 45% of households (Mertz *et al.*, 2010), underlining the importance of forage services for local livelihoods.

4.3.2 Sampling design

We stratified sampling in three rainfall zones oriented along the south-north gradient of increasing climatic aridity (Figure 4-2). In each zone, our sampling approach was designed to assess local environmental gradients of interest (i.e. gradients in topo-edaphic factors and grazing pressure; (Shipley, 2010). This was achieved by choosing sites that maximised the range of grazing and topo-edaphic gradients. For grazing gradients, we explicitly included heavily grazed sites close to settlements and lightly grazed to ungrazed sites in protected areas (two per climate zone).

To capture regional variation in topo-edaphic factors, we used a geological map to select sites (with ≥3 km distance) in major geological units (see Ferner *et al.*, 2015). To capture local variation, we stratified our within-site sampling into slope position (upslope, midslope and lowland). We placed ≥3 plots per slope position and site in homogeneous vegetation (distance between plots ≥30 m; plot size 10 m x 10 m). Within each plot, we randomly placed three circular subplots of 1 m² for the assessment of vegetation attributes. To avoid seasonal bias and to capture intraseasonal ES dynamics, we sampled during two growth periods (June to October 2012 and 2013), and varied the time of sampling independent from other sources of variation. In total, we sampled 44 sites (14 in the most arid zone, 15 in the intermediate, and 15 in the least arid zone), and 300 plots.

4.3.3 Data collection

Climate variables

We obtained long-term climatic data (averaged over the period 1950-2000) for each site from WorldClim (http://www.worldclim.org/). Extracted variables were mean annual precipitation (MAP), mean annual temperature, minimum temperature of the coldest month (T_{Min}), maximum temperature of the warmest month, and mean temperature of the wettest quarter. We calculated the UNEP aridity index (AI) as the ratio of MAP to potential evapotranspiration (UNEP, 1997). For simplicity, we calculated and used a direct measure of aridity as 1 – AI in our analysis (Delgado-Baquerizo *et al.*, 2013). To capture effects of fluctuating climate on ESs, we obtained season's accumulated precipitation (SAP) until the month preceding field sampling from the global precipitation climatological centre (Schneider *et al.*, 2011).

Topo-edaphic variables

Besides slope position and bare soil cover, we recorded various abiotic variables to characterise plots' edaphic characteristics (see Appendix 10 for details). Following FAO (2006), we estimated the cover of surface fragments. To quantify physical and chemical top-soil properties, a composite sample from five soil cores (0–4 cm depth) per plot was collected. Samples were homogenised, air-dried (> 21 days) and sieved; only soil fractions < 2 mm were analysed. Particle size distribution was determined by laser diffraction method, using a Laser Particle Size Analyser (Horiba LA–960). Soil acidity was determined in a 1:2.5 water suspension. Plant-available phosphorus was measured via calcium-acetate-lactate (CAL) extraction (mg kg^{-1}), following standard protocols (VDLUFA, 2008). Soil N and C content was analysed by dry combustion with a CN analyser (Vario EL cube). Variables were categorised into 'slow' and 'fast' responding (soil attributes) to land-use pressure, based on findings from other African dryland rangelands (Angassa *et al.*, 2012; Linstädter & Baumann, 2013; Sandhage-Hofmann *et al.*, 2015); *cf.* Appendix 10). Fast variables (e.g. soil C and N) are mainly driven by direct inputs via herbivore excreta (Angassa *et al.*, 2012; Sandhage-Hofmann *et al.*, 2015). Slow variables (soil texture, soil acidity, bare soil cover and the cover of coarse surface fragments) are largely driven by underlying geology and local topography (see Vries *et al.*, 2012 for a similar approach). All analyses were performed at the Geographical Institute of the University of Bonn, Germany.

Land-use intensity variables

As main proxies for land-use intensity, we recorded four biotic surface characteristics with known positive (+) or negative (-) responses to increasing grazing pressure in savannas

(Zimmermann *et al.*, 2010; Linstädter *et al.*, 2014). The cover of cattle and donkey dung (+), smallstock droppings (+), litter (-), and moribund material (-) were visually estimated. We also combined physical evidence of grazing (trampling, dung, and the removal of standing biomass) in an expert assessment of recent grazing pressure (following Linstädter *et al.*, 2014).

Vegetation attributes

We visually estimated the ground cover of all vascular plant species within subplots, and measured species' vegetative height to the nearest centimeter. We focused on the herbaceous layer, but included seedlings and saplings (≤2 m) of woody species, following Le Roux *et al.* (1995). We also recorded species' phenological stage, using a simplified BBCH scale (Hess *et al.*, 1997), distinguishing germinating, sprouting, shooting, flowering, fruiting, and senescent.

Species' standing aboveground biomass (AGB_{Spec}; in kg dry matter (DM) ha^{-1}) was estimated via allometric equations. On 203 harvesting quadrats (1 m²) representing the full range of grazing pressure in Sudanian savannas, we recorded vascular plant species' vegetative height, ground cover and phenological stage. We then harvested plant biomass at stubble height (ca. 3 cm), and separated biomass into species, discarding moribund material. Samples were oven-dried (60°C, 48 hours) and weighed. For allometric models, we calculated species' biovolume per quadrat as cover x height (Jauffret & Visser, 2003) and established linear regressions with species' biomass per quadrat as response variable. Explanatory variables were – besides biovolume – species' growth form and phenological stage to account for their modulating effects on aboveground biomass (Byrne *et al.*, 2011; Rigge *et al.*, 2013). Model selection procedures rendered separate calibrations for two aggregate growth forms and four phenological stages (see Appendix 11 for details). Established equations performed well in predicting AGB_{Spec} (adjusted $R^2 = 0.74$) and were used for AGB_{Spec} estimation on all subplots. To evaluate indirect effects of biotic and abiotic drivers on ES delivery via their imprint on ecosystem structure and function, we calculated plant species richness on the plot level, and aggregated floristic composition into plant functional types (PFTs). Following recommendations of Díaz *et al.* (2007c) for regional scale studies, we established three-trait PFTs (Appendix 12), based on life history ('annual' or 'perennial'), growth form ('forb', 'graminoid', or 'woody'), and plant vegetative height ('small': ≤ 50 cm, 'tall': > 50 cm). Plant height was directly measured on subplots while species' life history and growth form affiliations were extracted from taxonomic literature (e.g. Poilecot, 1999; Clayton *et al.*, 2006; Schmidt *et al.*, 2011). Trait combinations resulted in ten PFTs (Appendix 13e). Relative abundances of PFTs were calculated based on AGB_{Spec} (see above). In analogy to community-aggregated functional traits (Vile *et al.*, 2006), we obtained an aggregated value for a community's phenological stage ('phenophase'). This was done by weighting species' phenological stage according to their relative contribution to the biomass of the plant community.

Approximating ecosystem services

We established plot-level proxies for two cardinal aspects of forage provision, i.e. forage quantity (total aboveground biomass, AGB; in kg DM ha^{-1}) and forage quality (metabolisable energy, ME; in MJ kg^{-1} DM). We estimated AGB by summing AGB_{Spec} data per subplot, and then averaging over a plot's three subplots. As no actions have been taken to prevent losses in biomass from herbivory before sampling, AGB may not serve as estimate for above ground primary production (Ruppert & Linstädter, 2014). However, given that our sampling efforts have covered the full range of grazing pressure in Sudanian savannas, we are very confident that it may serve as a reliable estimate of actual forage provision within years of sampling. For ME estimation, we used a portable spectro-radiometer (FieldSpec 3Hi-Res, ASD Inc., Boulder, CO, USA) to measure plant reflectances on subplots. With the aid of a regression model calibrated in the same area (Ferner *et al.*, 2015), we estimated ME and averaged to plot-level. Due to difficult measurement conditions in West Africa's Sudanian savannas (Gessner *et al.*, 2013; Ferner *et al.*, 2015), spectral data were obtained for 1–3 subplots per plot and for 1–9 plots per site. We combined AGB and ME in a single proxy of forage provision (metabolisable energy yield, MEY; in GJ ha^{-1}), the product of AGB and ME. As a proxy of the regulating ES 'erosion control', we used the cover of all perennial plants per plot.

4.3.4 Data analyses

To assess the relative importance of biotic and abiotic variables as drivers of ES supply, we used an integrated two-step approach. First, environmental variables (grouped into variable sets namely climate, topo-edaphic conditions, land-use and plant functional types) were selected as potential predictors; second, the relationship of selected potential predictors with ESs was explored, and important predictors were identified. In a third step, we explored the relationship between vegetation attributes and predictor sets which influence them (i.e. climate, topo-edaphic and land-use variables).

Selection of environmental variables as potential predictors of ES supply

We performed principal component analyses (PCAs) to select potential predictors of ES supply from six site-level variables (climatic variables from WolrdClim) and twenty-nine variables recorded on plot level (others). Separate PCAs were performed for five variable sets related to different biotic and abiotic factors: (i) climate, (ii) topo-edaphic variables with slow response or (iii) fast response to land-use, (iv) land-use intensity, and (v) plant functional types. We then identified variables highly loading ($\geq |0.8|$) on principal components (PC) with eigenvalues > 1 to reduce collinearity within predictor sets. In case of competing variables (several variables highly loading on the same PC), we chose the variable with the highest proportion of explained variance in single-variable models. We additionally chose study site, grazing pressure (GP), slope position (SP), season's accumulated precipitation (SAP), phenophase (Phen), species richness (SRic) and two interaction terms (GP x Phen, GP x SP). Given their ordinal or categorical nature, GP and SP could not be included in PCAs and were selected due to their prevalent importance (Augustine, 2003; Ouédraogo *et al.*, 2015). SAP and Phen were selected to account for intraseasonal variation in precipitation and forage provision, respectively (Brüser *et al.*, 2014). Interaction terms and SRic were selected based on expert knowledge, as we assumed important effects on ES supply. Multicollinearity of selected variables was checked using Spearman's rank correlation and variance inflation factors.

Exploring environmental variables' relationship with ESs

We used linear mixed-effect models (LMM) to explore the effect of selected variables on ESs. Initially, full LMMs – including all selected variables as fixed effects – were established for each ES in focus (four in total); 'site' was included as random-intercept term (e.g. ES proxy ~ climate variables + land-use variables + topo-edaphic variables + vegetation attributes + interactions + (1|site)). Due to the different units and scales of potential predictors, we first standardised all variables before performing LMMs. The initial full models were subject to (Bayesian information criteria) BIC-based model selection, using restricted maximum likelihood estimation (REML; Zuur *et al.*, 2009). LMMs were calculated using the lme4-package for R (Bates *et al.*, 2015).

To estimate the variance explained by fixed and random effects, we used the method proposed by Nakagawa and Schielzeth (2013) and extended by Johnson (2014) to obtain marginal and conditional R^2 (MR^2 and CR^2, respectively). MR^2 is the proportion of explained variance by fixed-effects, and CR^2 is the proportion explained by fixed plus random effects (Ruppert *et al.*, 2015). For each ES, variance explained by random effects was calculated as CR^2 minus MR^2. Final models were further explored using ANOVAs (Type III). We estimated the proportion of variance explained by individual predictors via classical eta-squared values. We plotted Moran's I spatial correlograms for final models to check for spatial autocorrelation (Legendre & Legendre, 1998; Griffith, 2009).

As a mean of validation and to estimate uncertainty in the standard errors (SEs) of our model parameters, we bootstrapped (10 000 repetitions with replacement) our final models and calculated the relative bias in SE. The relative bias of SE estimates for model parameters were calculated by comparing the bootstrap estimates and our LMM final model, following Thai *et al.* (2013):

$$RBias = \frac{SE_{Boot} - SE_{LMM}}{SE_{LMM}} x\ 100$$

Where $RBias$ is the relative bias

SE_{Boot} = Bootstrap standard errors averaged over the 10 000 runs

SE_{LMM} = Final LMM (selected from BIC model selection) standard errors

Following Thai *et al.* (2013), we classified model predictors as unbiased (RBias < ±5%); moderately biased (± 5-10%); and strongly biased (> ±10%). Bootstrapping was performed with the boot-package for R (Canty & Ripley, 2015). Statistical assumptions were explored visually as proposed by Zuur *et al.* (2010). To achieve normality of errors and homoscedasticity, we applied square-root transformation for PPC and logarithmic transformation for AGB and MEY. All analyses were conducted using the statistical software R in version 3.2.2 (R Core Team, 2015).

Exploring relationships between vegetation attributes and environmental variables

To test the relationships between vegetation attributes and (environmental) predictor sets with direct and indirect effects on ESs (i.e. climate, topo-edaphic and land-use variables), we performed LMMs for each retained vegetation attribute as response and the environmental variables as predictors.

4.4 Results

4.4.1 Selected potential predictors of ecosystem services

From the five PCAs, we selected fourteen variables (nine environmental and five PFTs) for further analyses (see Appendix 13 for PCA results). Soil sand content was dropped from the selected potential predictors due to its high correlation with soil nitrogen content (Appendix 14). In total, 21 variables (18 fixed-effects, two interactions, and one random effect) were selected as potential predictors of ES supply (Table 4-1).

Table 4-1: Selected variables for linear mixed-effect models. Fixed effects are grouped in five predictor sets. Two interaction terms and the random effect 'study site' are also considered. SD = standard deviation, Min. = minimum, Max. = maximum

Effect type	Predictor set	Potential predictor	Acronym (unit)	Mean	SD	Min.	Max.
Fixed	Climate	Climatic aridity[a]	CA (NA)	0.464	0.093	0.307	0.694
		Min. temperature of coldest month	T_{Min} (°C)	21.71	0.431	20.81	22.61
		Season's accumulated precipitation[b]	SAP (mm)	516.4	174.04	161.4	808.9
	Slow topo-edaphic variables	Slope position[c]	SP (NA)	-	-	1	3
		Soil acidity	pH (NA)	5.40	0.517	4.00	6.90
		Bare soil cover	BSC (%)	19.24	9.98	5.00	60.00
	Land-use	Grazing pressure[d]	GP (NA)	-	-	0	4
		Litter cover	LC (%)	3.00	3.95	0.00	25.00
		Moribund material cover	MMC (%)	0.502	1.53	0.00	15.00
	Fast topo-edaphic variables	Soil content of plant-available phosphorus	P (mg kg $^{-1}$)	14.20	17.10	1.00	147
		Soil nitrogen content	N (%)	0.090	0.054	0.031	0.324
	Vegetation attributes	Small annual forbs	SAF (% AGB)[e]	0.078	0.082	0.00	0.441
		Tall annual forbs	TAF (% AGB)[e]	0.115	0.094	0.00	0.558
		Small annual graminoids	SAG (% AGB)[e]	0.049	0.085	0.00	0.545
		Small perennial graminoids	SPG (% AGB)[e]	0.047	0.103	0.00	0.686
		Tall perennial graminoids	TPG (% AGB)[e]	0.283	0.240	0.00	0.991
		Species richness	SRic (#)	17.86	5.53	6	40
		Phenophase	Phen (CWM)[f]	2.55	0.616	2.00	4.85
Interaction	Interactions	Grazing pressure x Phenophase	GP*Phen	-	-	-	-
		Grazing pressure x Slope position	GP*SP	-	-	-	-
Random	Study site	Study site	Site	-	-	1	44

[a] 1 – AI, with AI = UNEP aridity index (mean annual precipitation/ potential evapotranspiration), following UNEP (1997)

[b] Antecedent rainfall of a rainy season until month preceding field sampling

[c] Categorical variable (1-3) – lowland (1), midslope (2), upslope (3)

[d] Ordinal scale (0-4) – 0 (very light GP), 1 (light GP), 2 (moderate GP), 3 (heavy GP), 4 (very heavy GP)

[e] AGB = total aboveground biomass per plot

[f] Community-weighted mean of phenology; species' phenological stage (0-5) weighted by their relative abundance (% AGB)

NA = not applicable

4.4.2 Performance of predictors across ES proxies

The importance, bias and direction of predictor effects for the four proxies of ES supply varied considerably (Figures 4-3 and 4-4). The ME model had a comparatively low overall explained variance (44%), while the other ES proxies had higher explained variance (MEY and PPC = 67%; AGB = 77%). The importance of the random factor 'site' (calculated as CR^2 minus MR^2) also varied considerably across ES proxies (Appendix 16). It was negligible for PPC (5% of variance) and still rather small for AGB (10%) and MEY (15%), but high for ME (26%). Following bootstrapping and the calculation of relative bias, we found that the ME model was also rather unreliable, since it had a high number of predictors with strongly biased standard errors – a ratio of four biased to three unbiased predictors (Table 4-2 and Figure 4-3).

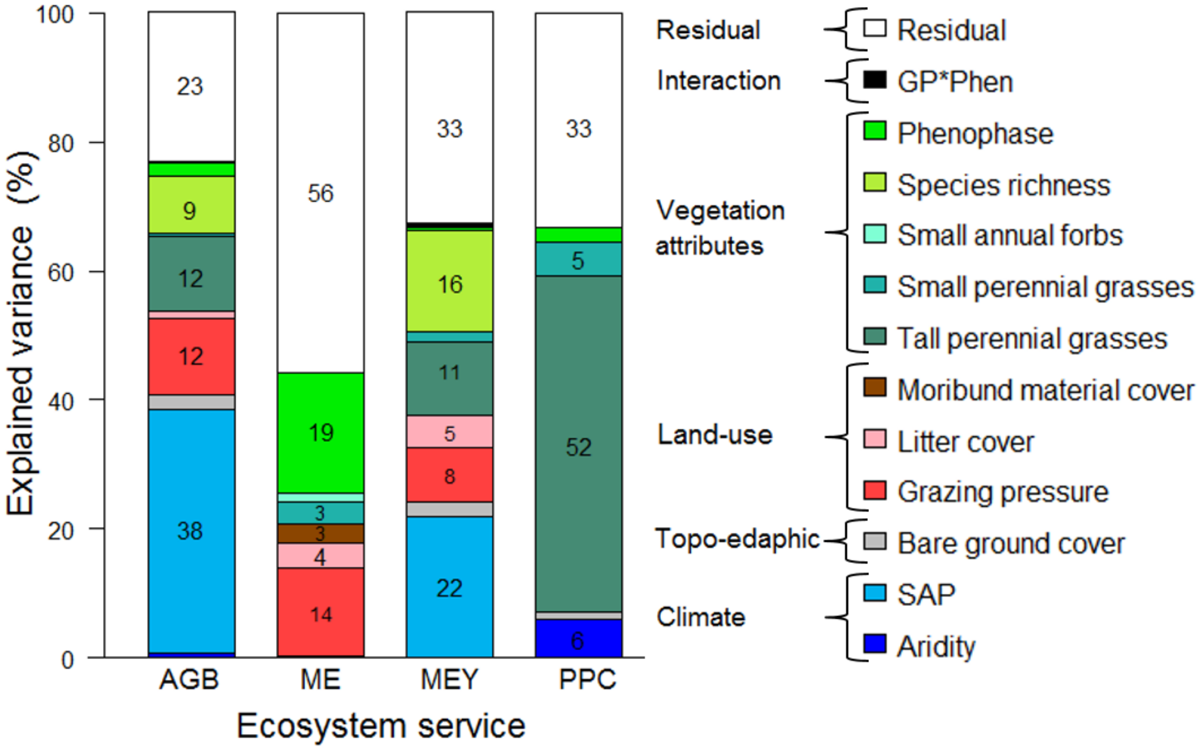


Figure 4-3: Percent of variance explained by biotic and abiotic drivers in linear mixed-effect models. For each ecosystem service, bars denote the percent of variance explained by each predictor (calculated as classical eta squared). Unexplained variance is included as residuals. SAP = Season's accumulated precipitation, GP = grazing pressure, Phen = phenophase; AGB = aboveground biomass, ME = metabolisable energy, MEY = metabolisable energy yield, PPC = perennial plant cover.

Table 4-2: Relative bias of the standard errors (SEs) for all predictors of ecosystem service supply (AGB = aboveground biomass, ME = metabolisable energy, MEY = metabolisable energy yield, PPC = perennial plant cover). Levels of bias are: unbiased, with relative bias < ±5% (given in brackets); moderately biased, with relative bias from ±5% to ±10%; and strongly biased, with relative bias > ±10% (given in bold). A dash (-) indicates that a predictor was not retained in the final model of the respective ecosystem service. Bootstrapping was performed using the boot-package in R (Canty & Ripley, 2015) and resampling within our data 10 000 times to estimate the uncertainty in model predictors.

Predictor set	Potential predictor	Relative bias of SEs (%)			
		AGB	ME	MEY	PPC
Climate variables	Climatic aridity	**-23**	-	-	**-24**
	Season's accumulated precipitation	**-23**	-	**-33**	**-**
Topo-edaphic variables	Bare soil cover	(1)	(0)	(3)	(-4)
Land-use variables	Grazing pressure	6	**-17**	(2)	-
	Litter cover	-5	**29**	(-3)	-
	Moribund material cover	**-**	-5	-	-
Vegetation attributes	Small annual forbs	**-**	**-11**	-	-
	Small perennial graminoids	**18**	**15**	6	-10
	Tall perennial graminoids	(4)	-	8	-5
	Species richness	5	-	(2)	-
	Phenophase	**14**	(-2)	**21**	**-21**
Interaction	Grazing pressure x Phenophase	10	-	8	-

4.4.3 Relationships between predictor sets and ES proxies

Climate variables

Climate variables (particularly SAP) were the most important predictors of AGB and MEY, with high levels of explained variance (39% and 22%, respectively; Figure 4-3). On the contrary, climate variables were less important for forage quality (ME) and erosion control (PPC). SAP had positive effects on AGB and MEY while climatic aridity negatively affected AGB and PPC (Figure 4-4).

Topo-edaphic variables

Effects of topo-edaphic variables were of secondary importance for all ESs: only bare soil cover was retained in final models (Appendix 15). This proxy was an unbiased predictor of all ESs, with negative effects on AGB, MEY and PPC, but positive effects on ME (Figure 4-4). However, it only explained a small portion of variance in ES proxies (< 5%; Figure 4-3).

Land-use variables

Grazing, litter cover and moribund material cover were important predictors for forage services, but were not relevant for PPC (Figure 4-3). Grazing pressure was the most important land-use predictor in all cases explaining 12% variance in AGB, 14% in ME and 8% in MEY. It had negative effects on AGB and MEY but positive effects on ME.

Vegetation attributes

Vegetation attributes were important predictors for all ES proxies and had strong positive effects in all cases except Phen which was negatively related to ME and PPC (Figure 4-4). SRic, SAF, SPG, TPG, and Phen were important for forage services while only a subset (SPG, TPG, Phen) were important for PPC (Figures 4-3 and 4-4). ME was mainly driven by phenophase (19%) and grazing pressure (14%), while PPC was mainly driven by TPG (52%). Vegetation attributes contributed high levels of variance (greater than 20%) for all ES proxies.

Interactions

Of the two interactions tested, only the interaction of grazing pressure with phenophase was important for AGB and MEY (Figure 3 and Appendix 15) but explained less than 1% of variance in both cases.

4.4.4 Relationships between vegetation attributes and potential environmental predictors

The LMM results showed that plant functional types (SAF, SPG and TPG) were mainly driven by topo-edaphic and land-use variables with the exception of TPG which was additionally driven by climatic aridity (Table 4-3). SRic and Phen on the other hand were driven by season’s accumulated precipitation.

Table 4-3: Summary of LMM results showing relationship between vegetation attributes and environmental variables (climate, topo-edaphic and land-use variables). SAF = small annual forbs, SPG = small perennial graminoids, TPG = tall perennial graminoids, SRic = species richness, Phen = phenophase, n.s = nonsignificant but retained in final model.

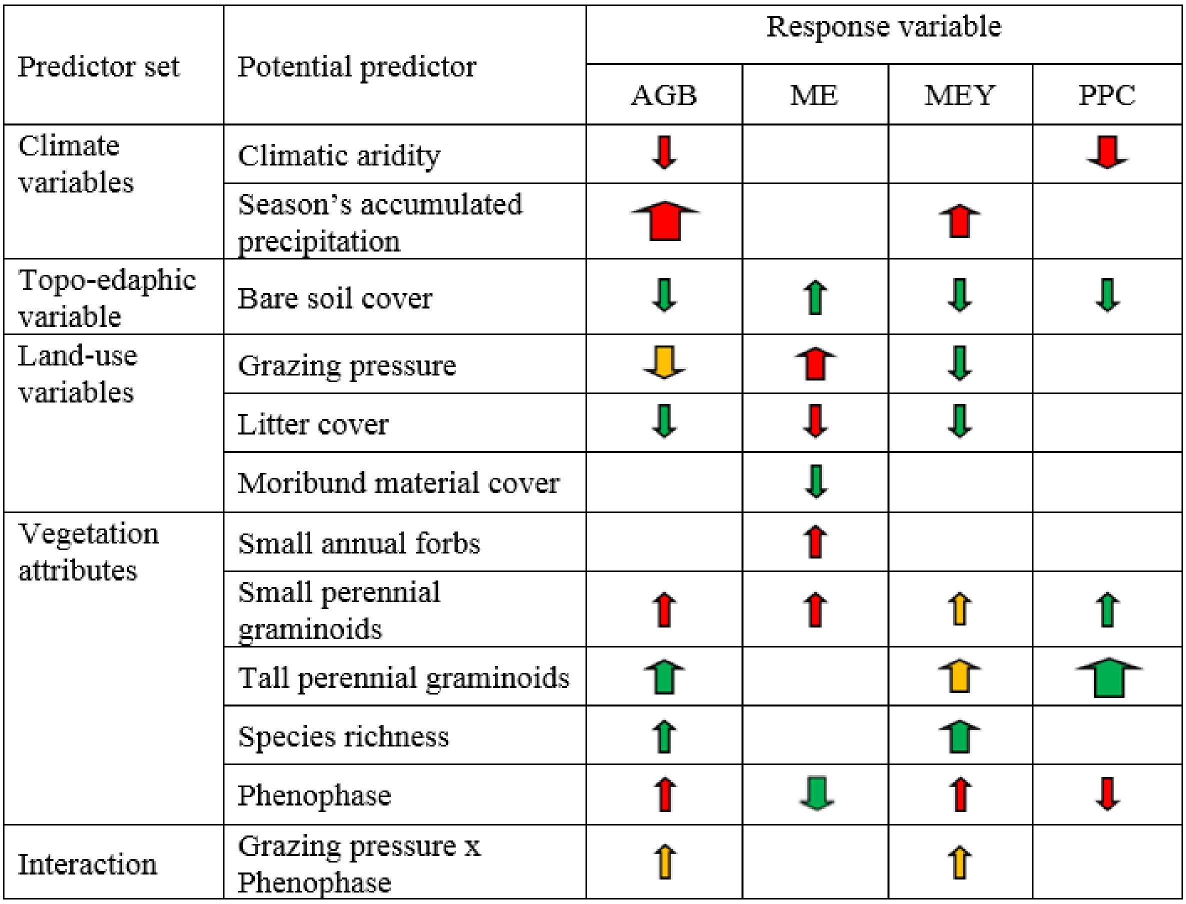
Predictor set	Potential predictor	SAF	SPG	TPG	SRic	Phen
Climate variables	Season’s accumulated precipitation				0.3 (**)	- 0.02 (n.s)
	Climatic aridity			-2.7 (**)		
	Min. temperature of coldest month					
Topo-edaphic variables	Slope position					
	Soil acidity	0.2 (***)	-0.2 (**)			
	Bare soil cover					
	Soil content of plant-available phosphorus			2.3 (***)		
	Soil nitrogen content		0.2 (**)			
Land-use variables	Grazing pressure	0.2 (**)	0.3 (***)	-2.2 (**)		
	Litter cover		0.2 (***)			
	Moribund material cover					
Interaction	Grazing pressure x Phenophase					

4.5 Discussion

Biotic and abiotic factors interactively affect ES supply. We assessed effects of various biotic and abiotic variables on vital ESs provided by African savannas. Our macroecological study gives valuable insights into the relative importance of climate, topo-edaphic conditions, land-use intensity and vegetation attributes as ES drivers at a regional scale. We found that the relative importance of predictor sets differed considerably across ES proxies, and that vegetation attributes always played an important role. This highlights that it is critical to consider a suite of biotic and abiotic variables as potential predictors of ESs supply (Kandziora *et al.*, 2013); and that variables reflecting vegetation structure are of primary importance (Gaitán *et al.*, 2014; Ruppert *et al.*, 2015). In the following, we will first discuss our results from a more methodological point of view, and then highlight the ecological context of predictor sets’ performance.

4.5.1 Performance of predictors across ES proxies

The importance, bias and direction of predictor effects for the four proxies of ES supply varied considerably (Figure 4-4). Since standard errors of model predictors were mostly unbiased for AGB, MEY and PPC, our sampling effort was sufficient for these ES models while the opposite is true for ME. An exception was the predictor set of climate; here, variables were always biased. We assume that this might be due to the fact that they were only available at site (and not plot) level. The fact that predictors explained a high proportion of variance in AGB, MEY and PPC (67-77%) and that site effects were comparatively small (5-15%) suggest that relevant predictor sets were used. However, our findings for ME are less convincing. The seven predictors retained in the final model explained only 44% of variance in ME; four of them were also highly biased. This finding is supported by the relative high amount of variance explained by the random factor 'site' (26%). Hence, important drivers of ME supply were not taken into account, either because we did not record them in the field, and/or because variable selection missed them. We assume that the large number of plant species' included in this study (with varying forage properties) may have driven ME differences. More generally, our results underline that it is still a major challenge to identify key biotic and abiotic drivers for spatio-temporal patterns in ES supply (Díaz *et al.*, 2007b; Kandziora *et al.*, 2013).



Predictor set	Potential predictor	Response variable			
		AGB	ME	MEY	PPC
Climate variables	Climatic aridity	⇩			⇩
	Season's accumulated precipitation	⇧		⇧	
Topo-edaphic variable	Bare soil cover	⇩	⇧	⇩	⇩
Land-use variables	Grazing pressure	⇩	⇧	⇩	
	Litter cover	⇩	⇩	⇩	
	Moribund material cover		⇩		
Vegetation attributes	Small annual forbs		⇧		
	Small perennial graminoids	⇧	⇧	⇧	⇧
	Tall perennial graminoids	⇧		⇧	⇧
	Species richness	⇧		⇧	
	Phenophase	⇧	⇩	⇧	⇩
Interaction	Grazing pressure x Phenophase	⇧		⇧	

Figure 4-4: Importance and direction of predictor effects on ES supply. Arrows indicate that a predictor was retained in the final ES model, visualise a predictor's effect size class (after Cohen, 1988)[1], direction of effect[2] and level of bias[3]. AGB = aboveground biomass, ME = metabolisable energy, MEY = metabolisable energy yield, PPC = perennial plant cover.

[1] Arrow width indicates predictors’ effect size (classical eta squared); ⬆ = very small effect (< 0.1), ⬆ = small effect (0.1 - 0.3) and ⬆ = medium effect (0.3 - 0.5).

[2] Arrow direction indicates relationship; upward/downward arrows = positive/negative relationship of predictors with response variable.

[3] Arrow colour indicates relative bias of predictors; green = unbiased (relative bias < ±5%), yellow = moderately biased (relative bias from ±5% - ±10%) and red = strongly biased (relative bias > ±10%).

4.5.2 Relationships between predictor sets and ES supply

Climate variables

Contrary to our initial hypothesis, the long-term climate regime of a given site was of minor importance for forage provision: forage quality (ME) was not predicted by any climate variable, while AGB and MEY were more driven by antecedent rainfall than by climatic aridity. Our results corroborate earlier findings that effects of climatic aridity on forage production may be overridden by fluctuations in rainfall (Ruppert *et al.*, 2012). As we designed our study to (also) capture intraseasonal variation in ESs and their drivers, it is not surprising that a season’s accumulated precipitation played – like in other dryland rangelands – an important role for forage production (Brüser *et al.*, 2014; Wang *et al.*, 2016).

The strong negative relationship between PPC and climatic aridity corroborates earlier findings (Linstädter *et al.*, 2014). In our study, tall perennial grasses only dominated near-natural vegetation in the two rainfall zones with intermediate and high MAP (results not shown). We deduce that non-protected areas in the northern Sudanian savannas are particularly prone to soil erosion. , and also to losses of other soil-mediated ESs such as carbon storage (Orwin *et al.*, 2015).

Topo-edaphic variables

Among the various proxies within this predictor set, five were selected for further analyses, and only bare soil cover was retained as a significant predictor in final models. Although it was an unbiased predictor of all ESs, it always had very small effects (Figure 4-4). The ecological interpretation is challenging: bare soil is an unspecific indicator, reflecting not only edaphic aridity but also other aspects of environmental harshness such as climatic aridity and disturbances (Augustine, 2003; Linstädter *et al.*, 2014). It has also been described as an indicator of low ecosystem integrity (Kandziora *et al.*, 2013). The negative relationship between PPC and bare soil cover – notwithstanding the potential existence of autocorrelation – might relate to the fact that environmental harshness favours bare soil cover and annual plant cover (Linstädter *et al.*, 2014). The very small effects by topo-edaphic variables indicate that in West Africa’s Sudanian savannas, they are of minor importance for ES supply from herbaceous vegetation. This is somewhat surprising, as other regional studies from African savannas found topo-edaphic conditions as a major source of spatial heterogeneity in herbaceous vegetation, e.g. in floristic composition and/or ANPP (Augustine, 2003; Viljoen *et al.,* 2014). However, the relative importance of environmental conditions for ESs (also) depends on gradient length. We assume that the broad range in land-use intensity captured in our study area has masked the comparatively small variation in topo-edaphic conditions. Our considerations are in congruence with a global study on environmental constraints of savannas, which found that both soil fertility and topographic complexity were of local and divergent importance (Lehmann *et al.*, 2011).

Land-use variables

Grazing, litter cover and moribund material cover were significant predictors for forage provision, but only had small to very small effects. In agreement with earlier findings (e.g. Schönbach *et al.*, 2012), grazing had a strong negative relationship with AGB and MEY (Figure 4-4). Our results are in line with findings from dryland rangelands elsewhere (Linstädter & Baumann, 2013; Gaitán *et al.*, 2014; Changwony *et al.*, 2015), and underline that it is critical for ES studies to (also) consider management effects on ecosystem function (de Bello *et al.*, 2010). In accordance with previous studies from dryland rangelands (Schönbach *et al.*, 2012; Changwony *et al.*, 2015), we found a strong positive relationship between ME and grazing (Figure 4-4). This is probably due to modulatory effects of grazing on phenophases. Grazing typically delays plant phenology (Han *et al.*, 2015); as advanced phenological stages have lower nutritive values (Moreno García *et al.*, 2014; Changwony *et al.*, 2015), grazing indirectly increases forage quality.

Vegetation attributes

Species richness (SRic), phenophase (Phen), tall perennial graminoids (TPG), small perennial graminoids (SPG), and small annual forbs (SAF) were important predictors for forage services, but only Phen, SPG and TPG could predict PPC. In agreement with other research findings, especially from experimental sites (e.g. Marquard *et al.*, 2009), there was a significant positive relationship between SRic and AGB. Positive effects of species diversity on productivity (estimated here as AGB) can be due to a number of mechanisms (see Craven *et al.*, 2016 for a recent review), such as species complementarity or facilitation, or the presence of key species/functional groups that have a disproportionately positive effect on community performance. It is noteworthy that the relationship between SRic and productivity is contentious and Tredennick *et al.* (2015) argue that the relationship might be site-specific.

Our findings highlight the critical role of SRic for maintaining functioning in rangelands, and provide additional evidence of its role in providing key ESs (Cardinale *et al.*, 2012).

The positive relationship between AGB and TPG is consistent with findings by Laliberté *et al.* (2012), who suggested that a strong dominance of tall species, rather than a co-dominance of species with varying heights, could result in higher above- and below-ground production. In contrast to forage quantity (AGB), we only found weak effects of PFTs on forage quality; the positive effects of two 'small' PFTs (SPG and SAF) were very small and strongly biased (Figure 4-4). Apparently our PFT approach was successful in aggregating species with similar effects on forage quantity but not on forage quality. This is somewhat surprising, as we explicitly distinguished between 'tall' and 'small' forbs and graminoids to account for the typically higher forage quality of 'small' (low-stature) grasses and forbs, as found in African grazing lawns (Hempson *et al.*, 2015). In agreement with earlier findings (Schönbach *et al.*, 2012; Changwony *et al.*, 2015), we found ME to be negatively related to phenophase (Figure 4-4), which is mainly due to a reduction in leaf-to-stem ratio at advanced phenological stages (Ball *et al.*, 2001). Our result of a positive relationship between PPC and the relative abundance of perennial graminoids is not surprising; it implies that ecosystems dominated by perennial grasses (e.g. in protected areas) are comparatively little affected by accelerated erosion, but should also have a good capacity to capture and retain water and nutrients (Soliveres *et al.*, 2014). More generally, it underlines that management efforts aiming at erosion control in African rangelands and savannas should focus on the retention of perennial grasses. In support of this recommendation, a modelling study from the southwestern United States found that declines in perennial vegetation cover resulted in exponential increases in wind erosion (Munson *et al.*, 2011).

4.5.3 Indirect effects of climate, topo-edaphic and land-use variables on ESs

In dryland ecosystems, environmental variables (climate, topo-edaphic conditions and land-use) are major drivers of vegetation structure (Augustine, 2003; Linstädter *et al.*, 2014), exerting both direct and indirect effects on ecosystem functions and services (Gaitán *et al.*, 2014). The indirect effects can be estimated via vegetation attributes which have the potential to modify the effects of biotic and abiotic factors on ecosystems (Fry *et al.*, 2013). Our result that climate, topo-edaphic and land-use variables drive vegetation attributes (which were direct drivers of ESs) points to the indirect effects of environmental variables on ESs. Vegetation attributes were more important predictors (explained more variance) than climate, topo-edaphic and land-use variables for all ESs except AGB. Our results suggest that land managers can achieve considerable success by conserving or introducing specific functional groups. Our approach provides important insights on the relative importance of environmental variables and vegetation attributes for driving ES supply in African savannas.

4.6 Conclusion

A main strength of our study is its macroecological approach at a regional scale, including a large number of study sites and spanning across a large area of varying environmental conditions. The study aimed at determining the drivers of ES supply and their relative importance in West African Sudanian rangelands. Our findings are useful for rangeland management and conservation within the context of ongoing climate change. Studies along steep climatic gradients may enhance our understanding of climate change effects on ES supply via a space- time substitution. Our results indicate that climate change will indeed have an impact on the sustainability of ES supply from the region both directly and indirectly via its effects on vegetation attributes. However, the higher importance of antecedent rainfall compared to climatic aridity over a 50-year period suggests that the received rainfall of a year could override the effects of long-term climatic conditions. Considering the importance of grazing pressure as a driver of forage supply and erosion control, we deduce that appropriate land management strategies (such as an adaptive regulation of stocking densities on a local and regional scale) can potentially mitigate negative effects of climate change on ES supply.

5 General conclusion

This study investigated the impacts of biotic and abiotic variables on three important aspects of herbaceous vegetation in the Sudanian savannas of West Africa; namely the species composition, the diversity and the provision of ecosystem services (ESs). One main strength of this study is that it uses a macroecological approach at a regional scale, including a large study area (~106 000 km²) and a considerably high number of vegetation relevés (450 plots).

Studies along steep climatic gradients and using a space-time substitution approach (as done in this study) may enhance our understanding of climate change effects on vegetation. The results, for all the investigated aspects of vegetation, suggest that climate is more important than land-use (assessed via grazing pressure), topography and soil at a regional scale. This indicates that climate change will indeed affect vegetation composition, ecosystem functioning and hence ES supply. However, the higher importance of antecedent rainfall (for biomass production) compared to climatic aridity over a 50-year period suggests that the received rainfall of a year could override the effects of long-term climatic conditions for some aspects of vegetation.

Considering the importance of grazing pressure and topo-edaphic variables as drivers of vegetation composition, diversity and ES supply, we deduce that appropriate land management strategies can potentially mitigate negative effects of climate change on vegetation. This suggests that local site conditions (in soil, topography, land-use etc) could determine to which extent climate change effects on plant communities are actually translated into changes in ecosystem structure and function.

Although it is easier and quicker to measure taxonomic diversity indices, correlations between them and functional diversity indicate that they are not recommended for use as surrogates of ecosystem functioning.

The findings of this study are useful for scientists, land managers and policy makers; it can be used to support the management and conservation activities in general and particularly in West Africa’s savanna ecosystems. We opine that the combined gradient approach, simultaneously including climatic, topo-edaphic and land-use gradients, to disentangle climatic and land-use effects was successful in this study. Longer term studies will be required to better understand vegetation responses to environmental conditions. We also recommend that future works aiming to study the combined effects of climate, topo-edaphic and land-use factors on vegetation should consider including more information on land-use such as cropping patterns, fertiliser inputs and length of fallows among others.

6 References

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7 Appendices

Appendix 1 Description of biotic and abiotic variables used in section 2. These were obtained at site level (for climate) or at plot level (other categories).

Variable set	Variable	Description and categories (when applicable)	Unit
Geographic location	Longitude	Angle from 0° (at the equator) to 90° (North or South) at the poles	°
	Latitude	Angular distance of a point east or west of the Greenwich meridian	°
Regional scale drivers[a]	Aridity index[b]	UNEP aridity index: Mean annual precipitation/ annual potential evaporation	NA
	Mean annual precipitation	Mean annual precipitation over 50 years	mm
	Mean annual temperature	Mean annual temperature over 50 years	°C
	Minimum temperature of coldest month	Mean over 50 years	°C
	Maximum temperature of warmest month	Mean over 50 years	°C
	Mean temperature of wettest quarter	Mean over 50 years	mm
	Precipitation of the wettest month	Mean over 50 years	mm
	Precipitation of the wettest quarter	Mean over 50 years	mm
	Precipitation seasonality	Mean over 50 years	%
	Temperature seasonality	Mean over 50 years	%
	Isothermality	Mean over 50 years	°C
Local scale drivers	Slope position	Categorical (upslope, midslope, lowland)	NA
	Fine material cover[c]	Cover of fine material (< 0.2 cm) at plot surface	%
	Fine gravel cover[c]	Cover of fine gravel (0.2-0.6 cm) at plot surface	%
	Medium gravel cover[c]	Cover of medium gravel (0.6-2 cm) at plot surface	%
	Coarse gravel cover[c]	Cover of coarse gravel (2-6 cm) at plot surface	%
	Stone cover[c]	Cover of stones (6-20 cm) at plot surface	%
	Bare soil cover	Plot surface covered by bare soil	%
	Soil N content	Total nitrogen content in topsoil (0-4 cm)	%
	Soil C content	Total carbon content in topsoil (0-4 cm)	%

Appendix 1 continued

Variable set	Variable	Description and categories (when applicable)	Unit
Local scale drivers continued	Soil content of plant-available phosphorus	Plant-available phosphorus of topsoil	mg kg^{-1}
	Soil sand content	Percent of sand in topsoil (0-4 cm)	%
	Soil silt content	Percent of silt in topsoil (0-4 cm)	%
	Soil clay content	Percent of clay in topsoil (0-4 cm)	%
	Soil acidity	Topsoil pH (0-4 cm) in 1:2.5 water suspension	NA
	Litter cover	Plot surface covered by litter	%
	Moribund material cover	Plot surface covered by moribund vegetation	%
	Earthworm excrements	Plot surface covered by earthworm excrements	%
	Biological soil crusts	Plot surface covered by biological soil crusts	%
	Cattle & donkey dung	Plot surface covered by dung of cattle and donkeys	%
	Smallstock droppings	Plot surface covered by smallstock droppings (goats, sheep)	%
	Wild ungulate droppings	Plot surface covered by wild ungulate droppings	%
	Recent grazing pressure	Expert estimate of recent grazing pressure, based on physical evidence of grazing (trampling, dung, removal of standing biomass): 0 = very light, 1 = light, 2 = moderate, 3 = heavy, 4 = extreme	NA

[a] Regional scale drivers = Climate data: Taken from WorldClim.

[b] UNEP aridity index = Mean annual precipitation/ annual potential evaporation

[c] Estimation of coarse surface fragments follows FAO (2006)

NA = not applicable.

Appendix 2 Results of principal component analysis for section 2. The variables are divided into two sets, namely regional scale drivers and local scale drivers of vegetation composition.

Variable	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11	PC12	PC13	PC14	PC15	PC16	PC17	PC18	PC19	PC20
(a) Regional scale drivers																				
UNEP aridity index	0.86	0.38	-0.32	0.03	-0.08	0.06	0.05	-0.01	0.06	0.00	0.00									
Mean annual precipitation	0.91	0.38	-0.08	0.03	-0.08	0.06	0.05	-0.01	0.02	0.02	0.00									
Mean annual temperature	-0.26	-0.24	**0.94**	0.02	0.01	0.00	0.00	0.03	0.00	0.00	0.00									
Min temperature of the coldest month	0.67	0.03	0.73	-0.08	0.00	0.00	-0.01	-0.08	0.00	0.00	0.01									
Max temperature of the warmest month	-0.82	-0.29	0.48	0.07	0.01	0.00	0.01	0.09	0.00	0.00	0.01									
Mean temperature of the wettest quarter	-0.56	-0.56	0.55	0.25	-0.04	-0.03	0.01	0.01	0.00	0.00	0.00									
Precipitation of the wettest month	0.14	**0.97**	-0.17	0.03	0.02	-0.12	-0.01	-0.01	0.00	0.00	0.00									
Precipitation of the wettest quarter	0.42	0.88	-0.11	-0.06	-0.03	0.18	0.01	0.00	0.00	0.00	0.00									
Precipitation seasonality	**-0.99**	-0.11	0.02	-0.01	0.10	-0.03	-0.03	-0.01	0.03	0.01	0.00									
Temperature seasonality	-0.92	-0.35	0.03	0.09	-0.07	0.02	0.11	0.01	0.00	0.00	0.00									
Isothermality	0.95	0.21	-0.02	-0.11	0.18	-0.03	-0.02	0.00	0.00	0.00	0.00									
Eigenvalue	**2.77**	**1.45**	**1.01**	0.35	0.24	0.14	0.10	0.09	0.05	0.02	0.01									
Proportion of Variance	0.70	0.19	0.09	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00									

Appendix 2 continued

Variable	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11	PC12	PC13	PC14	PC15	PC16	PC17	PC18	PC19	PC20
Cumulative Proportion	0.70	0.89	0.98	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00									
(b) Local scale drivers																				
Fine material cover	-0.17	-0.06	-0.66	-0.50	-0.26	-0.14	-0.10	-0.11	0.00	0.19	0.05	-0.01	-0.02	0.01	0.02	0.00	-0.34	0.01	0.12	0.00
Fine gravel cover	0.00	-0.03	0.07	-0.06	**0.97**	0.09	0.01	-0.02	-0.02	-0.09	-0.02	-0.05	-0.02	0.03	0.01	0.01	0.17	0.00	0.00	0.00
Medium gravel cover	0.16	0.01	0.41	0.10	0.29	0.14	0.04	0.02	0.01	-0.15	-0.05	-0.04	0.04	0.01	0.01	0.01	0.81	0.00	0.01	0.00
Coarse gravel cover	0.08	-0.01	**0.97**	0.10	-0.01	0.08	0.03	0.02	-0.01	-0.13	-0.02	-0.04	0.03	-0.03	0.02	-0.02	0.14	0.00	0.03	0.00
Stone cover	0.15	0.11	0.19	**0.92**	-0.10	0.08	0.10	0.15	0.00	-0.12	-0.05	0.07	0.00	0.02	-0.04	0.05	0.05	0.00	0.01	0.00
Bare soil cover	-0.03	-0.03	0.05	0.14	-0.02	-0.01	0.00	0.97	0.03	-0.04	-0.01	0.07	0.10	0.03	-0.05	0.06	0.02	0.00	0.00	0.00
Soil nitrogen content	**0.89**	0.29	0.10	0.14	0.01	0.05	0.14	-0.01	0.06	-0.03	0.05	0.04	0.02	-0.04	0.15	0.15	0.07	-0.11	-0.01	0.00
Soil carbon content	0.89	0.29	0.09	0.08	0.01	0.10	0.15	-0.03	0.04	-0.02	0.06	0.04	0.03	-0.05	0.20	0.05	0.08	0.11	0.00	0.00
Soil content of plant-available phosphorus	0.26	0.07	0.01	-0.04	0.01	0.03	0.02	-0.05	0.01	0.00	0.03	0.01	-0.02	-0.01	0.96	0.00	0.01	0.00	0.00	0.00
Soil acidity	0.11	-0.09	0.13	0.09	0.10	**0.95**	0.06	-0.01	-0.03	-0.12	0.04	0.04	0.01	-0.05	0.04	0.03	0.09	0.00	0.00	0.00
Soil sand content	-0.29	-0.87	-0.02	-0.09	0.01	0.03	-0.38	0.02	0.02	0.01	-0.04	-0.03	0.03	0.03	-0.04	-0.04	-0.01	0.00	0.00	0.00
Soil silt content	0.24	**0.96**	-0.01	0.05	-0.02	-0.08	0.03	-0.02	0.00	0.05	0.06	0.06	-0.04	-0.02	0.05	0.04	0.00	0.00	0.00	0.00
Soil clay content	0.25	0.32	0.08	0.12	0.02	0.08	0.89	0.00	-0.05	-0.12	-0.02	-0.04	0.02	-0.04	0.02	0.02	0.04	0.00	0.00	0.00
Litter cover	0.03	-0.05	0.04	0.00	-0.02	0.01	0.01	0.09	0.04	-0.06	0.04	0.07	0.98	0.00	-0.01	0.05	0.02	0.00	0.00	0.00

Appendix 2 continued

Variable	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11	PC12	PC13	PC14	PC15	PC16	PC17	PC18	PC19	PC20
Moribund material cover	0.05	0.07	-0.04	0.06	-0.05	0.04	-0.03	0.07	-0.03	-0.01	0.11	0.98	0.07	-0.05	0.01	0.00	-0.02	0.00	0.00	0.00
Earthworm excrements	-0.03	0.04	-0.20	-0.14	-0.10	-0.13	-0.10	-0.05	0.09	0.93	-0.03	-0.01	-0.07	0.00	0.00	0.03	-0.11	0.00	0.00	0.00
Biological soil crusts	-0.06	-0.04	-0.03	0.01	0.03	-0.05	-0.03	0.03	-0.01	0.00	-0.04	-0.05	0.00	0.99	-0.01	0.03	0.00	0.00	0.00	0.00
Cattle & donkey dung	0.06	-0.01	-0.01	0.00	-0.02	-0.03	-0.04	0.03	0.98	0.08	-0.04	-0.03	0.05	-0.01	0.01	0.17	0.00	0.00	0.00	0.00
Smallstock droppings	0.15	0.06	-0.03	0.05	0.01	0.03	0.02	0.07	0.20	0.03	0.23	0.00	0.05	0.03	0.00	0.93	0.00	0.00	0.00	0.00
Wild herbivore droppings	0.07	0.07	-0.04	-0.05	-0.02	0.04	-0.01	-0.01	-0.04	-0.03	0.96	0.12	0.04	-0.04	0.03	0.21	-0.03	0.00	0.00	0.00
Eigenvalue	**2.12**	**1.70**	**1.31**	**1.22**	**1.16**	**1.05**	0.99	0.96	0.93	0.90	0.84	0.76	0.72	0.67	0.67	0.60	0.54	0.16	0.11	0.00
Proportion of Variance	0.22	0.14	0.09	0.07	0.07	0.05	0.05	0.05	0.04	0.04	0.04	0.03	0.03	0.02	0.02	0.02	0.01	0.00	0.00	0.00
Cumulative Proportion	0.22	0.37	0.45	0.53	0.60	0.65	0.70	0.75	0.79	0.83	0.86	0.89	0.92	0.94	0.97	0.98	1.00	1.00	1.00	1.00

Appendix 3 Correlation of environmental variables with individual NMDS ordination axes. Significance of correlations are indicated by *** ($p < 0.001$), ** ($p < 0.01$), * ($p < 0.05$).

Variable	NMDS axis 1		NMDS axis 2		NMDS axis 3	
	R^2	p value	R^2	p value	R^2	p value
Latitude	0.0005	0.670	**0.4874**	0.001***	0.0036	0.211
Longitude	0.1035	0.001***	0.1276	0.001***	0.0254	0.001***
Mean annual temperature	0.0727	0.001***	0.0444	0.001***	0.0010	0.592
Precipitation seasonality	0.0037	0.216	**0.4241**	0.001***	0.0200	0.002**
Precipitation of the wettest month	0.0519	0.001***	0.1945	0.001***	**0.1163**	0.001***
Phenophase	0.0155	0.014*	0.2390	0.001***	0.0273	0.001***
Total nitrogen	0.0024	0.305	0.0192	0.005**	0.0049	0.139
Soil acidity	0.0643	0.001***	0.0271	0.001***	0.0106	0.032*
Soil silt content	0.0007	0.596	0.0068	0.076*	0.0247	0.001***
Fine gravel cover	0.0008	0.539	0.0209	0.002**	0.0001	0.854
Coarse gravel cover	0.0677	0.001***	0.0185	0.007**	0.0080	0.058*
Stone cover	0.0186	0.004**	0.0696	0.001***	0.0488	0.001***
Slope position	0.0752	0.001***	0.0055	0.280	0.0312	0.003**
Grazing pressure	**0.2880**	0.001***	0.0351	0.002**	0.0593	0.001***

Appendix 4 Description of biotic and abiotic variables used for section 3. These were obtained at site level (for climate) or at plot level (other categories).

Variable set	Variable	Description and categories (when applicable)	Unit
Geographic location	Longitude	Angle from 0° (at the equator) to 90° (North or South) at the poles	^{o}
	Latitude	Angular distance of a point east or west of the Greenwich meridian	^{o}
Climate data[a]	Aridity index[b]	UNEP aridity index: Mean annual precipitation/ annual potential evaporation	NA
	Mean annual precipitation	Mean annual precipitation over 50 years	mm
	Mean annual temperature	Mean annual temperature over 50 years	^{o}C
	Minimum temperature of coldest month	Mean over 50 years	^{o}C
	Maximum temperature of warmest month	Mean over 50 years	^{o}C
	Mean temperature of wettest quarter	Mean over 50 years	mm
	Precipitation of the wettest month	Mean over 50 years	mm
	Precipitation of the wettest quarter	Mean over 50 years	mm
	Precipitation seasonality	Mean over 50 years	%
	Temperature seasonality	Mean over 50 years	%
	Isothermality	Mean over 50 years	^{o}C
Slow topo-edaphic variables	Slope position	Categorical (upslope, midslope, lowland)	NA
	Medium gravel cover[c]	Cover of medium gravel (0.6-2 cm) at plot surface	%
	Coarse gravel cover[c]	Cover of coarse gravel (2-6 cm) at plot surface	%
	Stone cover[c]	Cover of stones (6-20 cm) at plot surface	%
	Boulder cover[c]	Cover of boulders (6-20 cm) at plot surface	%
	Soil sand content	Percent of sand in topsoil (0-4 cm)	%
	Soil silt content	Percent of silt in topsoil (0-4 cm)	%
	Soil clay content	Percent of clay in topsoil (0-4 cm)	%
	Soil acidity	Topsoil pH (0-4 cm) in 1:2.5 water suspension	NA

Appendix 4 continued

Variable set	Variable	Description and categories (when applicable)	Unit
Disturbances	Recent grazing pressure	Expert estimate of recent grazing pressure, based on physical evidence of grazing (trampling, dung, removal of standing biomass): 0 = very light, 1 = light, 2 = moderate, 3 = heavy, 4 = extreme	NA
	Fire frequency		NA
Fast topo-edaphic variables	Soil N content	Total nitrogen content in topsoil (0-4 cm)	%
	Soil C content	Total carbon content in topsoil (0-4 cm)	%
	Soil organic carbon content	Total organic carbon content in topsoil (0-4 cm)	%
	Soil content of plant-available phosphorus	Plant-available phosphorus of topsoil	mg kg^{-1}
	Fine material cover [c]	Cover of fine material (< 0.2 cm) at plot surface	%
	Fine gravel cover [c]	Cover of fine gravel (0.2-0.6 cm) at plot surface	%

[a] Climate data: Taken from WorldClim.

[b] UNEP aridity index = Mean annual precipitation/ annual potential evaporation

[c] Estimation of coarse surface fragments follows FAO (2006); visual cover estimation of fragments including those that are partly buried were performed.

NA = not applicable.

Appendix 5 Results of principal component analysis for section 3. The variables are divided into three sets, namely climate, topo-edaphic variables with slow response to land-use, and topo-edaphic variables with fast response to land-use. High factor loadings ($\geq \lvert 0.8 \rvert$) on principal components (PC) with eigenvalues > 1 are shown in bold. Variables selected as predictors for ecosystem service supply are also in bold.

Variable	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11
(a) climate											
Mean annual temperature	-0.26	-0.24	**0.94**	0.02	0.01	0.00	0.00	0.03	0.00	0.00	0.00
Mean annual precipitation	0.91	0.38	-0.08	0.03	-0.08	0.06	0.05	-0.01	0.02	0.02	0.00
Maximum temperature of warmest month	0.67	0.03	0.73	-0.08	0.00	0.00	-0.01	-0.08	0.00	0.00	0.01
Minimum temperature of coldest month	-0.82	-0.29	0.48	0.07	0.01	0.00	0.01	0.09	0.00	0.00	0.01
Temperature seasonality	-0.92	-0.35	0.03	0.09	-0.07	0.02	0.11	0.01	0.00	0.00	0.00
Precipitation seasonality	**-0.99**	-0.11	0.02	-0.01	0.10	-0.03	-0.03	-0.01	0.03	0.01	0.00
Precipitation of the wettest quarter	0.42	0.88	-0.11	-0.06	-0.03	0.18	0.01	0.00	0.00	0.00	0.00
Precipitation of the wettest month	0.14	**0.97**	-0.17	0.03	0.02	-0.12	-0.01	-0.01	0.00	0.00	0.00
Mean temperature of wettest quarter	-0.56	-0.56	0.55	0.25	-0.04	-0.03	0.01	0.01	0.00	0.00	0.00
Aridity index	0.86	0.38	-0.32	0.03	-0.08	0.06	0.05	-0.01	0.06	0.00	0.00
Isothermality	0.95	0.21	-0.02	-0.11	0.18	-0.03	-0.02	0.00	0.00	0.00	0.00
Eigenvalue	**2.77**	**1.45**	**1.01**	0.35	0.24	0.14	0.10	0.09	0.05	0.02	0.01
Proportion of Variance	0.70	0.19	0.09	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Cumulative Proportion	0.70	0.89	0.98	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00
(b) Topo-edaphic factors with slow response to land-use											
Clay content	0.32	**0.92**	-0.06	0.09	0.13	0.06	0.08	0.11	0.00		
Silt content	**0.99**	0.06	0.00	-0.07	0.07	-0.02	0.00	0.06	0.00		
Sand content	-0.90	-0.42	0.02	0.02	-0.11	-0.01	-0.03	-0.09	0.00		
Soil depth	-0.01	-0.05	**0.98**	0.00	-0.07	-0.09	-0.07	-0.16	0.00		

Appendix 5 continued

Variable	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11
Soil acidity	-0.07	0.08	0.00	0.97	0.05	0.10	0.14	0.08	0.00		
Medium gravel cover	0.02	0.07	-0.08	0.16	0.04	0.28	0.93	0.08	0.00		
Coarse gravel cover	-0.01	0.06	-0.11	0.10	0.02	0.94	0.28	0.13	0.00		
Stone cover	0.11	0.11	-0.19	0.10	0.20	0.14	0.09	0.93	0.00		
Boulder cover	0.12	0.12	-0.07	0.05	0.96	0.02	0.03	0.18	0.00		
Eigenvalue	**1.70**	**1.40**	**1.04**	0.96	0.82	0.75	0.71	0.63	0.00		
Proportion of Variance	0.32	0.22	0.12	0.10	0.08	0.06	0.06	0.04	0.00		
Cumulative Proportion	0.32	0.54	0.66	0.76	0.84	0.90	0.96	1.00	1.00		
(b) Topo-edaphic factors with fast response to land-use											
Soil nitrogen content	**0.96**	0.16	-0.16	0.00	0.09	-0.12					
Soil carbon content	0.95	0.22	-0.12	0.00	0.15	0.12					
Soil content of plant-available phosphorus	0.25	**0.96**	0.02	0.01	0.08	0.00					
Soil organic carbon content	0.70	0.20	-0.19	0.01	0.66	0.00					
Fine material cover	-0.20	0.02	0.96	-0.19	-0.08	0.00					
Fine gravel cover	-0.01	0.01	-0.17	0.98	0.00	0.00					
Eigenvalue	**1.78**	**1.13**	0.90	0.70	0.48	0.17					
Proportion of Variance	0.53	0.21	0.13	0.08	0.04	0.00					
Cumulative Proportion	0.53	0.74	0.87	0.96	1.00	1.00					

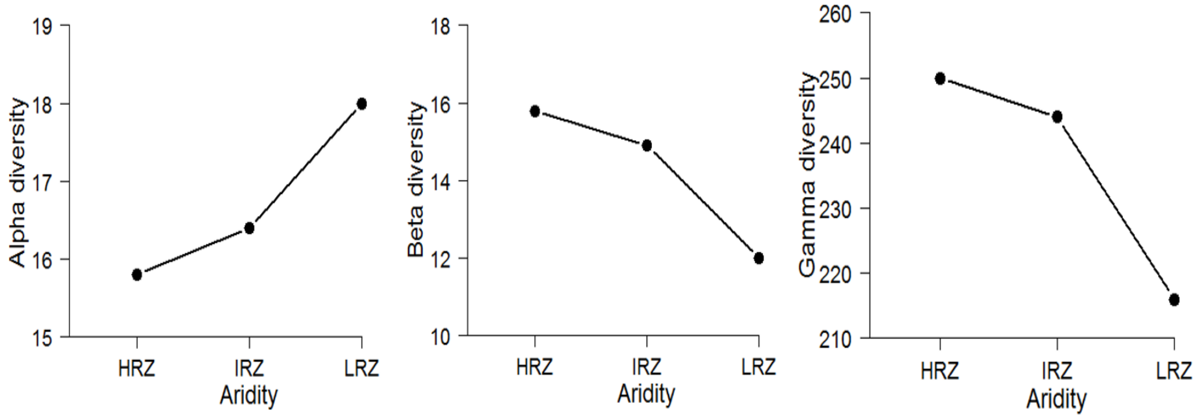
Appendix 6 Correlation between selected variables for section 3. Values shown in bold indicate a high correlation (>│0.5│).

Variable	PS	MAT	PWM	SP	Silt	Clay	SDep	GP	Fire	N	P
Precipitation seasonality (PS)	1.00	0.30	-0.24	0.01	0.13	0.15	-0.18	0.24	0.03	0.05	-0.05
Mean annual temperature (MAT)	0.30	1.00	-0.43	0.01	0.10	-0.13	-0.15	0.46	-0.01	-0.15	-0.17
Precipitation of the wettest month (PWM)	-0.20	-0.43	1.00	-0.01	-0.04	-0.24	0.35	-0.35	0.39	-0.01	0.23
Slope position (SP)	0.00	0.01	-0.01	1.00	-0.17	-0.03	-0.20	0.01	0.00	0.03	-0.06
Silt content(Silt)	0.10	0.10	-0.04	-0.17	1.00	0.38	-0.02	0.04	0.03	**0.51**	0.17
Clay content (Clay)	0.20	-0.13	-0.24	-0.03	0.38	1.00	-0.15	-0.07	-0.01	0.47	0.12
Soil depth (SDep)	-0.20	-0.15	0.35	-0.20	-0.02	-0.15	1.00	-0.14	0.07	-0.15	0.04
Grazing pressure (GP)	0.20	0.46	-0.35	0.01	0.04	-0.07	-0.14	1.00	-0.18	-0.02	-0.15
Fire frequency (Fire)	0.00	-0.01	0.39	0.00	0.03	-0.01	0.07	-0.18	1.00	-0.02	0.20
Soil nitrogen content (N)	0.10	-0.15	-0.01	0.03	**0.51**	0.47	-0.15	-0.02	-0.02	1.00	0.40
Soil content of plant-available phosphorus (P)	-0.10	-0.17	0.23	-0.06	0.17	0.12	0.04	-0.15	0.20	0.40	1.00

Appendix 7 Correlations between taxonomic diversity indices and functional diversity indices. Bold values indicate significant correlations (at $p < 0.05$).

Diversity indices	Species richness	Species evenness	Simpson's index
Functional richness	**0.62**	**0.14**	**0.26**
Functional evenness	**-0.24**	0.01	**-0.11**
Rao's quadratic entropy	**0.12**	**0.59**	**0.58**

Appendix 8 Effects of aridity on alpha, beta and gamma diversity.



Appendix 9 Summary of linear mixed-effect model results testing the effects of grazing pressure on the functional diversity of individual plant traits.

Traits	Grazing pressure	
	Estimate	P value
Life history	-0.0028	0.7279
Life form	0.0006	0.9527
Photosynthetic pathway	0.0299	0.0014**
Nitrogen fixation	0.0252	0.0018**
Height	-0.0012	0.9076
Growth habit	0.0301	0.0024**

Appendix 10 Description of biotic and abiotic variables used in section 4. These were obtained at site level (for climate) or at plot level (other categories).

Variable set	Variable	Description and categories (when applicable)	Unit
Spatial data	Longitude	Angle from 0° (at the equator) to 90° (North or South) at the poles	°
	Latitude	Angular distance of a point east or west of the Greenwich meridian	°
Climate data[a]	Climatic aridity	1 – UNEP aridity index[b]	NA
	Mean annual precipitation	Mean annual precipitation over 50 years	mm
	Mean annual temperature	Mean annual temperature over 50 years	°C
	Min. temperature of coldest month	Mean over 50 years	°C
	Max. temperature of warmest month	Mean over 50 years	°C
	Mean temperature of wettest quarter	Mean over 50 years	mm
	Season's accumulated precipitation[c]	Accumulated season's rainfall until month preceding field sampling	mm
Slow topo-edaphic variables[d]	Slope position	Categorical (upslope, midslope, lowland)	NA
	Medium gravel cover[e]	Cover of medium gravel (0.6-2 cm) at plot surface	%
	Coarse gravel cover[e]	Cover of coarse gravel (2-6 cm) at plot surface	%
	Stone cover[e]	Cover of stones (6-20 cm) at plot surface	%
	Boulder cover[e]	Cover of boulders (> 20 cm) at plot surface	%
	Bare soil cover	Plot surface covered by bare soil	%
	Soil sand content	Percent of sand in topsoil (0-4 cm)	%
	Soil silt content	Percent of silt in topsoil (0-4 cm)	%
	Soil clay content	Percent of clay in topsoil (0-4 cm)	%
	Soil acidity	Topsoil pH (0-4 cm) in 1:2.5 water suspension	NA
Land-use	Litter cover	Plot surface covered by litter	%
	Moribund material cover	Plot surface covered by moribund vegetation	%
	Cattle & donkey dung	Plot surface covered by dung of cattle and donkeys	%
	Smallstock droppings	Plot surface covered by smallstock droppings (goats, sheep)	%
	Grazing pressure	Expert estimate of recent grazing pressure, based on physical evidence of grazing (trampling, dung, removal of standing biomass): 0 = very light, 1 = light, 2 = moderate, 3 = heavy, 4 = extreme	NA
Fast topo-edaphic variables[f]	Soil N content	Total nitrogen content in topsoil (0-4 cm)	%

Appendix 10 continued

Variable set	Variable	Description and categories (when applicable)	Unit
	Soil C content	Total carbon content in topsoil (0-4 cm)	%
	Soil content of plant-available phosphorus	Plant-available phosphorus of topsoil	mg kg^{-1}
	Fine material cover	Cover of fine material (< 0.2 cm) at plot surface	%
	Fine gravel cover	Cover of fine gravel (0.2-0.6 cm) at plot surface	%
Vegetation attributes	Species richness	Number of vascular plant species on plot (100 m^2)	#
	Relative abundance of 10 PFTs[g]	Relative aboveground biomass of 10 PFTs on plot	%
Seasonality	Phenophase	Community-aggregated phenological stage; obtained by weighting species' phenological stage (0 = germinating, 1 = sprouting, 2 = shooting, 3 = flowering, 4 = fruiting, 5 = senescent) with their contribution to the biomass of the plant community.	NA

[a] Climate data: Taken from WorldClim database.

[b] UNEP aridity index = Mean annual precipitation/ annual potential evaporation

[c] Taken from the Global Precipitation Climatology Centre dataset

[d] Variables with slow response to land-use pressure; largely driven by geology and topography (see Vries *et al.*, 2012 for a similar approach).

[e] Estimation of coarse surface fragments follows FAO (2006)

[f] Variables with fast response to land-use pressure; mainly driven by direct inputs via herbivore excreta (Angassa *et al.*, 2012; Sandhage-Hofmann *et al.*, 2015). Fine gravel cover quantifies the residual accumulation of plinthic concretions due to soil erosion (Da Costa *et al.*, 2015).

[g] For the definition of PFTs (plant functional types), see Appendix 12.

NA = not applicable

Appendix 11 Predicting species' biomass via allometric equations from biovolume, phenology and growth form.

Given the spatial extent of the present study, it was not feasible to destructively sample all 1350 subplots for plant biomass. Given the allometry between plants' biovolume, i.e. the product of height and cover, and biomass (Byrne & Wentworth, 1988; Johnson *et al.*, 1988), we opted to destructively sample a representative fraction of plots and species to establish allometric equations. As allometry may vary with plants' growth form and current phenology (Barnes, 2002; Byrne *et al.*, 2011), we included these information in our sampling and modelling efforts.

Data collection

We selected biomass harvesting quadrats (1 m²) to represent the full range of grazing pressure in West Africa's Sudanian savannas, including heavily grazed and protected sites. On each quadrat, all vascular plants of the herbaceous layer were identified to the species level, and the phenological stage of species' current season's biomass was determined using a simplified BBCH-scale of growth stages (Hess *et al.*, 1997): germinating, sprouting, shooting, flowering, fruiting, and senescent. Mean height of each species was measured to the nearest centimetre, and canopy cover [cm²] was obtained via visual estimation. Subsequently all vascular plants of the herbaceous layer were clipped to stubble height (ca. 3 cm) using hand shears. Plant material was separated into species, discarding moribund material. Samples were oven-dried (68 °C, 48 hours) and weighed to nearest 0.01 g to determine species-specific dry biomass in g m^{-2} (Hooper & Vitousek, 1997). During digitalisation of data and based on a literature review, species were grouped into seven growth forms: (1) annual erect graminoids, (2) annual prostrate graminoids, (3) perennial erect graminoids, (4) perennial prostrate graminoids, (5) erect herbs, (6) prostrate herbs and (7) woody species. Altogether, we obtained 1883 biomass samples from 105 species sampled across 203 harvesting quadrats.

Allometric models

It has frequently been found that the biomass-biovolume relationship is nonlinear, more precisely of a power-law type (e.g. Nafus *et al.*, 2009). Most researchers have countered this 'undesired feature' by log-transformation to both the predictor(s) and the response variable in order to analyse the relationship by means of linear regression. However, recently this common practice has come into criticism as being potentially biased (Packard, 2009). Bearing this in mind, we explored error distribution of the biomass-biovolume relationship prior to model formulation following the likelihood approach of Xiao et al. (2011). Supporting recent findings (Oliveras *et al.*, 2014), the biomass-biovolume relationship in our data showed a multiplicative error distribution and hence rendered eligible to be analysed using the log-transformation plus linear regression approach. We started with a full model using (natural log-transformed) species' aboveground biomass per quadrat [g m^{-2}] as response variable and the full-factorial combination of (natural log-transformed) biovolume [cm^3 m^{-2}], growth form, and phenological stage as predictor variables. The full-factorial model was subject to an AIC-based model-selection algorithm that ultimately ruled out all interaction terms and only retrieved the main effects. Hence, the final model formulation was:

log(biomass) ~ log(biovolume) + growth form + phenological stage

Tukey HSD as well as coefficient estimates revealed that not all levels of the factorial predictors 'growth form' and 'phenological stage' were significantly different from another, hence, levels were lumped according to these findings. Ultimately, the model built upon the simplified growth form and phenological stage classifications which retained two growth forms and four phenological stages.

In the case of growth form, the class of (2) annual prostrate graminoids was dropped due to missing observations. Furthermore, the two classes of (3) perennial erect graminoids and (4) perennial prostrate graminoids were lumped into a group of 'perennial graminoids', all other growth forms were lumped to 'other growth forms'. For phenological stages, the levels 'fruiting' and 'flowering' were lumped, and 'germinating' had to be dropped due to the lack of observations.

Predictive performance of the final model was assessed using cross-validation. Mean squared prediction error from leave-one-out cross-validation was 1.2089 which translates into a normalised root mean squared prediction error of 14.95 % (normalization was achieved using the amplitude between maximum and minimum observed residuals). The good predictive performance was also matched by a high explained variance in the final model (R^2=0.74, adjusted R^2=0.74). Biovolume explained most variance (partial ε^2=0.70), while phenological stage (partial ε^2=0.03) and growth form (partial ε^2=0.01) were of minor importance.

Statistical analyses were performed in R, version 3.2.2 (R Core Team, 2015). Distribution error was analysed using the R-script provided by Xiao et al. (2011; therin in Supp. 2). Cross-validation was performed with the boot-package in version 1.3-17 (Canty & Ripley, 2015). We used the final allometric models to estimate species' aboveground biomass (AGB_{Spec}) for all subplots from non-destructive measurements of morphological and phenological parameters, and from species' growth form. We estimated plot level total aboveground biomass (AGB) by summing AGB_{Spec} data per subplot and then averaging over a plot's three subplots. The unit of AGB was converted from g m^{-2} to kg ha^{-1} (by applying a multiplication factor of 10) in order to ease comparability to MEY which is given per hectare. Logarithmic bias was not corrected (Baskerville, 1972).

Final model

Variable/parameter	Estimate	Std. Error	p
Intercept	-0.07093	0.03613	*
Log (Biovolume)	0.60339	0.00922	***
Growth form: quasi perennial graminoids	0.40760	0.08707	***
Phenostage: senescent	0.16246	0.06975	*
Phenostage: shooting	-0.45499	0.07554	***
Phenostage: sprouting	-0.48376	0.15086	**

*p-values: *** < 0.001; ** < 0.01; * < 0.05*
$r^2 = 0.7388$*, residual prediction error = 1.098, residual df = 1877*
normalised cross-validation prediction error = 14.95 %

Allometric equations to predict species' aboveground biomass (AGB_{Spec}) from biovolume, growth form and phenological stage

	Formula (in power-law format)
Growth form 1[a]	
Sprouting	$AGB_{Spec} = 0.8632 * biovolume^{0.60339}$
Shooting	$AGB_{Spec} = 0.8884 * biovolume^{0.60339}$
Flowering or fruiting	$AGB_{Spec} = 1.4003 * biovolume^{0.60339}$
Senescent	$AGB_{Spec} = 1.6473 * biovolume^{0.60339}$
Growth form 2[b]	
Sprouting	$AGB_{Spec} = 0.5743 * biovolume^{0.60339}$
Shooting	$AGB_{Spec} = 0.5910 * biovolume^{0.60339}$
Flowering or fruiting	$AGB_{Spec} = 0.9315 * biovolume^{0.60339}$
Senescent	$AGB_{Spec} = 1.0958 * biovolume^{0.60339}$

AGB_{Spec} *[g* m^{-2}*], biovolume [*cm^3*]*
[a] *Erect and prostrate perennial graminoids, prostrate annual graminoids*
[b] *Erect annual graminoids, annual herbs, perennial herbs and woody species*

Appendix 12 Plant traits and trait attributes used for defining plant functional types (PFTs).

Trait	Trait attribute	Acronym[a]	Description
Height	Small	S	Max. vegetative height 0 - 50 cm
	Tall	T	Max. vegetative height > 50 cm
Life history	Annual	A	Plants living for only one growing season
	Perennial	P	Plants living for more than one growing season
Growth form	Forbs	F	Herbaceous non-graminoid species
	Graminoids	G	Herbaceous graminoid species (grasses, sedges, rushes)
	Woody	W	Woody species (trees, shrubs, lianas)

[a] Components of PFT acronyms, e.g. TAF = tall annual forb

Appendix 13 Results of principal component analysis (PCA) for section 4. The variables were grouped into five sets, namely (a) climate, (b) topo-edaphic variables with slow response to land-use, (c) land-use, (d) topo-edaphic variables with fast response to land-use and (d) plant functional types – a subgroup of the predictor set 'vegetation attributes'. High factor loadings (≥│0.8│) on principal components (PC) with eigenvalues > 1 are shown in bold. Variables selected as predictors for ecosystem service supply are also in bold.

Variable	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
(a) Climate variables										
Mean annual temperature	-0.58	0.72	0.32	0.22	0.00	-0.01	-	-	-	-
Mean annual precipitation	0.93	0.29	-0.23	0.02	0.03	0.00	-	-	-	-
Climatic aridity	**0.96**	0.09	-0.26	-0.03	-0.02	0.01	-	-	-	-
Min temperature of the coldest month	0.34	**0.94**	-0.01	-0.05	0.00	0.01	-	-	-	-
Maximum temperature of the warmest month	-0.89	0.05	0.35	0.28	0.00	0.00	-	-	-	-
Mean temperature of the wettest quarter	-0.71	0.17	0.69	0.05	0.00	0.00	-	-	-	-
Eingenvalue	**2.10**	**1.30**	0.40	0.20	0.00	0.00	-	-	-	-
Proportion of Variance	0.70	0.30	0.00	0.00	0.00	0.00	-	-	-	-
Cumulative Proportion	0.70	1.00	1.00	1.00	1.00	1.00	-	-	-	-
(b) Topo-edaphic variables with slow response to land-use										
Medium gravel at surface	-0.03	0.17	0.03	0.02	0.28	0.94	0.10	0.08	-	-
Coarse gravel at surface	0.01	0.13	0.06	0.02	0.94	0.27	0.13	0.06	-	-
Stones	-0.10	0.08	0.14	0.21	0.13	0.10	0.94	0.12	-	-
Boulders	-0.13	0.04	0.14	0.95	0.02	0.02	0.20	0.13	-	-
Soil sand content	0.93	0.01	-0.01	-0.13	0.01	-0.03	-0.10	-0.31	-	-
Soil clay content	-0.37	0.09	0.02	0.16	0.07	0.09	0.14	0.89	-	-

Appendix 13 continued										
Variable	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
Bare ground cover[a]	-0.01	-0.05	**0.98**	0.13	0.06	0.03	0.13	0.01	-	-
Soil acidity	0.01	**0.97**	-0.05	0.04	0.12	0.15	0.07	0.07	-	-
Eingenvalue	**1.62**	**1.24**	**1.09**	0.89	0.78	0.72	0.66	0.56	-	-
Proportion of Variance	0.33	0.19	0.15	0.10	0.08	0.06	0.05	0.04	-	-
Cumulative Proportion	0.33	0.52	0.67	0.77	0.84	0.91	0.96	1.00	-	-
(c) Land-use variables										
Litter cover	**0.97**	0.07	0.11	0.05	0.03	-0.22	-	-	-	-
Moribund material cover	0.07	**0.98**	0.03	0.11	0.05	-0.16	-	-	-	-
Cattle & donkey dung	0.03	0.05	0.24	0.08	0.96	-0.14	-	-	-	-
Smallstock droppings	0.11	0.03	0.96	-0.01	0.24	-0.06	-	-	-	-
Green vegetation cover	-0.23	-0.18	-0.06	-0.05	-0.14	0.94	-	-	-	-
Wild herbivores' droppings	0.05	0.11	0.00	0.99	0.07	-0.05	-	-	-	-
Eingenvalue	**1.45**	**1.08**	0.98	0.87	0.77	0.63	-	-	-	-
Proportion of Variance	0.35	0.20	0.16	0.13	0.10	0.07	-	-	-	-
Cumulative Proportion	0.35	0.55	0.71	0.84	0.93	1.00	-	-	-	-
(d) Topo-edaphic variables with fast response to land-use										
Fine material cover	-0.21	0.01	-0.18	0.96	0.00	-	-	-	-	-
Fine gravel cover	0.00	0.01	0.99	-0.17	0.00	-	-	-	-	-
Soil nitrogen content[b]	**0.97**	0.11	0.00	-0.18	-0.12	-	-	-	-	-
Soil carbon content[b]	0.95	0.26	0.01	-0.13	0.14	-	-	-	-	-

Appendix 13 continued

Variable	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
Soil content of plant-available phosphorus	0.23	**0.97**	0.01	0.01	0.00	-	-	-	-	-
Eingenvalue	**1.54**	**1.12**	0.90	0.72	0.18	-	-	-	-	-
Proportion of Variance	0.48	0.25	0.16	0.10	0.01	-	-	-	-	-
Cumulative Proportion	0.48	0.73	0.89	0.99	1.00	-	-	-	-	-
(e) Plant functional types										
Small annual forbs	0.07	0.02	0.05	0.00	**0.99**	-0.05	-0.09	0.04	0.00	0.00
Tall annual forbs	-0.07	**0.99**	0.01	-0.07	0.02	0.00	0.02	0.05	0.01	0.00
Small annual graminoids	0.10	0.01	**0.99**	0.02	0.05	0.02	-0.10	0.01	-0.05	0.00
Tall annual graminoids	0.92	-0.24	-0.07	-0.14	-0.08	-0.20	-0.10	-0.11	-0.05	0.00
Small perennial forbs	-0.04	0.06	0.01	0.14	0.04	-0.06	-0.03	0.98	-0.02	0.00
Tall perennial forbs	-0.06	0.00	0.02	-0.04	-0.05	0.99	-0.06	-0.06	-0.02	0.00
Small perennial graminoids	0.03	-0.07	0.02	**0.98**	0.00	-0.05	-0.10	0.15	-0.04	0.00
Tall perennial graminoids	**-0.86**	-0.16	-0.28	-0.23	-0.24	-0.13	-0.14	-0.08	0.04	0.00
Small woody perennials	-0.06	0.01	-0.05	-0.04	0.00	-0.02	-0.03	-0.02	1.00	0.00
Tall woody perennials	0.01	0.02	-0.10	-0.09	-0.09	-0.06	0.98	-0.03	-0.03	0.00
Eingenvalue	**1.39**	**1.23**	**1.11**	**1.09**	**1.04**	0.93	0.90	0.85	0.81	0.00
Proportion of Variance	0.19	0.15	0.12	0.12	0.11	0.09	0.08	0.07	0.06	0.00
Cumulative Proportion	0.19	0.34	0.47	0.59	0.69	0.78	0.86	0.94	1.00	1.00

[a] Bare soil cover was tricky to classify – exhibiting both fast and slow responses depending on land-use intensity and other prevailing conditions such as climate – but we chose to group it among variables that respond slowly to land-use pressure.

[b] Due to the high correlation of soil nitrogen and soil carbon content with soil sand content, neither sand nor carbon content was selected for LMMs.

Appendix 14 Correlation between selected variables for section 4. Values shown in bold indicate a high correlation (>|0.5|) between variables; in these cases, the term that performed better in single-variable models was chosen for subsequent statistical analyses.

	CA	T_{Min}	SAP	Sand	BSC	pH	LC	MMC	N	P	TPG	TAF	SAG	SPG	SAF	GP	SP	SRic	PHEN
CA	1.0																		
T_{Min}	0.4	1.0																	
SAP	-0.3	-0.5	1.0																
Sand	0.2	0.0	0.1	1.0															
BSC	-0.1	0.0	-0.3	-0.1	1.0														
pH	-0.1	-0.2	0.1	0.0	-0.1	1.0													
LC	-0.1	-0.2	-0.0	0.1	0.2	0.0	1.0												
Mori	0.1	0.1	-0.1	-0.1	0.3	0.0	0.2	1.0											
N	-0.2	0.0	-0.2	**-0.7**	0.1	0.2	0.0	0.1	1.0										
P	0.1	0.0	0.1	-0.2	-0.1	0.2	0.0	-0.1	0.3	1.0									
TPG	0.4	0.1	0.0	-0.2	-0.1	0.1	0.1	0.1	0.1	0.3	1.0								
TAF	0.2	0.1	-0.2	0.0	0.1	-0.2	0.0	0.0	0.0	0.0	-0.1	1.0							
SAG	-0.1	0.1	-0.1	0.2	0.0	0.0	0.0	-0.1	-0.2	-0.1	-0.4	0.0	1.0						
SPG	-0.2	0.1	-0.3	0.1	0.2	-0.1	0.2	0.1	0.2	-0.1	-0.2	-0.1	0.1	1.0					
SAF	-0.3	0.1	-0.1	-0.1	0.1	0.1	0.1	-0.1	0.1	-0.1	-0.3	0.0	0.1	0.0	1.0				
GP	-0.4	0.1	-0.4	-0.1	0.3	0.0	0.1	-0.1	0.1	-0.1	-0.4	-0.1	0.3	0.4	0.4	1.0			
SP	0.0	0.0	0.0	0.1	0.2	0.2	0.1	0.0	-0.1	-0.1	-0.1	0.0	0.0	-0.1	0.0	0.0	1.0		
SRich	0.0	-0.2	0.2	0.1	-0.2	0.1	0.0	-0.2	-0.2	0.0	-0.2	0.1	0.1	-0.1	0.0	-0.2	0.0	1.0	
PHEN	-0.3	-0.2	0.5	0.0	-0.2	-0.1	0.0	0.0	0.0	-0.1	-0.1	-0.2	0.0	-0.1	-0.1	-0.2	0.0	0.1	1.0

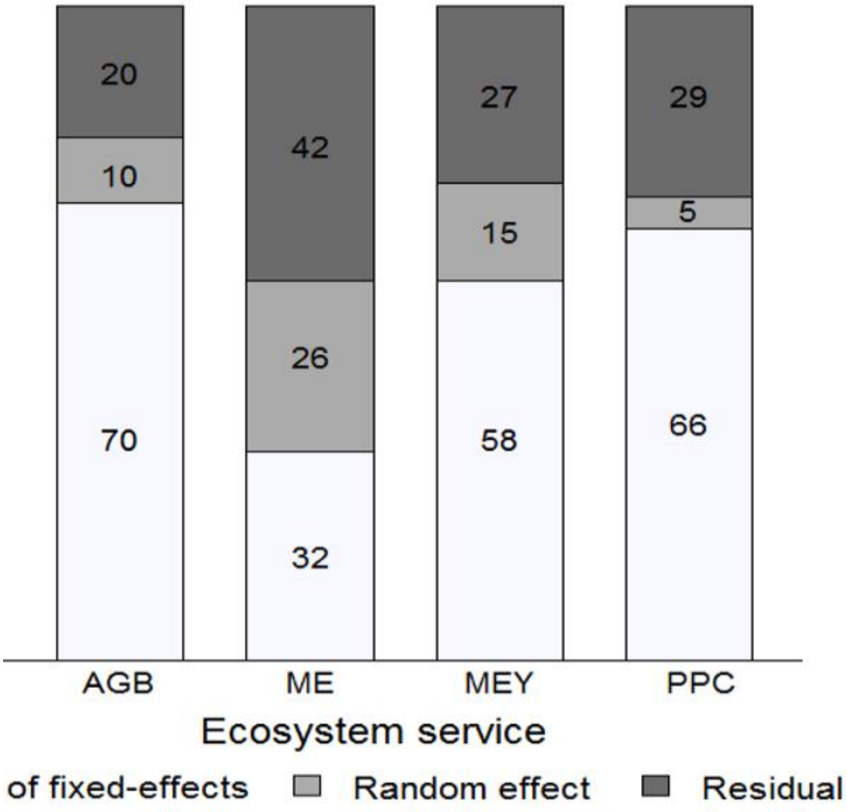
AI = aridity index, T_{Min} = minimum temperature of the coldest month, SAP = Season's accumulated precipitation, Sand = soil sand content, BSC = bare soil cover, pH = soil acidity, LC = litter cover, MMC = moribund material cover, N = soil nitrogen content, P = plant-available phosphorus content, TPG = tall perennial graminoids, TAF = tall annual forbs, SAG = small annual graminoids, SPG = small perennial graminoids, SAF = small annual forbs, GP = grazing pressure, SP = slope position, SRic = species richness, PHEN = phenophase.

Appendix 15 Effects of climate, topo-edaphic variables, land-use and vegetation attributes on ES supply based on type III ANOVAs (AGB = aboveground biomass, ME = metabolisable energy, MEY = metabolisable energy yield, PPC = perennial plant cover).

Predictor set	Predictor	AGB		ME		MEY		PPC	
		F value	*P* value	*F* value	*P* value	*F* value	*P* value	*F* value	*P* value
Climate variables	Climatic aridity	5.63	0.021*	-	-	-	-	17.88	< 0.001***
	Season's accumulated precipitation	27.98	< 0.001***	-	-	14.65	< 0.001***	-	-
Slow topo-edaphic variables	Bare soil cover	19.95	< 0.001***	5.83	0.016*	10.58	0.0013**	15.99	< 0.001***
Land-use variables	Grazing pressure	16.85	< 0.001***	9.83	0.002**	11.41	< 0.001***	-	-
	Litter cover	9.67	0.0021**	14.04	< 0.001***	24.10	< 0.001***	-	-
	Moribund material cover	-	-	8.06	0.0049**	-	-	-	-
Vegetation attributes	Small annual forbs	-	-	7.81	0.0056**	-	-	-	-
Seasonality	Small perennial graminoids	8.58	0.0037**	13.07	< 0.001***	15.89	< 0.001***	65.64	< 0.001***
	Tall perennial graminoids	37.51	< 0.001***	-	-	39.46	< 0.001***	273.5	< 0.001***
	Species richness	48.34	< 0.001***	-	-	59.48	< 0.001***		
	Phenophase	29.44	< 0.001***	18.82	< 0.001***	8.63	0.0036	9.55	0.002**
Interaction	Grazing*Phen-ophase	8.91	< 0.0031**	-	-	10.49	0.0014**	-	-

*p-values: *** < 0.001; ** < 0.01; * < 0.05*

Appendix 16 Percent variance explained by linear mixed-effects models, with the four ecosystem services as response variables (AGB = aboveground biomass, ME = metabolisable energy, MEY = metabolisable energy yield, PPC = perennial plant cover). Variance explained by fixed-effects is based on marginal R^2 values; for random-effects (variance explained by site alone), it is based on conditional R^2 values minus marginal R^2 values. Residuals quantify unexplained variance for the respective ecosystem service.



Appendix 17 List of species used in this study. The species were collected within sample plots in Ghana and Burkina Faso. The list includes grasses, forbs and seedlings of woody species (trees and shrubs) which were found in the herbaceous layer (< 2 m).

Species	Family
Acacia gourmaensis A.Chev.	Leguminosae
Acacia hockii De Wild.	Leguminosae
Acacia indica (Poir.) Desv.	Leguminosae
Acacia macrostachya DC.	Leguminosae
Acacia nilotica (L.) Delile	Leguminosae
Acacia pennata (L.) Willd.	Leguminosae
Acacia senegal (L.) Willd.	Leguminosae
Acalypha ciliata Forssk.	Euphorbiaceae
Acanthospermum hispidum DC.	Compositae
Achyranthes aspera L.	Amaranthaceae
Acroceras amplectens Stapf	Poaceae
Aeschynomene indica L.	Leguminosae
Ageratum conyzoides (L.) L.	Compositae
Alysicarpus ovalifolius (Schum.) Leonard	Leguminosae
Alysicarpus rugosus (Willd.) DC.	Leguminosae
Amorphophallus aphyllus (Hook.) Hutch.	Araceae
Ampelocissus leonensis (Hook.f.) Planch.	Vitaceae
Andropogon chinensis (Nees) Merr.	Poaceae
Andropogon fastigiatus Sw.	Poaceae
Andropogon gayanus Kunth	Poaceae
Andropogon pseudapricus Stapf	Poaceae
Andropogon schirensis Hochst.	Poaceae
Andropogon tectorum Schumach. & Thonn.	Poaceae
Aneilema lanceolatum Benth.	Commelinaceae
Aneilema paludosum A.Chev.	Commelinaceae
Aneilema setiferum A.Chev.	Commelinaceae
Annona senegalensis Pers.	Annonaceae
Anogeissus leiocarpa (DC.) Guill. & Perr.	Combretaceae
Arachis hypogaea L.	Fabaceae
Aristida adscensionis L.	Poaceae
Aristida hordeacea Kunth	Poaceae
Aristida kerstingii Pilg.	Poaceae
Ascolepis protea Welw.	Cyperaceae
Asparagus africanus Lam.	Asparagaceae
Aspilia africana (Pers.) C.D.Adams	Compositae
Aspilia bussei O.Hoffm. & Muschl.	Compositae
Aspilia helianthoides (Schumach. & Thonn.) Oliv. & Hiern	Compositae

Species	Family
Aspilia paludosa Berhaut	Compositae
Aspilia rudis Oliv. & Hiern	Compositae
Axonopus compressus (Sw.) P.Beauv.	Poaceae
Azadirachta indica A.Juss.	Meliaceae
Balanites aegyptiaca (L.) Delile	Zygophyllaceae
Bidens bipinnata L.	Compositae
Blepharis maderaspatensis (L.) B.Heyne ex Roth	Acanthaceae
Blumea viscosa (Mill.) V.M.Badillo	Compositae
Boerhavia diffusa L.	Nyctaginaceae
Bombax costatum Pellegr. & Vuillet	Malvaceae
Brachiaria deflexa (Schumach.) C.E.Hubb. ex Robyns	Poaceae
Brachiaria jubata (Fig. & De Not.) Stapf	Poaceae
Brachiaria lata (Schumach.) C.E.Hubb.	Poaceae
Brachiaria stigmatisata (Mez) Stapf	Poaceae
Brachiaria villosa (Lam.) A.Camus	Poaceae
Buchnera hispida Buch.-Ham. ex D.Don	Orobanchaceae
Bulbostylis abortiva (Steud.) C.B.Clarke	Cyperaceae
Bulbostylis barbata (Rottb.) C.B.Clarke	Cyperaceae
Bulbostylis hispidula (Vahl) R.W.Haines	Cyperaceae
Caperonia serrata (Turcz.) C.Presl	Euphorbiaceae
Cardiospermum halicacabum L.	Sapindaceae
Cassia sieberiana DC.	Leguminosae
Ceratotheca sesamoides Endl.	Pedaliaceae
Chamaecrista nigricans (Vahl) Greene	Leguminosae
Chamaecrista pratensis (R.Vig.) Du Puy	Leguminosae
Chasmopodium caudatum (Hack.) Stapf	Poaceae
Chloris pilosa Schumach. & Thonn.	Poaceae
Chrysanthemum americanum (L.) Vatke ex Weberl. & Lagos	Asteraceae
Chrysopogon nigritanus (Benth.) Veldkamp	Poaceae
Cienfuegosia heteroclada Sprague	Malvaceae
Cissus cornifolia (Baker) Planch.	Vitaceae
Cissus populnea Guill. & Perr.	Vitaceae
Cissus rufescens Guill. & Perr.	Vitaceae
Citrullus colocynthis (L.) Schrad.	Cucurbitaceae
Cleome viscosa L.	Cleomaceae
Cochlospermum planchonii Hook.f. ex Planch.	Bixaceae
Cochlospermum religiosum (L.) Alston	Bixaceae
Cochlospermum tinctorium Perrier ex A.Rich.	Bixaceae
Combretum adenogonium Steud. ex A.Rich.	Combretaceae
Combretum collinum Fresen.	Combretaceae

Species	Family
Combretum glutinosum Perr. ex DC.	Combretaceae
Combretum microphyllum Klotzsch	Combretaceae
Combretum molle R.Br. ex G.Don	Combretaceae
Combretum sericeum G.Don	Combretaceae
Commelina nigritana Benth.	Commelinaceae
Commelina umbellata Schumach. & Thonn.	Commelinaceae
Corchorus tridens L.	Malvaceae
Crinum biflorum Rottb.	Amaryllidaceae
Crinum paludosum Verd.	Amaryllidaceae
Crossopteryx febrifuga (Afzel. ex G.Don) Benth.	Rubiaceae
Crotalaria goreensis Guill. & Perr.	Leguminosae
Crotalaria hyssopifolia Klotzsch	Leguminosae
Crotalaria macrocalyx Benth.	Leguminosae
Crotalaria microcarpa Benth.	Leguminosae
Crotalaria retusa L.	Leguminosae
Ctenium elegans Kunth	Poaceae
Ctenium newtonii Hack.	Poaceae
Cucumis melo L.	Cucurbitaceae
Curculigo pilosa (Schumach. & Thonn.) Engl.	Hypoxidaceae
Cyanotis lanata Benth.	Commelinaceae
Cymbopogon giganteus Chiov.	Poaceae
Cymbopogon schoenanthus (L.) Spreng.	Poaceae
Cynodon dactylon (L.) Pers.	Poaceae
Cyperus amabilis Vahl	Cyperaceae
Cyperus denudatus L.f.	Cyperaceae
Cyperus digitatus Roxb.	Cyperaceae
Cyperus dilatatus Schumach.	Cyperaceae
Cyperus iria L.	Cyperaceae
Cyperus michelianus (L.) Delile	Cyperaceae
Cyperus reduncus Hochst. ex Boeckeler	Cyperaceae
Cyperus rotundus L.	Cyperaceae
Cyperus squarrosus L.	Cyperaceae
Cyperus tenuiculmis Boeckeler	Cyperaceae
Dactyloctenium aegyptium (L.) Willd.	Poaceae
Daniellia oliveri (Rolfe) Hutch. & Dalziel	Leguminosae
Desmodium gangeticum (L.) DC.	Leguminosae
Desmodium hirtum Guill. & Perr.	Leguminosae
Desmodium triflorum (L.) DC.	Leguminosae
Detarium microcarpum Guill. & Perr.	Leguminosae
Dichrostachys cinerea (L.) Wight & Arn.	Leguminosae

Species	Family
Dicoma tomentosa Cass.	Compositae
Digitaria argillacea (Hitchc. & Chase) Fernald	Poaceae
Digitaria ciliaris (Retz.) Koeler	Poaceae
Digitaria debilis (Desf.) Willd.	Poaceae
Digitaria eriantha Steud.	Poaceae
Digitaria gayana (Kunth) A.Chev.	Poaceae
Digitaria horizontalis Willd.	Poaceae
Digitaria nuda Schumach.	Poaceae
Diospyros mespiliformis Hochst. ex A.DC.	Ebenaceae
Dioscorea togoensis R.Knuth	Dioscoreaceae
Echinochloa colona (L.) Link	Poaceae
Eleusine indica (L.) Gaertn.	Poaceae
Elionurus ciliaris Kunth	Poaceae
Elionurus elegans Kunth	Poaceae
Entada africana Guill. & Perr.	Leguminosae
Eragrostis amabilis (L.) Wight & Arn.	Poaceae
Eragrostis aspera (Jacq.) Nees	Poaceae
Eragrostis cilianensis (All.) Janch.	Poaceae
Eragrostis egregia Clayton	Poaceae
Eragrostis gangetica (Roxb.) Steud.	Poaceae
Eragrostis pilosa (L.) P.Beauv.	Poaceae
Eragrostis tremula Hochst. ex Steud.	Poaceae
Eragrostis turgida (Schumach.) De Wild.	Poaceae
Eriosema pellegrinii Tisser.	Leguminosae
Eucalyptus camaldulensis Dehnh.	Myrtaceae
Euclasta condylotricha (Steud.) Stapf	Poaceae
Euphorbia convolvuloides Hochst. ex Benth.	Euphorbiaceae
Euphorbia hirta L.	Euphorbiaceae
Evolvulus alsinoides (L.) L.	Convolvulaceae
Excoecaria grahamii Stapf	Euphorbiaceae
Faidherbia albida (Delile) A.Chev.	Leguminosae
Ficus exasperata Vahl	Moraceae
Fimbristylis debilis Steud.	Cyperaceae
Fimbristylis dichotoma (L.) Vahl	Cyperaceae
Fimbristylis ferruginea (L.) Vahl	Cyperaceae
Fimbristylis littoralis Gaudich.	Cyperaceae
Flueggea virosa (Roxb. ex Willd.) Royle	Phyllanthaceae
Fuirena umbellata Rottb.	Cyperaceae
Gardenia erubescens Stapf & Hutch.	Rubiaceae
Gardenia ternifolia Schumach. & Thonn.	Rubiaceae

Species	Family
Gladiolus gregarius Welw. ex Baker	Iridaceae
Gomphrena celosioides Mart.	Amaranthaceae
Gomphrena globosa L.	Amaranthaceae
Grewia cissoides Hutch. & Dalziel	Malvaceae
Grewia mollis Juss.	Malvaceae
Guiera senegalensis J.F.Gmel.	Combretaceae
Gymnosporia senegalensis (Lam.) Loes.	Celastraceae
Hackelochloa granularis (L.) Kuntze	Poaceae
Heliotropium strigosum Willd.	Boraginaceae
Heteropogon contortus (L.) P.Beauv. ex Roem. & Schult.	Poaceae
Hibiscus asper Hook.f.	Malvaceae
Hibiscus sidiformis Baill.	Malvaceae
Hibiscus squamosus Hochr.	Malvaceae
Hoslundia opposita Vahl	Lamiaceae
Hybanthus enneaspermus (L.) F.Muell.	Violaceae
Hygrophila micrantha (Nees) T.Anderson	Acanthaceae
Hygrophila senegalensis (Nees) T.Anderson	Acanthaceae
Hyparrhenia cyanescens (Stapf) Stapf	Poaceae
Hyparrhenia glabriuscula (Hochst. ex A.Rich.) Andersson ex Stapf	Poaceae
Hyparrhenia involucrata Stapf	Poaceae
Hyparrhenia rufa (Nees) Stapf	Poaceae
Hyparrhenia smithiana (Hook.f.) Stapf	Poaceae
Hyphaene thebaica (L.) Mart.	Arecaceae
Hyptis spicigera Lam.	Lamiaceae
Hyptis suaveolens (L.) Poit.	Lamiaceae
Indigofera aspera DC.	Leguminosae
Indigofera berhautiana J.B.Gillett	Leguminosae
Indigofera bracteolata DC.	Leguminosae
Indigofera congolensis De Wild. & T.Durand	Leguminosae
Indigofera dendroides Jacq.	Leguminosae
Indigofera geminata Baker	Leguminosae
Indigofera hirsuta L.	Leguminosae
Indigofera kerstingii Harms	Leguminosae
Indigofera leprieurii Baker f.	Leguminosae
Indigofera leptoclada Harms	Leguminosae
Indigofera macrocalyx Guill. & Perr.	Leguminosae
Indigofera nigritana Hook.f.	Leguminosae
Indigofera nummulariifolia (L.) Alston	Leguminosae
Indigofera paniculata Pers.	Leguminosae
Indigofera spicata Forssk.	Leguminosae

Species	Family
Indigofera tinctoria L.	Leguminosae
Ipomoea coscinosperma Hochst. ex Choisy	Convolvulaceae
Ipomoea eriocarpa R. Br.	Convolvulaceae
Isoberlinia doka Craib & Stapf	Leguminosae
Jatropha gossypiifolia L.	Euphorbiaceae
Justicia insularis T.Anderson	Acanthaceae
Kohautia grandiflora DC.	Rubiaceae
Kohautia tenuis (Bowdich) Mabb.	Rubiaceae
Kyllinga pumila Michx.	Cyperaceae
Lannea acida A.Rich.	Anacardiaceae
Lepidagathis anobrya Nees	Acanthaceae
Leptadenia lancifolia (Schumach. & Thonn.) Decne.	Apocynaceae
Leucas martinicensis (Jacq.) R.Br.	Lamiaceae
Lindernia exilis Philcox	Linderniaceae
Lippia chevalieri Moldenke	Verbanaceae
Lonchocarpus sericeus (Poir.) DC.	Leguminosae
Loudetia simplex (Nees) C.E.Hubb.	Poaceae
Loudetia togoensis (Pilg.) C.E.Hubb.	Poaceae
Ludwigia hyssopifolia (G.Don) Exell	Onagraceae
Ludwigia octovalvis (Jacq.) P.H.Raven	Onagraceae
Macrotyloma biflorum (Schum. & Thonn.) Hepper	Leguminosae
Melanthera elliptica O.Hoffm.	Compositae
Melochia corchorifolia L.	Malvaceae
Nesphostylis holosericea (Baker) Verdc.	*Leguminosae*
Microchloa indica (L.f.) P.Beauv.	Poaceae
Mimosa pudica L.	Fabaceae
Mitracarpus hirtus (L.) DC.	Rubiaceae
Mitragyna inermis (Willd.) Kuntze	Rubiaceae
Mollugo nudicaulis Lam.	Molluginaceae
Monechma ciliatum (Jacq.) Milne-Redh.	Acanthaceae
Monocymbium ceresiiforme (Nees) Stapf	Poaceae
Nelsonia canescens (Lam.) Spreng.	Acanthaceae
Ocimum americanum L.	Lamiaceae
Oldenlandia corymbosa L.	Rubiaceae
Ophioglossum reticulatum L.	Ophioglossaceae
Orthosiphon rubicundus (D.Don) Benth.	Lamiaceae
Oryza longistaminata A.Chev.& Roehr.	Poaceae
Oxycaryum cubense (Poepp. & Kunth) Palla	Cyperaceae
Ozoroa insignis Delile	Anacardiaceae
Pandiaka angustifolia (Vahl) Hepper	Amaranthaceae

Species	Family
Pandiaka involucrata (Moq.) B.D.Jacks.	Amaranthaceae
Panicum anabaptistum Steud.	Poaceae
Panicum laetum Kunth	Poaceae
Panicum maximum Jacq.	Poaceae
Panicum subalbidum Kunth	Poaceae
Parkia biglobosa (Jacq.) G.Don	Leguminosae
Paspalum scrobiculatum L.	Poaceae
Paspalum vaginatum Sw.	Poaceae
Pennisetum pedicellatum Trin.	Poaceae
Pennisetum setaceum (Forssk.) Chiov.	Poaceae
Pentanema indicum (L.) Ling	Compositae
Pergularia tomentosa L.	Apocynaceae
Phyllanthus amarus Schumach. & Thonn.	Phyllanthaceae
Phyllanthus maderaspatensis L.	Phyllanthaceae
Phyllanthus muellerianus (Kuntze) Exell	Phyllanthaceae
Physalis angulata L.	Solanaceae
Piliostigma reticulatum (DC.) Hochst.	Leguminosae
Piliostigma thonningii (Schum.) Milne-Redh.	Leguminosae
Platostoma africanum P.Beauv.	Lamiaceae
Plectranthus gracillimus (T.C.E.Fr.) Hutch. & Dandy	Lamiaceae
Polycarpaea eriantha Hochst. ex A.Rich.	Caryophyllaceae
Polycarpaea linearifolia (DC.) DC.	Caryophyllaceae
Polygala arenaria Willd.	Polygalaceae
Polygala capillaris E.Mey. ex Harv.	Polygalaceae
Polygala erioptera DC.	Polygalaceae
Polygala guineensis Willd.	Polygalaceae
Polygala multiflora Poir.	Polygalaceae
Portulaca oleracea L.	Portulacaceae
Pseudocedrela kotschyi (Schweinf.) Harms	Meliaceae
Pteleopsis suberosa Engl. & Diels	Combretaceae
Pycreus lanceolatus (Poir.) C.B.Clarke	Cyperaceae
Rhynchosia minima (L.) DC.	Leguminosae
Sacciolepis micrococca Mez	Poaceae
Sarcocephalus latifolius (Sm.) E.A.Bruce	Rubiaceae
Schizachyrium brevifolium (Sw.) Buse	Poaceae
Schizachyrium sanguineum (Retz.) Alston	Poaceae
Schoenefeldia gracilis Kunth	Poaceae
Schwenckia americana L.	Solanaceae
Scleria melanotricha Hochst. & A.Rich.	Cyperaceae
Sclerocarya birrea (A.Rich.) Hochst.	Anacardiaceae

Species	Family
Scoparia dulcis L.	Plantaginaceae
Senna obtusifolia (L.) H.S.Irwin & Barneby	Leguminosae
Senna occidentalis (L.) Link	Leguminosae
Setaria barbata (Lam.) Kunth	Poaceae
Setaria pumila (Poir.) Roem. & Schult.	Poaceae
Setaria sphacelata (Schumach.) Stapf & C.E.Hubb. ex Moss	Poaceae
Sida acuta Burm.f.	Malvaceae
Sida cordifolia L.	Malvaceae
Sida rhombifolia L.	Malvaceae
Sida spinosa L.	Malvaceae
Sida urens L.	Malvaceae
Siphonochilus aethiopicus (Schweinf.) B.L.Burtt	Zingiberaceae
Spermacoce chaetocephala DC.	Rubiaceae
Spermacoce filifolia (Schumach. & Thonn.) J.-P.Lebrun & Stork	Rubiaceae
Spermacoce radiata (DC.) Hiern	Rubiaceae
Spermacoce radiata (DC.) Hiern	Rubiaceae
Spermacoce stachydea DC.	Rubiaceae
Sporobolus pectinellus Mez	Poaceae
Sporobolus pyramidalis P.Beauv.	Poaceae
Sporobolus virginicus (L.) Kunth	Poaceae
Stachytarpheta angustifolia (Mill.) Vahl	Verbenaceae
Stereospermum kunthianum Cham.	Bignoniaceae
Sterculia setigera Delile	Malvaceae
Striga asiatica (L.) Kuntze	Orobanchaceae
Striga brachycalyx Skan	Orobanchaceae
Striga dalzielii Hutch.	Orobanchaceae
Striga gesnerioides (Willd.) Vatke	Orobanchaceae
Striga hermonthica (Delile) Benth.	Orobanchaceae
Struchium sparganophorum (L.) Kuntze	Compositae
Strychnos innocua Delile	Loganiaceae
Strychnos spinosa Lam.	Loganiaceae
Stylosanthes erecta P.Beauv.	Leguminosae
Stylochiton hypogaeus	Araceae
Synedrella nodiflora (L.) Gaertn.	Compositae
Tacca leontopetaloides (L.) Kuntze	Dioscoreaceae
Thalia geniculata L.	Maranthaceae
Tephrosia bracteolata Guill. & Perr.	Leguminosae
Tephrosia elegans Schum.	Leguminosae
Tephrosia gracilipes Guill. & Perr.	Leguminosae
Tephrosia mossiensis A.Chev.	Leguminosae

Species	Family
Tephrosia nana Schweinf.	Leguminosae
Tephrosia pedicellata Baker	Leguminosae
Terminalia avicennioides Guill. & Perr.	Combretaceae
Terminalia catappa L.	Combretaceae
Terminalia laxiflora Engl.	Combretaceae
Terminalia macroptera Guill. & Perr.	Combretaceae
Terminalia mollis M.A.Lawson	Combretaceae
Tinnea barteri Gürke	Lamiaceae
Tragia senegalensis Müll.Arg.	Euphorbiaceae
Trema orientalis (L.) Blume	Cannabaceae
Trianthema portulacastrum L.	Aizoaceae
Tribulus terrestris L.	Zygophyllaceae
Tridax procumbens (L.) L.	Compositae
Tripogon minimus (A.Rich.) Hochst. ex Steud.	Poaceae
Triumfetta lepidota K.Schum.	Malvaceae
Triumfetta pentandra A.Rich.	Malvaceae
Triumfetta rhomboidea Jacq.	Malvaceae
Uraria picta (Jacq.) DC.	Leguminosae
Urena lobata L.	Malvaceae
Vangueria agrestis (Schweinf. ex Hiern) Lantz	Leguminosae
Vernonia nigritiana Oliv. & Hiern	Compositae
Vigna filicaulis Hepper	Leguminosae
Vigna heterophylla A.Rich.	Leguminosae
Vigna longifolia (Benth.) Verdc.	Leguminosae
Vigna racemosa (G.Don) Hutch. & Dalziel	Leguminosae
Vitex doniana Sweet	Lamiaceae
Vitex madiensis Oliv.	Lamiaceae
Vitellaria paradoxa C.F.Gaertn.	Sapotaceae
Waltheria indica L.	Malvaceae
Wissadula amplissima (L.) R.E.Fr.	Malvaceae
Ximenia americana L.	Olacaceae
Ziziphus mauritiana Lam.	Rhamnaceae
Ziziphus mucronata Willd.	Rhamnaceae
Zornia glochidiata DC.	Leguminosae