

Vegetation Heterogeneity of the Savuti-Mababe-Linyanti ecosystem of northern Botswana: Understanding Drivers of Functional Heterogeneity and Herbivore Movements

by

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Disclaimer

The work contained in this thesis was completed by the author at the Okavango Research institute (University of Botswana) between 01/08/2014 to 15/12/2017. It is original work except where reference is made and has not been submitted for any award at other universities.

Dedication

This work is dedicated to my son, Fryxell Chendo who passed away during the last phase of this study.

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Chapter 7: Functional heterogeneity for large herbivores in wetland - dryland landscapes of northern Botswana: **A synthesis**.

Abstract

Vegetation classification and baseline mapping of the Savuti-Mababe-Linyanti ecosystem (SMLE, northern Botswana) is important for conservation planning and animal habitat use studies. This study aimed to develop a baseline vegetation map of the SMLE, and use it for various wildlife habitat use studies currently being conducted there, and for understanding the functional heterogeneity and ecology of the SMLE. The vegetation of the SMLE were determined and mapped using Landsat 8 and RapidEye imagery. Cover of all species was estimated using 40 m x 20 m plots. Forage characteristics in four habitat types; two wetland habitats (wet sandveld and sedgelands), and two dryland habitats (mopane and sandveld) around the distal reaches of the Okavango Delta were sampled during the late dry season of 2015. Vegetation composition, structure and richness in two different vegetation types (mopane and sandveld woodland) at three distance zones (0-5, 10-15 and > 20 km) from the permanent water of the Okavango Delta and Linyanti Swamps were surveyed. In this survey, relationships between vegetation and herbivory in relation to distance from permanent water was determined. The seasonal movements and habitat selection of three buffalo Syncerus caffer caffer and six zebra *Equus quaqqa* herds were determined using GPS enabled collars in the SMLE.

Non-Metric Multidimensional Scaling identified seven communities on deep Kalahari sandy soils, four on alluvial loamy soils and four on lacustrine clay soils. Communities on sandy soils were dominated by *Terminalia sericea* and *Philenoptera nelsii* in sandveld and *Baikiaea plurijuga* in Baikiaea forest, while various indicator species defined other communities. Mopane woodland farther away from riparian woodland was common on less sandy alluvial soils, whereas tall open grasslands and acacia grasslands in the sump of a paleolake system, the Mababe Depression (MD) are supported by mineral-rich heavy clay soils, supporting grasses higher in minerals (P, Ca, Na and K), thereby making this region an important wet season range for the migratory zebra population. High quality taller grasses in the mosaic of sandveld and mopane woodland communities providesl grazing for taller grass grazers such as buffalo, roan *Hippotragus equinus* and sable *Hippotragus niger* antelope during the wet season, while wetland communities provide reliable green forage and surface water to various herbivores including elephant *Loxodonta Africana* during the dry season. Wet sandveld in wetlands was characterized by the highest protein content of all habitat types though grass height and biomass were very low in this habitat. Of the wetland habitats sedgelands had the highest biomass of adequate-quality forage, while dryland habitats had the lowest quantity and quality of forage during the dry season.

Trees favoured by elephants during the dry season occurred as pollarded populations within 5 km of permanent water while mature tall populations of these species were found farther from water (> 10-15 km). Short high-quality grazing grasses were higher in abundance within 5 km of permanent water whereas taller high-quality perennial grasses peaked in abundance beyond 20 km from permanent water. Herbaceous richness with distance from water depended upon vegetation type, while tree richness did not change with distance from water. Spatial refuges in waterless regions of landscapes facilitate the creation of heterogeneity of vegetation structure, composition and richness by large herds of mammalian herbivores. Buffalo herds had greater activities in the mopane-sandveld woodland mosaic farther away from permanent water for drinking, but moved to wetland habitats where there was permanent water and forage during the dry season. Conversely, zebra herds in the Linyanti Swamp region migrated from their dry season range in the Linyanti region into the mineral rich paleolake

system of the MD during the wet season. Zebra wet season range was characterized by extensive open grasslands on higher - quality soils, and their dry season range was characterized by woodland systems adjacent the Linyanti Swamps, and wetland habitats along the Linyanti Swamps and Savuti Channel, which provided greenery forage during the dry season.

In conlcuion, gradients of soil texture and wetness allowed development of critical heterogeneity in vegetation composition and phenology, which enabled herbivores to adapt to seasonal variability in forage and water availability. Herbivory on the large distance gradients away from permanent water (> 20 km) in the SMLE has created key diversity, compositional and structural heterogeneity in grass, forb and woody species that is likely to result in greater niche diversity and adaptive foraging options that will enhance biodiversity and herbivore population stability and productivity. This study shows that spatial refuges for both grass and woody species occurred beyond 15 km from permanent water of the Okavango Delta and Linyanti Swamps. Water provision in the form of artificial water holes in the dryland woodlands of the SMLE will allow elephants, buffalo and other herbivores to spend a long time farther from permanent water during the dry season, leading to over-grazing of taller tufted and high-quality grasses and destruction of tall woodland, ultimately homogenising vegetation composition and structure across large landscapes, with negative consequences for biodiversity. Therefore artificial water provision in woodlands distant from permanent surface water in this ecosystem should be limited as it will have dramatic effects on both large herbivores and vegetation.

Thesis outline

Chapter 1 provides a general background about the study, the study area and the problem statement. Chapters 2 to 6 are a series of manuscripts published or under review in specific journals. Chapter 2 provides a baseline vegetation classification and mapping of the Savuti-Mababe-Linyanti ecosystem (SMLE, northern Botswana) while chapter 3 compares the forage dynamics of wetland habitats used by buffalo during the dry season against dryland habitats used during the wet season. Chapter 4 describe the effects of herbivory on plant species diversity, composition and structure with distance from permanent water, while chapter 5 provides a study of habitat selection by buffalo in the SMLE in relation to the availability of resources. Chapter 6 provides an analysis of seasonal habitat selection by migrating plains zebra in an unfragmented landscape in northern Botswana. Chapter 7 provides a synthesis of the overall study.

Definition of terms

Environmental heterogeneity	Involves the spatial heterogeneity, complexity, diversity,
	structure or variability in the environment (Stein and Kreft
	2015).
Vegetation heterogeneity	Includes the physical structure of the vegetation and its
	taxonomic or functional composition such as plant diversity
	(Stein et al. 2014).
Functional heterogeneity	Spatial and temporal variations in grass height (structure),
	productivity, phenology, composition in savanna plant
	communities (Fynn et al. 2016).
Plant community	An assemblage of plant species that occur together and
	interact with each other in a common environment (Little
	and Jones 1980).
Habitat	Includes the physical and biological features where a species
	can berform its normal activities such as searching for food,
	shelter, protection and mates for reproduction.
Habitat selection	A proportion of habitat use against habitat availability
	(defined in chapters 5 and 6).
Woodland	A habitat covered with ancient trees.
Forest	a land area of more than 0.5 ha, with a tree canopy cover of
	more than 10% (FAO 2010).
Migrations	Seasonal movements of animals from and to geographically
	separate homeranges (Dingle and Drake 2007).

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Chapter 1: General Introduction

African savannas are important in supporting the diversity and abundance of domestic and wild herbivores (Smithers 1983, Coppock et al. 1986, Scholte et al. 2007, Homewood 2008, Fynn and Bonyongo 2011), and their long-range migrations (Homewood 2008, Harris et al. 2009, Fynn et al. 2015). As a result these savannas are considered important for global conservation. Historically, pastoral communities and their domestic herbivores such as cattle Bos taurus, camels Camelus bactrianus, donkeys Equus asinus, sheep Ovis aries and goats Capra hircus coexisted with wildlife. The movements of these communities and their domestic herbivores followed the seasonal migratory and foraging patterns of wild herbivores (Homewood 2008, Fynn et al. 2015). However, with changes in landuse, these movements of both domestic and wild herbivores have been disrupted. Literature to date suggests that most protected areas are limited in supporting the needs of migratory species, which often satisfy varying requirements by moving between habitats offering functionally different resources (Harris et al. 2009, Craigie et al. 2010, Fynn and Bonyongo 2011). These long-distance movements and migrations are important as adaptive responses to environmental gradients, patchy rainfall and fire occurrences, thereby maintaining the carrying capacity and sustainability of both domestic and wild herbivore populations (Owen-Smith 2004, Fryxell et al. 2005, Hobbs et al. 2008, Augustine 2010, Fynn and Bonyongo 2011).

Literature suggests that agriculture and developments in seasonal ranges of herbivores have promoted ecosystem fragmentation (Serneels et al. 2001, Baudron et al. 2011). Growing human populations and land use policy changes, and their associated impacts such as overgrazing and the dispersal of homesteads have also promoted ecosystem fragmentation (Ogutu et al. 2009, Western et al. 2009), resulting in a decline of herbivore populations across Africa (Harris et al. 2009, Western et al. 2009, Craigie et al. 2010, Fynn and Bonyongo 2011), and impoverished pastoral communities (Pamo 1998, Homewood 2008). Ecosystem fragmentation is elevated when local communities get no or little financial benefits from protected areas (Norton-Griffiths and Said 2010). However, Fynn et al (2016) suggested that ecosystem fragmentation can be minimised when local communities are allowed to benefit directly from protected areas through various means: "promote access for communities to key ecosystem services and economic benefits within landscapes that encompass one or more protected areas (national parks, game reserves and wildlife management areas). These benefits could occur in the form of direct payments to local communities to revise landuse policies or practices to facilitate wildlife use of key habitats and migratory corridors outside protected areas".

The northern conservation area of Botswana remains one of the few relatively unfragmented, open, wildlife systems in Africa (Fynn and Bonyongo 2011). This region supports large populations of herbivores such as African elephant *Loxodonta africana*, Cape buffalo *Syncerus caffer caffer*, plains zebra *Equus quaqqa* and populations of rare antelope, roan *Hippotragus equinus* and sable *Hippotragus niger* (Chase 2011, Chase et al. 2016). This region contains extensive savanna woodlands between the permanent water sources of the Okavango Delta and Linyanti Swamps. Because it is an open system, wildlife populations in northern Botswana freely move between habitats offering a variety of resources: buffalo move to dryland woodlands during the wet season in northern Botswana, and back to wetland habitats in the Okavango Delta and Linyanti Swamps region and Savuti Channel over the dry season (Bennitt et al. 2014, Sianga et al. 2017a). Similarly, zebra populations in northern Botswana migrate from wetland habitats into paleolake systems during the wet season, and back to wetland habitats over the dry season: from the Boteti River in the dry season to Makgadikgadi Pans saline grasslands in the wet season (Brooks 2005, Bradley 2012), from the Okavango Delta floodplains and grasslands in the dry season to Makgadikgadi Pans saline grasslands in the wet season (Bartlam-Brooks et al. 2011), and from the Chobe River floodplains in the dry season to Nxai Pan saline grasslands in the wet season (Naidoo et al. 2014a), and between the Linyanti Swamps and adjacent woodlands in the dry season to the Mababe Depression in the wet season (Joos-Vandewalle 2000, Sianga 2014). These migrations are important adaptive strategies for meeting elevated resource requirements for growth and reproduction, as documented elsewhere in Africa (Murray 1995, Hopcraft et al. 2010, Fynn and Bonyongo 2011), and also important in accessing surface water and green grass which are available in wetland habitats during the dry season owing to shallow water tables (Vesey-FitzGerald 1960, McNaughton 1985, Fryxell 1987, Fryxell et al. 1988).

The northern part of Botswana occurs in the Kalahari sedimentary basin (Mendelsohn et al. 2010), which covers about 2.5 million km², extending across parts of many southern African countries such as Botswana, Zambia, Zimbabwe, Namibia, Angola and South Africa. This basin is characterized by relatively homogenous substratum, flat topography and a clearly defined northeast or southwest precipitation gradient (Scholes et al. 2002). The origin of the Kalahari basin is related to the break-up of the supercontinent Gondwanaland during the Mesozoic era through tectonic activities (Thomas and Shaw 1991). This resulted in the evolution of hydrological patterns and the deposition of the Kalahari Group sediments which arose from the erosional processes in the Kalahari basin (Rust 1975). Through the process, rifting of tectonic plates which occurred during the time also influenced the sedimentation rates of the Kalahari Group of sediments (Rust 1975). Similarly, the thermal expansion of the crust during this rifting

led to the development of the Great escarpment (Summerfield 1985) where the Kalahari Group sediments were deposited (Thomas and Shaw 1988). Small scale tectonic activities also play an important role in the sedimentation rates throughout the basin. For example, in northern Botswana, seismic and hydrological studies highlighted the occurrence of geologic faults running northeast – southwest (Du Toit 1926). The Kalahari Group of sediments which were deposited during the initial stages of this tectonic activities were reworked through generations by water and wind (Bullard et al. 1995), and interactions between water, wind and sediments had major implications for the geomorphology of the region (Bullard and Livingstone 2002). However, extensive studies demonstrated that the Kalahari Group of sediments can be grouped into six groups: Kalahari sands, sandstones, marl, conglomerate and gravel, alluvium and lacustrine deposits, and duricrusts (Thomas and Shaw 1991).

Recent studies in northern Botswana demonstrated that Kalahari sands are dominant in terms of spatial extent and are characterized by sandy soils that are acidic and nutritionally poor relative to other Kalahari Group of sediments (Wang et al. 2007). Another important group of sediments is the alluvium and lacustrine deposits which dominate paleolake systems. In northern Botswana, the paleolakes Mababe Depression, Makgadikgadi pans, Nxai Pan and Lake Ngami are characterized by clay and silts eroded from watersheds in the Angolan highlands (Gamrod 2009). The progressive desiccation and evaporative concentration of solutes, erosion of calcium and phosphorus rich calcrete-silcrete in local watersheds deposited large amounts of phosphorus and other minerals in these paleolake systems (McCarthy and Ellery 1995, Kampunzu et al. 2007, Teter 2007), and hence they are dominated by short saline grasslands where grasses such as *Urochloa trichopus, Chloris virgata* and *Sporobolus ioclados* prevail, and thus provide high quality forage for various herbivores during the wet season (Sinclair 1979, Sianga and Fynn

2017, Sianga et al. in review). Generally, this variation in the surface expression of the Kalahari Group of sediments, and interactions with other factors such as fire, soil moisture and herbivory are responsible for vegetation heterogeneity in the region (Sianga and Fynn 2017).

Vegetation heterogeneity defined by assemblages of plant species distributed unevenly across an ecosystem (Burrows 1990), is related to different factors at different spatial scales (Crawley and Harral 2001, Gillson 2004, Bisigato et al. 2009) (figure 1).



Figure 1: A conceptual framework of the factors that lead to vegetation heterogeneity (adapted from Hopcraft et al. 2010). This shows the interaction of the abiotic factors, herbivory and disturbance to generate

heterogeneity in forage quality, quantity, plant growth forms and vegetation structure. The description of these factors is given in the following sections.

The differences brought by these various factors may lead to seasonal or permanent differences in forage greenness, digestibility and nutrient concentrations, thereby leading to functional heterogeneity (McNaughton 1985, Western and Gichohi 1993, Fryxell et al. 2005, Verweij et al. 2006, Sensenig et al. 2010, Fuhlendorf et al. 2017, Fynn et al. 2017), and thus important in enhancing the sustainability and productivity of herbivore populations that can access it (Illius and O'Connor 2000, Owen-Smith 2002, Owen-Smith 2004, Hobbs et al. 2008, Hopcraft et al. 2010, Fynn 2012, Fynn et al. 2017). For example, in Tanzania, the Lake Manyara buffalo balance their intake of protein and fibre in forage by foraging adaptively between *Cynodon dactylon* and *Cyperus laevigatus* sedgelands grasslands during the dry season (Prins and Beekman 1989).

Vegetation communities that are components of vegetation heterogeneity are complex to understand without the use of appropriate tools (Symstad 2002). As a result various vegetation classification techniques are used by plant ecologists to better understand this complexity (Symstad 2002). Vegetation classification began in the 19th century when scientists shifted from classifying plants into species to classifying vegetation communities in relation to the dominant species within them (Mueller-Dombois and Ellenberg 1974). The key objective of these techniques is to simplify the complexity of plant communities while keeping the important information required in achieving specific research goals (Running et al. 1995, Noble and Gitay 1996).

1.1.1 Ecological gradients

Savannas in Africa experience patchy rainfall, frequent droughts and long dry seasons (Barry and Chorley 2003, Fynn et al. 2014), which lead to drying out of forage and declining forage quality well below maintenance requirements of pregnant and lactating herbivores (Ellis and Swift 1988, Owen-Smith 2008, Hopcraft et al. 2010). As a result, herbivores are forced to adapt spatially and temporally to this variation in forage resources and surface water availability. This involves adaptive movements between habitats varying in forage quality and quantity as a strategy to access green grass linked with patchy rainfall (Fryxell et al. 2005). As a result, this may lead to seasonal habitat selection patterns by herbivores (Zweifel-Schielly et al. 2009). This may also involve some seasonal migrations between wet and dry season habitats offering optimal forage resources, and this is important in maintaining productive and stable populations of herbivores (Scoones 1995, Illius and O'Connor 2000, Owen-Smith 2002, Owen-Smith 2004, Fynn 2012).

During the wet season, rainfall provides ephemeral water in pans, lifting the restriction imposed by water limitation on regional access to woodlands during the dry season. As a result, herbivores may move adaptively from their dry season ranges into their wet season ranges when there is adequate water in the pans, and back to permanent water sources when water in the pans get depleted (Bartlam-Brooks et al. 2011, Sianga 2014). Apart from water availability, forage quality also plays a role in determining movements and habitat selection patterns by herbivores (McNaughton 1988, 1990, Murray 1995).

Forage quality in low-rainfall regions and shallow-upland soils is generally higher than in productive grasslands (Breman and de Wit 1983, McNaughton and Banyikwa 1995, Murray 1995), because minerals, protein and energy are less diluted by low biomass in these systems (Jarrell and Beverly 1981). Similarly, low rainfall which leads to low leaching of minerals in low

productivity habitats, results in high concentration of minerals in the soil. The key mechanisms giving rise to salinity in low rainfall areas are water loss through soil evaporation and evapotranspiration in closed (endorheic) lakes (Teter 2007), volcanic deposits (Sinclair 1979), geological type, leaching of minerals upslope and deposition in seep zones downslope - sodic sites (Grant and Scholes 2006). These low productivity habitats are dominated by short grasses that are highly digestible and richer in minerals than taller grasses in productive habitats (Fynn and Bonyongo 2011, Fynn et al. 2015). As a result these short and nutritious grasses are generally selected by herbivores as wet season resources, particularly important for maximising minerals, energy and protein intake during lactation or pregnancy (Kreulen 1975, Murray 1995, Parker et al. 1999, Parker et al. 2009). For example, in northern Botswana and Namibia, short saline grasslands in paleolake systems such as Etosha Pan (Berry 1997, Fynn and Bonyongo 2011), the Mababe Depression, Nxai Pan and Makgadikgadi pans were found to be key wet season habitats for zebra populations (Joos-Vandewalle 2000, Bradley 2012), while the Serengeti short-grass plains (Kreulen 1975, Maddock 1979), the Loita plains (Serneels and Lambin 2001, Serneels et al. 2001, Ogutu et al. 2009, Western et al. 2009, Ogutu et al. 2011), the Athi-Kapiti plains (Imbahale et al. 2008) and the Simanjiro plains (Kahurananga and Silkiluwasha 1997) are key wet season habitats for various herbivores in East Africa. However, when forage and water availability declines in the ephemeral pans in wet season habitats (Ellis and Swift 1988, Mduma et al. 1999, Illius and O'Connor 2000), high productivity areas become significant in the provision of green grass during the dry season (Vesey-FitzGerald 1960, McNaughton 1985, Fryxell 1987, Fryxell et al. 1988). During this time, herbivores select for dry season habitats offering adequate-quality forage and surface water, hence minimising their body store loss throughout the dry season. Dry season habitats may include floodplain grasslands (VeseyFitzGerald 1960, Sheppe and Osborne 1971, Fryxell and Sinclair 1988, Adams 1993, Pamo 1998), dambo grasslands (Roberts 1988, Scoones 1995) or high-rainfall regions (McNaughton 1985, Fynn and Bonyongo 2011). Deep rooted perennial grasses grow in floodplain grasslands or high-rainfall regions over the dry season due to the availability of soil moisture (McNaughton 1985, Roberts 1988, Scoones 1995, Fynn and Bonyongo 2011). Patchy rainfall which may occur during the wet or dry season provide soil moisture for grasses to grow during this time (McNaughton 1979, Verlinden and Masogo 1997, Fryxell et al. 2005) and herbivores may select for habitats offering green grass during this period. For example, red hartebeest *Alcelaphus buselaphus* in the Kalahari (Botswana) were found to be abundant on green grass growth after patchy rainfall (Verlinden and Masogo 1997), and in the Serengeti Plains, Thompson's gazelles *Eudorcas thomsonii* are adapted to move within the plains in response to seasonal forage availability as a result of stochastic rainfall (Fryxell et al. 2005).

Plant species favoured by large herbivores may be spared from excessive herbivore impact in regions of landscapes farther from permanent water (O'Connor et al. 2007), and as a result rare antelope such as sable and roan depend upon these waterless, backcountry parts of landscapes to avoid higher concentrations of predators and other herbivore species closer to permanent water (Harrington et al. 1999, Hensman et al. 2013, Haveman 2014). These species have narrow mouths specialised for foraging on taller grasses (Codron et al. 2008). Similarly, apex predators, such as African wild dog *Lycaon pictus*, may also be forced by competition with larger carnivores to focus their hunting in regions of landscapes with lower abundances of their preferred prey (Mills and Gorman 1997). However, the establishment of artificial water points in the Kruger National Park (South Africa) removed the spatial heterogeneity provided by the natural landscapes and resulted in zebra populations moving into roan and sable ranges, elevating

competition for resources between these species, which ultimately resulted in a decline in roan and sable populations. These water points also removed the predation refuge provided by water limitation in the landscapes, and lion *Panthera leo* settled in roan and sable ranges and ultimately resulted in a decline of these antelope species (Harrington et al. 1999).

Vegetation heterogeneity therefore provides plant diversity which permits portioning into niches by herbivores and thus enriching biodiversity (Hutchinson 1959, Schoener 1974, Ricklefs 2008, Kartzinel et al. 2015, Fynn et al. 2016). This niche separation limits competition for resources between species and thus prevents the extinction of one species as a result of another species, and allows the coexistence of species (Kartzinel et al. 2015). Resource partitioning by various herbivores is achieved mainly through variation in body size and mouth anatomy (Arsenault and Owen-Smith 2008, Fynn et al. 2016). In general, smaller bodied herbivores are associated with larger relative metabolic requirements, and therefore rely on high quality forage resources, whereas larger bodied herbivores rely on more abundant but lower quality forage resources (Jarman 1974, Illius and Gordon 1987, Steuer et al. 2014). For example, smaller bodied herbivores (e.g. impala Aepyceros melampus and Thomson's gazelle) rely on high quality short grasslands to enhance their maintenance and reproductive requirements. In contrast, larger bodied herbivores utilise taller grasslands to enhance their bite size and intake rate in response to higher demands of their large absolute food requirements (Illius and Gordon 1987, Wilmshurst et al. 2000). Mouth anatomy also contributes to resource partitioning between herbivores; narrowmouthed herbivores select high quality green leaves while avoiding low quality stems and dead leaves, whereas broad mouthed herbivores are adapted to utilise dense swards of grasslands (Murray and Illius 2000, Codron et al. 2008). For example, narrow-mouthed herbivores including reedbuck Redunca arundinum (Jungius 1971), sable (Grobler 1981, Codron et al. 2008,

Hensman et al. 2013) and roan (Haveman 2014) favour intermediate to taller grass habitats, while wildebeest and Thompson gazelles in the Masai-Mara Game Reserve favour shorter grasslands (Bhola et al. 2012). Broad mouthed herbivores such as buffalo prefer taller grass habitats as they rely on their adaptive tongue sweep strategy to enhance their bite size and larger absolute food requirements (Illius and Gordon 1987).

Interactions between small and medium sized short-grass specialists can lead to facilitation effects in productive habitats such as in high-rainfall areas, floodplains, swamps, and lowlands (Western and Gichohi 1993, Fryxell et al. 2005, Verweij et al. 2006), as grass biomass and height may increase to higher levels thereby limiting herbivore intake rates (Wilmshurst et al. 2000, Owen-Smith 2002). This positive interaction occurs when grazing by one species limits grassland senescing into less digestible taller grasses, thereby promoting the regrowth of high-quality plants (Vesey-FitzGerald 1960). Various studies across different ecosystems have also demonstrated that large herbivores are important in facilitating forage for smaller-sized herbivores; hippopotamus *Hippopotamus amphibius* and kob *Kobus kob* in Benue National park Cameroon (Verweij et al. 2006) and elephants, buffalo and hippopotamus in the Rukwa Valley, South-western Tanganyika territory, Tanzania are examples (Vesey-FitzGerald 1960).

However, despite the importance of vegetation environmental heterogeneity, its effects on species richness are scale dependent (Stein et al. 2014). Environmental heterogeneity- species richness relationships increase positively with spatial scales because larger sampling areas would incorporate more environmental differences (Van Rensburg et al. 2002, Kallimans et al. 2008, Stein et al. 2014). Rowe (2009) and Qian and Kissling (2010) also argue that environmental heterogeneity is important in species richness relationships at landscape scales. This positive relationships result from mechanisms that promote species coexistence, persistence and diversification (Stein et al. 2014). The stronger environmental heterogeneity- species richness relationships can be attributed to more variability in environmental heterogeneity. In addition, allopatric speciation and species turnover are more significant at larger spatial scales (Van Rensburg et al. 2002). Constranstly, Tamme et al (2010) and Laanisto et al (2013) argued that negative environmental heterogeneity – species richness relationships may become stronger at smaller spatial scales, increasing species extinction risks because of isolation and habitat loss. Similarly, Gazol et al (2013) suggested that at smaller scales heterogeneity, dominant species which are adapted to this heterogeneity conditions may decrease species diversity.

1.1.2 Soil

Soil type plays an important role in determining the floristic composition and abundance of species. For example, plant community composition changes dramatically on soil texture gradients (Bisigato et al. 2009), on soil depth gradients (Allison et al. 2007) and on soil fertility gradients (Grime 1979, Gibson and Hulbert 1987, Gaudet and Keddy 1995, Fynn et al. 2005). Soil characteristics such as nutrients and moisture availability are dependent on the parent material and organic matter that forms soil (Wild 1993). The bedrock from which soil is formed determines soil particle size, which influences soil properties such as texture, soil aeration, infiltration, water storage capacity and soil fertility (Miller and Gardiner 1958, Wild 1993). Sandy soils are defined by content of the sand, and thus characterized by large pores between soil particles, good aeration and infiltration abilities but have low water and nutrient holding capacity, low cation exchange capacity, and higher leaching. Sandy soils stores a large proportion of the rainfall received during the wet season, though little is lost through evaporation or runoff from coarse sandy soils relative to fine-textured clay soils (Alizai and Hulbert 1970,

Noy-Meir 1973). Generally, water in sandy soils infiltrates easily through the coarse textured particles and gets stored below the evaporative zone over the dry season than clay soils, enabling deep rooted plants to continue growing even when rainfall has ceased during the dry season (Alizai and Hulbert 1970, McNaughton and Banyikwa 1995, Fynn 2012). Conversely, clay soils are characterized by higher clay contents and cation exchange capacity, and are defined as fertile soils because they retain nutrients and water effectively (Miller and Gardiner 1958).

1.1. 3 Flooding

Plant growth and greenness in African savanna ecosystems is limited by soil moisture availability (Knapp et al. 2006). As a result dryland woodland habitats distant from long-term surface water are associated with limited plant growth and green leaf during the dry season, due to their deep water tables. However, plant growth and green leaf provision during the dry season characterizes wetland habitats such as floodplains, swamps and dambo grasslands, due to their shallow water tables (Vesey-FitzGerald 1960, Roberts 1988, Pamo 1998, Fynn et al. 2014, Fynn et al. 2015). Consequently, wetland habitats and associated riverine habitats are critically important in the provision of green forage to large herbivores during the dry season when their favoured wet season forage has dried out or been depleted (Vesey-FitzGerald 1960, Fryxell and Sinclair 1988, Bartlam-Brooks et al. 2011, Fynn et al. 2014, Naidoo et al. 2014b) and forage protein and energy levels have fallen below maintenance requirements (Ellis and Swift 1988, Owen-Smith 2008, Hopcraft et al. 2010). For example, wetland habitats (i.e. floodplains) along the Sobat River and its tributary (i.e. Pibor River) in South Sudan, provide reliable dry season forage for wildlife (Fryxell and Sinclair 1988, Howell et al. 1988) and also attract transhumant pastoralists during the dry season (Duany 1999). In northern Botswana, buffalo populations in

the Savuti-Mababe-Linyanti Ecosystem utilize the Linyanti swamps during the dry season, where there is adequate surface water and green forage (Fynn et al. 2014, Sianga 2014), whereas zebra populations in northern Botswana utilise various wetland habitats during the dry season: the Boteti River (Brooks 2005, Bradley 2012), Okavango Delta floodplains and grasslands (Bartlam-Brooks et al. 2011), Chobe River floodplains (Naidoo et al. 2014a), and the Linyanti Swamps and adjacent woodlands (Joos-Vandewalle 2000, Sianga 2014).

Grazing in wetland habitats during the dry season removes the dead and above ground biomass, which are low in quality due to the accumulation of structural components (i.e. lignin, cellulose and silica) while maturing (Wilmshurst et al. 2000, Mosimane 2015). This new regrowth acts as a bridging resource for herbivores during the late dry season, a time when forage is limiting in most habitats (Owen-Smith 2002, Fynn et al. 2015). Wetland habitats also buffer herbivores against starvation and mortality during extended dry seasons or droughts through the provision of forage resources (e.g., reeds, sedges and stems of wetland grasses) which are often not consumed during good dry seasons (when there is adequate forage in dry seasons) as they are relatively low in quality (Owen-Smith 2002).

The frequency and duration of flooding in wetland habitats is important in maintaining resource heterogeneity throughout the dry season. For example, Fynn et al (2015) stated that "Plant zonation on flood frequency and duration gradients occurs in predictable sequences across Africa, and this variation combined with increasing retention of soil moisture for plant growth over the dry season with increasing flooding provides critical resource heterogeneity for herbivores". This suggest that floodplain grasslands of different depths experience different degrees of seasonal flooding (Mendelsohn et al. 2010), thereby providing variable foraging options for herbivores throughout the dry season (Fynn et al. 2015). For example, sitatunga

Tragelaphus spekii and red lechwe Kobus leche favour permanent swamps and seasonal floodplains of the Okavango Delta during the dry season, respectively, while elephant, zebra, buffalo, wildebeest, tsessebe Damaliscus lunatus and warthog Phacochoerus africanus utilize the floodplains over the dry season (Chase 2011). As the depth and duration of flooding increases in wetland habitats, floodplains become increasingly dominated by taller more productive sedges and swamp grasses (Murray-Hudson et al. 2014, Fynn et al. 2015). Though the deeper parts of floodplains provide more reliable green forage during the late dry season, their tall fibrous grasses and sedges are of lower digestibility and quality owing to greater cellulose and lignin content (Wilmshurst et al. 2000). Similarly, wetland grasses and sedges are characterised by a higher silica content in tissues which lowers their digestibility and palatability (Mosimane 2015). Thus, herbivores foraging between regions of floodplains varying in frequency and gradients ensures a balanced protein and fibre intake during the late dry season, as was demonstrated for buffalo foraging between taller Cyperus laevigatus sedgelands and short but higher quality Cynodon dactylon grasslands around Lake Manyara (Manyara National Park, Tanzania), as a strategy to balance protein and fibre intake during the dry season (Prins and Beekman 1989). Similalry, in the Bangweulu swamps and Kafue flats (Zambia), black lechwe Kobus leche utilised the termitaria grasslands and floodplain edges during the flooding season, but moved farther into floodplains as the floods recede (Sheppe and Osborne 1971, Kamweneshe 2000), whereas populations of large herbivores such as elephants and buffalo in northern Botswana favour dryland woodland habitats during the wet season but favour wetlands as the water recede (Chase 2011, Fynn et al. 2014, Sianga 2014).

Variation in flooding depth and duration in wetlands provides key heterogeneity in forage quantity and quality to enable herbivores to balance protein against fibre intake (Fynn et al. 2015). The wetland community composition in the Okavango Delta differs by gradients of flood depth and duration, with *C. dactylon* often associated with the parts of the gradient with the lowest depth and duration of flooding, while *Panicum repens* and *Setaria sphacelata* often characterise areas with intermediate depth and duration of flooding, whereas tall sedges and grasses such as *Oryza longistaminata* and *Vossia cuspidata* characterise areas of the gradient with the largest depth and duration of flooding (Murray-Hudson et al. 2011, Murray-Hudson et al. 2014, Fynn et al. 2015).

This variation in composition and phenology on flooding gradients is important in providing the variation in green forage supply for herbivores from the early to late dry season, owing to variation in availability of soil moisture for growth, allowing for adaptive foraging options over the dry season. Edges of floodplain grasslands and shallow – intermediate depth floodplains are favoured by herbivores over the early dry season, while deep floodplains and swamps are used over the late dry season and during droughts (Fynn et al. 2015).

1.1. 4 Light, temperature, soil water and nutrients

Terrestrial plants require light from above the soil surface and mineral nutrients and water extracted from soil layers for survival. Different plant species require particular optimal quantities of nutrients and light to enable photosynthesis and ensure optimal growth. When plants are exposed to limited quantities of light, most of its growth will be allocated to leaves and stems, rather than to the roots. Adequate light intensity at soil surface is therefore critically important for the growth of newly established seedlings and shoots (Tilman 1988). Conversely, plants limited by nutrient availability will mostly allocate their growth to roots rather than to leaves or stems (Tilman 1988). Tilman (1988) suggests that this trade-off causes the patterns we

notice in natural plant communities because each unique pattern of vegetation and soil resources benefits plants with specific morphology, physiology and life-history traits, and hence resulting in vegetation heterogeneity. However, Tilman (1988) highlighted that growth of seedlings leads to loss of the required resources through uptake by plants. For example, seedling establishment uses variable resources such as water, light and nutrients, thereby reducing their availability in the soil, while seedling predation, disturbance and herbivory reduces the stress exerted on these resources. Thus the growth of plants in habitats is balanced by the reduction in the available resources and through predation (Tilman 1988). Thus the physiognomy of vegetation heterogeneity is strongly determined by factors that regulate the amount of light and limiting nutrients received by plants (Tilman 1988). Plants require soil moisture to take up nutrients through the process of diffusion. Low soil moisture content restricts root and shoot growth. The stronger cohesion of soil particles in drier soils is seen to be the key factor restricting root growth rather than water limitation (Wild 1993). In addition, temperatures below or above the optimum levels for particular plant species can hinder the growth and development of roots and shoots (Vapaavuori et al. 1992, Wild 1993). Temperature has a major influence on the photosynthetic rates of many plants (Berry and Bjorkman 1980), and hence plant species inhabiting different climatic regions evolved different photosynthetic responses (Berry and Bjorkman 1980). Species native to cool climates generally show higher photosynthetic rates at lower temperatures while those in warmer climates have higher photosynthetic rates at higher temperatures (Bjorkman et al. 1975, Berry and Bjorkman 1980).

1.1. 5 Herbivory and fire

Grazing by large herbivores promotes plant diversity across ecosystems (Glenn and Collins 1990, Turner et al. 1995, Knapp et al. 1999). The short-term effects of grazing involve photosynthesis increase in growing plant species (McNaughton 1979, Wallace 1990, Knapp et al. 1999). For example, a higher photosynthetic rate (53 %) was reported in grazed plants than in ungrazed plants in the Konza prairie grasslands, northeastern Kansas (Knapp et al. 1999). This was attributed to increased light availability and reduced soil moisture stress for species in grazed patches (Fahnestock and Knapp 1993, Mbatha and Ward 2010). Also, photosynthesis enhancement in grazed patches resulted from the translocation of carbon reserves from underground to aboveground tissues (Knapp et al. 1999). Grazing contributes to forage quality through the addition of nitrogen in the form of urine and faeces (Ross and Tate 1984, Knapp et al. 1999, Stark et al. 2002), and through the creation of grazing lawns (Arnold et al. 2014). For example, plant species growing on urine patches showed higher quality and leaf nitrogen content than those in patches without urine (Day and Detling 1990).

Grazing lawns are "areas where large mammal grazers effect a drastic reduction of canopy height and the activation of tillers that lead to a prostrate dense canopy" (McNaughton 1984). Grazing lawns are found on three areas: (i) sodic sites - areas where minerals, particularly sodium accumulated over time (Grant and Scholes 2006), (ii) nutrient hotspots - localized patches of N or P enrichment (Augustine and McNaughton 2006, Gosling et al. 2012), and (iii) around water points where populations of grazers congregate (Hempson et al. 2015). Lawns concentrate plant biomass at soil surfaces, thereby making them important sources of nutritious and high-bulk density forage resources (McNaughton 1984, Verweij et al. 2006), where plant regrowth is initiated by defoliation (Georgiadis et al. 1989, Anderson et al. 2006b, Anderson et

al. 2013). All grazing lawns are characterized by short and immature grasses (Archibald 2008, Cromsigt and Olff 2008, Hempson et al. 2015), though species composition may vary across lawns (Hempson et al. 2015). However, Hempson et al (2015) highlighted that despite differences in species composition between grazing lawns, lawn species can be categorized into three: (i) "species that spread laterally using horizontal stems (stolons), (ii) species that spread below the soil surface (rhizomes), and (iii) caespitose grasses that occur in dwarfed forms under heavy grazing".

Generally, grazing lawns are characterized by species with a high leaf: stem ratio, while leaf material has a lower C : N ratio than stem material, and is hence a highly digestible forage resource (Chaves et al. 2006). Relative to bunch grasses, lawn grasses are associated with a higher foliar N concentration (Stock et al. 2010). Repeated grazing hinders leaf blade tips from maturing, thereby promoting the existence of young and highly photosynthetic leaf blade tips closer to the intercalary meristems (Hempson et al. 2015). As a result, grazing lawns are important in the provision of high bulk density and nutritious forage (McNaughton 1976, 1985, Verweij et al. 2006). As demonstrated in East Africa savanna ecosystems, grazing promotes nutrient cycling in grazing lawns (McNaughton 1985, McNaughton et al. 1997). Grazers deposit decomposable dung and urine in lawns (Ruess and McNaughton 1987), a mechanism known to rapidly return nitrogen or nutrients to the plants. In the Serengeti, it was found that N mineralization in grazed patches was two times higher than in grasslands where grazing was limited (McNaughton et al. 1997). However, despite the importance of grazing lawns to herbivores, not all grazers have the ability to utilize them; probably because the grass is too short to enhance intake rates, which is important in meeting metabolic requirements (Owen-Smith 2002). Very small bodied herbivores such as impala and Thompson's gazelles have narrow

muzzles, but because of their small body size and their low absolute energy requirements they are able to get sufficient intake on grazing lawns but large bodied herbivores must have wide mouths to enhance intake rates (Murray and Illius 2000). Short grass specialists such as hippopotamus, wildebeest and white rhinoceros *Ceratotherium simum* are adapted to utilize grazing lawns to enhance their metabolic requirements for short - immature grasses (Arsenault and Owen-Smith 2008). Megaherbivores including hippopotamus and white rhinoceros were found to play key roles in the development of grazing lawns (Verweij et al. 2006, Waldram et al. 2008, Cromsigt and te Beest 2014). In the Benue National Park, northern Guinea, dry season crude protein in the hippopotamus grazing lawns species and on ungrazed plots were about 8% and 5% respectively (Verweij et al. 2006). This suggested that lawn grasses provide protein content above the minimum maintenance requirements for ruminants, which is about 5% (Crampton and Harris 1969).

Grazing lawns are not only nutritionally important to grazers; they are also important in minimizing predation risk for herbivores. Lawn grasses are relatively short in structure thereby providing greater visibility for grazers. As a result grazers can easily notice predators when they are still at a safer distance (Riginos and Grace 2008, Anderson et al. 2010, Hopcraft et al. 2010, Hempson et al. 2015). For example, in most African savannas, open areas with higher visibility are selected by some herbivores to minimize predation risk (Riginos and Grace 2008, Valeix et al. 2011).

The long-term effect of herbivory on grasslands involves the reduction in abundance of plant species, productivity of grasses and competition between dominant and subdominant species. Overall, this will result in flourishing of forbs, and increase in plant species richness and diversity and spatial heterogeneity (Hartnett et al. 1996, Knapp et al. 1999). Similarly, the

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deposition of dung and urine in grazed patches promotes species diversity at a microsite scale, and hence promotes spatial heterogeneity. Nitrogen deposition also promotes nutrient cycling processes and availability (Knapp et al. 1999, Mbatha and Ward 2010), which is critically important in the system as nitrogen is a key limiting nutrient in most grasslands (Owensby et al. 1970, Risser and Parton 1982, Seastedt et al. 1991, Blair 1997), and hence determines species composition (Gibson et al. 1993). Studies conducted in the Konza prairie grasslands (northeastern Kansas) demonstrated that grazing by American bison *Bison bison* is important in promoting nutrient cycling in the system (Frank and Evans 1997, McNaughton et al. 1997, Knapp et al. 1999).

The effect of grazing on grasslands varies along productivity gradients (Proulx and Mazumder 1998, Osem et al. 2002, Bakker et al. 2006, Burkepile et al. 2017) and with body sizes of the herbivores involved (Bakker et al. 2006). Grazing in unproductive habitats will result in reduced plant species richness, and the opposite may be true in productive habitats (Osem et al. 2002). Grazing in productive habitats removes the dominant and palatable species, thereby minimising the competitive interactions between species, for essential resources such light (Osem et al. 2002), water and nutrients. But in low productivity habitats grazing removes and tramples species that are able to withstand stress related limitation (Noy-Meir 1990), ultimately resulting in the reduction of plant species richness (Osem et al. 2002). However, the contrasting responses of species richness to grazing such as increasing or decreasing richness (Huston 1994, Proulx and Mazumder 1998) may vary with the grazing pressure experienced in the habitats involved. For example, the intermediate disturbance hypothesis (Figure 2) suggest that highest species richness is expected at intermediate grazing pressure (Connell 1978), while minimal grazing pressure may result in relatively low species richness because richness will be limited by

higher levels of competition between the plant species in the habitat (Figure 2) (Connell 1978). Species richness will decrease at higher grazing pressure because species will be taken-off faster than they grow (Gough et al. 1994, Gough and Grace 1998).

The effect of grazing on plant diversity varies with the body sizes of herbivores involved: large herbivores are known to increase plant diversity in productive habitats but may decrease diversity in less productive habitats (Bakker et al. 2006). Large herbivores promote diversity by impacting dominant species (Milchunas and Lauenroth 1993), ultimately reducing competition between species, which hinders the growth of new species (Grubb 1977, Huisman and Olff 1998, Huisman et al. 1999, Knapp et al. 1999). The removal of tall and dominant species through grazing by large herbivores (Huisman and Olff 1998, Huisman et al. 1999) enhances light availability to the remaining plants and also promotes the germination and establishment of seedlings (Jutila and Grace 2002). Conversely, smaller bodied herbivores with their selective feeding strategies may decrease diversity by selective consumption of highly nutritious plant species (Brown and Heske 1990).



Figure 2: The Intermediate Disturbance Hypothesis: I- at low grazing pressure species richness will be low, II- at intermediate levels of grazing, higher species richness, and III- highest levels of grazing, species richness will decrease (adapted from Connell 1978).

Grazing affects the frequency and intensity of fires in some systems (Knapp and Seastedt 1986, Savage and Swetnam 1990, Fuhlendorf and Engle 2004, Fuhlendorf et al. 2009) by keeping the fuel load relatively low (Knapp and Seastedt 1986), whereas browsing maintains woody plants within the flame zones (Scholes and Archer 1997). The grazer-browser-fire interaction (pyric herbivory) is particularly important in maintaining grass-tree savannas: the elimination of rinderpest in the early 1960s led to explosion of the Serengeti wildebeest population, which elevated the grazing pressure, minimized fire occurrences and grass competition, and promoted the growth of small trees (Sinclair 1979). Generally, the short term effects of fire include increase in grass quality by removing dead plant materials which hinders sunlight reaching the surface (Trollope and Tainton 1986, Trollope 1987). Fire enhances focal grazing in some ecosystems, and results in the maintenance of grazing lawns (McNaughton

1984, Anderson et al. 2006a). These patches will eventually develop into mosaics of disturbed patches across landscapes (Fuhlendorf and Engle 2001, Hassan et al. 2008), which are important in maintaining greater botanical and vegetation structural diversity (Fuhlendorf and Engle 2004). Thus the interaction between herbivory and fire promotes habitat heterogeneity and biological diversity and ecosystem functioning (Knapp and Seastedt 1986, Savage and Swetnam 1990, Fuhlendorf and Engle 2004, Fuhlendorf et al. 2009). Generally, primary productivity in some ecosystems worldwide could have declined if pyric herbivory was excluded in the management protocols of some ecosystems in North America (Boerner 1982), Serengeti grasslands in Africa (McNaughton 1979, McNaughton 1984) and the Taiga forest, Alaska (Van Cleve et al. 1983).

However, despite the importance of fires in savanna grasslands, frequent fires can be detrimental to these habitats. Frequent fires on large amounts of dry weight herbage contribute to a significant loss of total nitrogen content through volatilization (Ojima et al. 1994, Blair 1997, Fynn et al. 2003). In addition, frequent fires in agricultural soils are associated with a decrease in mineralizable nitrogen, and thereby decreasing the extractable mineral nitrogen available (Ojima et al. 1994, Blair 1997, Fynn et al. 2003).

1. 2 Problem statement

Adaptive foraging by herbivores declines with greater restriction on movements, and as a result the viability of wildlife populations is threatened (Hobbs et al. 2008, Hopcraft et al. 2010, Fynn 2012). This restriction on movements also reduces the resilience of vegetation to herbivore impacts. As found in Kruger National Park (South Africa), the establishment of artificial water points removed the spatial refuge provided by natural landscapes leading to competition for resources and declining herbivore populations (Harrington et al. 1999). When artificial water points are established in wet season dryland habitats of herbivores, migrating species are likely to settle in those habitats all year round, and may negatively affect the vegetation structure. Thus, competition for resources may escalate leading to shortage of forage, and mortality of wildlife populations. Predator species may also settle in these areas, and may affect the populations of rare species such as roan and sable which have adapted to utilise habitats distant from permanent water sources (Harrington et al. 1999, Hensman et al. 2013, Haveman 2014).

The northern conservation area of Botswana, extending into protected areas in Namibia and Zimbabwe, is one of the few remaining open wildlife systems in Africa (Fynn and Bonyongo 2011), with a wide diversity of large herbivores and carnivores and with medium and long distance migrations of several herbivore species. To understand what drives these migrations it is critical to have a detailed understanding of the vegetation and soil types, soil fertility and water availability. This information will improve our understanding of functional heterogeneity in the region (Hopcraft et al. 2010, Fynn et al. 2014). This region supports the large African elephant population globally, estimated at 130 000 individuals (Chase 2011, Chase et al. 2016). Owing to this large number of elephants, and buffalo and other herbivores, and their predicted impacts on vegetation in the ecosystem, it is therefore important to understand how spatial heterogeneity translates into functional heterogeneity for herbivores in the region. Herbivores become increasingly coupled to their resources as the opportunity for adaptive foraging declines with greater restrictions on movement and with decreasing heterogeneity (Hobbs et al. 2008, Hopcraft et al. 2010, Fynn 2012). Thus, extensive heterogeneous landscapes, where herbivores are able to move seasonally between functionally-different habitats and avoid heavily-utilized areas and where large distances from permanent water exist, are likely to be more resilient to the impacts of large herbivore populations. This resilience is likely to decline with increasing modification of ecosystems by agriculture, fencing and artificial water provision. Similarly, optimized land use management needs to be based on remote sensing data, combined with field data to create spatial baseline and time-series information. This information is important for conservation planning and implementation for this region. While there are already some useful spatial information products for the region (http://okavangodata.ub.bw/ori/), there have been inadequate studies to generate systematic and comprehensive spatial datasets to cover the entire northern Botswana region. At present, spatial information products are mostly case study based (Neuenschwander et al. 2005, Vanderpost et al. 2011) or largely generalized representations (McCarthy et al. 2005). Spatial analysis techniques involving remote sensing data are valuable in solving land use or land cover related problems such as land use conflicts, degradation and deforestation. They can be used to identify target zones for intervention and to provide scenarios for the improved management of ecosystem resources (Wessels et al. 2007).

Vegetation mapping and classification in northern Botswana will broaden the knowledgebase about this region and will help environmental and conservation policy-makers to formulate and implement policies that will foster interdisciplinary approaches to ecosystem management and increase the efficiency of environmental monitoring efforts. The product of this classification and mapping will also benefit wildlife studies currently being conducted in the region and studies to be carried out in the region in the future.

1.3 Objectives

The general aim of this study was to develop a better understanding of functional heterogeneity in northern Botswana. Such an understanding can only be developed by gaining knowledge of the key ecological gradients in the region and how vegetation, soil nutrient status, moisture
availability and forage quality are distributed along these gradients and, in turn, how different types of herbivores respond to this distribution of resources along these gradients. The study was designed to determine:

1. Key ecological gradients and vegetation types.

- 2. Forage quantity and quality, structure and the seasonal distribution of forage resources on these ecological gradients.
- 3. The effect of herbivory on plant composition, structure and diversity, as mediated by distance to water.
- 4. Habitat selection by zebra and buffalo within this functional heterogeneity of resources on these ecological gradients.

1. 4 Study area

This study was conducted in the Savuti-Mababe-Linyanti ecosystem (SMLE, -18.13-23.27N, -19.48-24.0S, -18.83-24.76E and -18.81-22.87W), northern Botswana (Figure 3), which provides the key ecological features needed to achieve the objectives of this study; an unfragmented ecosystem with key intact ecological gradients and a diverse guild of wildlife species.



Figure 3: Map of SMLE (study area) of northern Botswana

The SMLE is characterized by different vegetation types distributed on key ecological gradients of soil moisture and soil texture/fertility, including permanent swamps, floodplain grasslands and dambo grasslands and dryland woodlands (Sianga and Fynn 2017). Water in the ecosystem originates from the Angolan highlands, then passes through the Okavango Delta, Selinda Spillway, Linyanti Swamps and Savuti Channel, and results in the existence of floodplain grasslands along these water-bodies (Mendelsohn et al. 2010). As a result, herbivores in the SMLE are adapted to use these wetland habitats during the dry season (Figure 4; Smit 2011, Bennitt et al. 2014, Sianga 2014, Sianga and Fynn 2017, Sianga and Fynn in review), as a strategy to enhance intake of protein and minerals (Sianga and Fynn in review).



Figure 4: Dry season habitats in the SMLE, northern Botswana.

Dryland woodlands dominated by a mosaic of Colophospermum mopane or Philenoptera nelsii - Terminalia sericea woodlands (Figure 5) occupy alluvial loam and aeolian sandy soils respectively (Sianga and Fynn 2017), while mixed woodland communities dominated by species such as *Combretum imberbe* occur in old low-lying drainage systems (Mendelsohn et al. 2010). Dryland woodlands farther away from permanent water are key wet season grazing habitats for large herbivores such as buffalo (Bennitt et al. 2014, Sianga 2014, Sianga and Fynn 2017, Sianga and Fynn in review), sable and roan (Hensman et al. 2013, Haveman 2014), and elephants, probably because of the abundance of high quality grasses such as *Digitaria eriantha* and Schmidtia pappophoroides (Figure 5) which experience reduced herbivore pressure closer to permanent water (Sianga et al. 2017b). The Mababe Depression (MD), a large paleolake system, occurs in the terminus portion of the Okavango Delta (Figure 3), and is characterized by clays of lacustrine origin (Baert 1989, Bekker 1990, Teter 2007, Sianga and Fynn 2017), shaping the vegetation types that grow there. These clay soils are dominated by Acacia spp and savanna grasslands (Figure 6) which are of higher quality than the sandveld woodlands (Fynn et al. 2014, Sianga and Fynn 2017).



Figure 5: Wet season habitats in the SMLE, northern Botswana.



Figure 6: Wet season habitats for Plains zebra in the Mababe Depression, northern Botswana.

1. 5 Brief description of the materials and methods

To address the objectives of this study the following key areas were investigated:

1. To determine the key ecological gradients and vegetation types.

The major vegetation units of the SMLE were determined from satellite imagery and field visits and then mapped using Landsat 8 and RapidEye imagery and Maximum Likelihood Classifier. These units were sampled using 40 m x 20 m (800 m²) plots in which cover of all plant species was estimated. Non - Metric Multidimensional Scaling was used to determine gradients influencing the distribution of the communities. 2. To determine forage quantity and quality, structure and the seasonal distribution of forage resources on these ecological gradients.

Forage characteristics (grass greenness, height, biomass and protein) were sampled in four habitat types around the distal reaches of the Tsam Tsam floodplains of the Okavango Delta during the late dry season of 2015; the habitat types were mopane and sandveld woodland farther away from floodplains (two dryland habitat types), sandveld habitats that receive soil moisture inputs from adjacent floodplains (wet sandveld) and sedgeland habitat within the floodplain. Data of grass greenness, height, biomass and protein were subjected to Shapiro-Wilk test (normality) and levene statistic (homogeneity of variance) and failure to meet these assumptions resulted in the use of Kruskal-Wallis test.

3. To determine the effect of herbivory on plant composition, structure and diversity.

Vegetation composition, structure and richness in two different vegetation types (mopane and sandveld woodland) at three distance zones (0-5, 10-15 and > 20 km) from the permanent water of the Okavango Delta and Linyanti Swamps were surveyed. I controlled for environmental effects by selecting only mopane and sandveld woodland because these are dryland plant communities that occur in all three distance zones. Vegetation response of the most abundant species to herbivory in relation to distance from permanent water was modelled, and fire frequency included as a covariate.

4. To determine habitat selection by zebra and buffalo to functional heterogeneity of resources on these ecological gradients.

Three cows and six mares from different herds found during the collaring exercise were fitted with GPS enabled collars to establish their seasonal movement and habitat selection patterns, in relation to a detailed habitat map and according to seasonal changes in forage quality and quantity in the SMLE. GPS coordinates from collars were used to locate positions and habitats used by buffalo and zebra herds during the wet and dry seasons. Forage characteristics (grass greenness, height and biomass) of habitats used by these herbivores were analysed.

Finally the results of these four areas of study were synthesised to provide the main insights and concepts derived from the study.

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Chapter 2

The vegetation and wildlife habitats of the Savuti-Mababe-Linyanti Ecosystem, northern Botswana

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ABSTRACT

This study classified the vegetation of the Savuti-Mababe-Linyanti ecosystem (SMLE, northern Botswana) and developed a detailed map that provides a reliable habitat template of the SMLE for future wildlife habitat use studies. The major vegetation units of the SMLE were determined from satellite imagery and field visits and then mapped using Landsat 8 and RapidEye imagery and Maximum Likelihood Classifier. These units were sampled using 40 x 20 m (800 m²) plots in which cover of all plant species was estimated. Non Metric Multidimensional Scaling (NMS) demonstrated that plant communities were determined by gradients in soil texture/fertility and wetness. NMS axis 1 represented a gradient of soil texture with seven woodland communities on sandy soils (sandveld communities and Baikiaea forest) dominated by *Baikiaea plurijuga* in Baikiaea forest and *Terminalia sericea* and *Philenoptera nelsii* in sandveld, with various indicator species differentiating the various sandveld community types. Mopane woodland further from and riparian woodland adjacent to permanent water was common on less sandy alluvial soils. Mineral-rich heavy clay soils in the sump of a large paleolake system support open grassland and Acacia savanna, with the mineral rich soils supporting grasses high in minerals such as P, Ca, Na and K and thus this region is a critical wet season range for migratory zebra. Taller high-quality grasses in the mosaic of sandveld and mopane woodland communities provides critical grazing for taller grass grazers such as buffalo, roan and sable antelope, while wetland communities provide reliable green forage during the dry season for a variety of herbivores, including elephant. This study has provided a detailed classification and mapping of wildlife habitats of the SMLE, which can be used for conservation planning and animal habitat use studies and acts a base paper for these studies.

Key words: Drylands, functional habitat heterogeneity, multivariate analysis, plant communities, savanna, vegetation classification and wetlands

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Introduction

There is growing recognition of the importance of spatial heterogeneity in determining biodiversity (MacFayden et al. 2016) and in determining adaptive foraging options for herbivores (Owen-Smith 2004; Hobbs et al. 2008; Hopcraft et al. 2010) and predators (Hopcraft et al. 2005) and for facilitating predation avoidance and avoidance of competition among guilds of herbivores or carnivores (Mills & Gorman 1997; Rettie & Messier 2000). Spatial heterogeneity is strongly associated with vegetation heterogeneity and detailed vegetation maps derived from remote-sensed spectral variation are likely to represent a large proportion of spatial heterogeneity (MacFayden et al. 2016). Plant community variation on environmental gradients is associated with complex combinations of environmental factors and associated plant species composition, richness and physiognomy, leading to distinct habitat attributes for animals such as seasonal resources, predation avoidance and shelter (Hopcraft et al. 2010; Fynn et al. 2014). Functional differences among different plant communities in meeting the seasonally varying needs of animals has been referred to as functional habitat heterogeneity and plays a key role in determining the viability of herbivore populations (Owen-Smith 2004; Hopcraft et al. 2010). Environmental factors such as soil fertility, forage quality and water availability, which co-vary strongly with vegetation, may also influence human settlement, crop field and livestock distribution patterns.

Development of detailed vegetation maps is, therefore, essential for (i) understanding the distribution of biodiversity across a region, (ii) research on wildlife species home range and habitat use, (iii) conservation planning and (iv) understanding socio-ecological interactions. Vegetation maps are especially useful for determining seasonal habitat use of collared wildlife species where thousands of GPS locations may be obtained from a collared animal, which cannot

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easily be followed up on, especially in vast wilderness regions with little road access, such as in northern Botswana. Currently, no detailed vegetation map exists for northern Botswana with the best available product being the elephant habitat map of northern Botswana, which lacks the detail and accuracy needed for comprehensive wildlife habitat use studies (Ringrose 2006).

A key region for wildlife in northern Botswana is the regional scale contrast of extensive floodplains of the Okavango Delta and the Linyanti Swamps with the vast woodland systems adjacent these wetland systems. The Savuti-Mababe-Linyanti ecosystem (SMLE) with its extensive wetlands and woodlands and the open grasslands of the Mababe Depression has excellent functional habitat heterogeneity for wildlife (Fynn *et al.* 2014), as well as great aesthetic features for tourism, providing the basis for it forming the core region for wildlife and tourism in Botswana. Thus the SMLE is a region of key conservation importance being one of the few remaining relatively unfragmented ecosystems in Africa with important heterogeneity of seasonal habitats that support a wide diversity of wildlife species, including important populations of rare species such as wild dog, eland, sable and roan antelope, as well as long-range migrations of several herbivore species (Sianga 2014; Fynn *et al.* 2014; Naidoo *et al.* 2014).

Thus apart from the need for a detailed vegetation classification and habitat map for conservation planning in the SMLE and for future wildlife habitat use studies in the region, this paper provides baseline ecosystem-level data on the SMLE, which allows the various herbivore and carnivore studies to be analysed in relation to the same habitat map.

The objectives of this study were to (i) classify the vegetation of the SMLE of northern Botswana, (ii) develop a detailed vegetation map that provides a reliable habitat template of the SMLE for wildlife habitat use studies and for future studies and (iii) discuss how the heterogeneity in vegetation and soils of the SMLE contribute to functional habitat heterogeneity for wildlife.

Materials and methods

Study area

This study was done in the Savuti-Mababe-Linyanti ecosystem (SMLE), northern Botswana (Figure 1), an extensive region of woodlands and open grasslands wedged between two major wetland systems - the Okavango Delta and the Linyanti Swamps. The SMLE is characterized by a semi-arid climate with annual rainfall of 500 mm in the western side (Okavango Delta) and increasing eastwards to around 600 mm (Chobe Enclave region) (Botswana Meteorological Services). The climate is characterized by a wet season (December-April), cool, early dry season (May-August) and a hot, late dry season (September-November) where daily maximum temperatures are regularly between 35 to 40 °C at this time (September-November) (Fynn et al. 2014). Water originating from the Angolan highlands into the ecosystem through the Okavango Delta, Linyanti Swamps, Selinda Spillway and Savuti Channel leads to the development of extensive floodplain grasslands and swamps adjacent the extensive woodland systems (Mendelsohn et al. 2010). Alluvial clays and aeolian sands in the ecosystem are occupied by Colophospermum mopane and Philenoptera nelsii-Terminalia sericea woodlands (dryland woodlands) respectively (Wolski & Murray-Hudson 2006) and low-lying drainage systems are dominated by woodlands of mixed communities (Combretum imberbe and others) (Mendelsohn et al. 2010). A large paleolake system known as the Mababe Depression (MD) (Figure 1), characterized by clays of lacustrine origin, occurs between the Okavango Delta and the Chobe region (Teter 2007). The extremely high clay soils of the MD provide key habitat heterogeneity

in the general landscape of the SMLE, which is dominated by Kalahari sands. Vegetation on the clay soils of the MD is characterized by open *Acacia spp*. savanna grasslands and higher forage quality (Fynn *et al.* 2014).



Figure 1. Study area depicting the SMLE ecosystem and locations of sampling positions.

Vegetation sampling

Vegetation composition was sampled using 40 x 20 m (800 m²) plots during the wet seasons of 2014 and 2015, with sampling conducted from January to the end of March to ensure plants had attained inflorescences for easier identification. Certain remote habitats on the MD on water-

logged heavy clay soils were inaccessible during the wet season and could only be sampled during the early dry season (April- mid May) once the soils had dried out. Plots were stratified within homogenous vegetation units (determined visually by extensive field surveys of the region) to ensure adequate sampling of all key vegetation types within the study area (Figure 1). 801 plots were located using two random numbers between 20 and 100, with the first random number taken along an access route such as a road and the second perpendicular from the road into the plant community. Plots were generally spaced at least 500 m apart in each plant community. The GPS coordinates of each plot were recorded using a Garmin GPS Map 62s. All plants (trees, grasses and forbs) rooted in the plots were identified, recorded and their percentage cover estimated. Unknown plants were pressed in the field and brought to the Peter Smith Herbarium (PSUB) collection at the Okavango Research Institute (Maun, Botswana) for identification. Nomenclature for all species follows (http://www.theplantlist.org). Five soil samples collected in each plot were mixed to form a composite sample which was brought to the Okavango Research Institute laboratory for textural and nutrients analysis.

Vegetation classification

The data for all 801 vegetation plots (% cover abundance of species, soil texture and nutrients) was standardized using relativizations by maximum in Principal Component Ordination 6 (PCORD) (McCune *et al.* 2002). These data was subjected to hierarchical cluster analysis (β linkage, β = -0.25, Sorensen distance) in PCORD 6 (McCune *et al.* 2002) comprising of species (505 species) occurring at more than one site based on species distribution across 801 plots. Indicator species analysis (ISA) (Dufrene & Legendre 1997) was used to identify levels to define ecological meaningful communities, and indicator values (IVs) were examined for statistical

significance in Monte Carlo technique in PCORD 6 (McCune *et al.* 2002). Differences between communities were examined using Multi-Response Permutation Procedure (MRPP) using Sorensen distance measure (McCune *et al.* 2002). In addition, non-metric multidimensional scaling (NMS) was used to plot the communities in ordination space in relation to key orthogonal gradients in the vegetation data using PCORD 6 (McCune *et al.* 2002). Such gradients are likely related to key environmental drivers and thus provide insights into how plant communities are structured in the ecosystem.

Vegetation mapping

Owing to the vast size of the SMLE, we were unable to purchase detailed RapidEye imagery for the entire ecosystem and thus purchased RapidEye imagery to map the core area of the ecosystem where we needed most detail for several herbivore studies currently being conducted there and then used Landsat 8 imagery to map the remainder of the ecosystem. A RapidEye composite image composed of 34 tiles and wet season Landsat Enhanced Thematic Mapper scenes from Earth Explorer USGS of the study area were radiometrically and atmospherically corrected in ENVI 4.8 (ENVI 2010). The Landsat images were mosaicked using seamless mosaic and Maximum Likelihood Classifier (supervised classification) in ENVI 4.8 (ENVI 2010) was used to map a subset of the 15 vegetation classes identified in the vegetation classification (reasons for mapping of a subset rather than all 15 vegetation classes is given in the results). A corrected RapidEye image was also mapped using Maximum Likelihood Classifier in ENVI 4.8 (ENVI 2010). The two classified images were seamlessly mosaicked together, and an area of interest was extracted by mask in ArcMap 10.2 (ESRI 2010). The area of each habitat was computed and converted into a minimum mapping unit in ArcMap 10.2 (ESRI 2010).

Results

Mapping

For mapping purposes we required a habitat map that presented functionally distinct classes for herbivores. Thus we grouped functionally similar classes (which, in addition, were generally difficult to distinguish from each other through remote sensing and thus difficult to map as separate communities) described by the cluster analysis (Figure S1 & Figure 2) and shown in the NMS (Figure 3). For example, the six sandveld types are not easily distinguished from each other through remote sensing and are functionally similar for herbivores, thus they can be mapped as one unit. By contrast, the communities on alluvial soils were very different functionally (eg wetland vs. mopane or riparian forests vs. dry floodplains) and could be easily distinguished through remote sensing and thus were be mapped separately. With regards the communities on heavy lacustrine clay soils two distinct functionally different communities occur, (i) the short acacia grasslands on silty soils and (ii) the tall open grasslands on vertisols (the communities on vertisols were difficult to distinguish through remote sensing), thus functionally for herbivores we chose to map them as two classes. Map accuracy was about 70 % (Table 1).



Figure 2. Map of Savuti-Mababe-Linyanti ecosystem Vegetation (northern Botswana).

Table 1: Accuracy assessment of a classified map of the SMLE

Overall Accuracy = 69.47 % (339/488)

• Kappa Coefficient = 0.644

Habitat	Producer accuracy	User	Producer	User accuracy
	(%)	accuracy (%)	accuracy	(Pixels)
			(pixels)	
Acacia grasslands	76.47	55.32	26/34	26/47
Baikiaea forests	94.29	73.33	33/35	33/45
Dry floodplains	68.18	71.43	30/44	30/42
Mopane	62.50	62.50	45/72	45/72
Riparian	56.57	68.29	56/99	56/82
Sandveld	61.21	73.96	71/116	71/96
Tall open grasslands	95.56	81.13	43/45	43/53
Wetland	81.40	68.63	35/43	35/51

Classification

A coincident minimum of ISA *p*-value and maximum number of significant indicator species was found at 7 and 9 communities. Another coincident minimum ISA *p*-value and maximum number of significant indicator species was found at 15 communities and was considered a meaningful ecological level of communities for a detailed vegetation classification. Thus hierarchical cluster analysis done on all 801 vegetation plots recognized 15 main vegetation communities within which many sub-communities occurred (Figure S1). MRPP tests of 15 communities suggested significant differences between communities (P < 0.000, Table S1) with chance-corrected within group agreement, A = 0.265. Pairwise comparisons between communities suggested significant differences (P < 0.000, Table S1).

The first axis of the non-metric multidimensional scaling analysis (NMS1) appears to be a gradient of soil texture and fertility, with communities on the most sandy contents having the most negative values, communities on loam soils having intermediate values and communities on extremely high-clay contents having the most positive values on NMS1, respectively (Figure 3; Table 2). The second NMS axis (NMS2) appears to be a weak gradient of wetness with communities having the most positive values on NMS2 being communities that receive some sort of seasonal flooding from the annual flood pulse into the Okavango and Linyanti systems (*Setaria sphacelata - Gomphocarpus fruticosus* community) or seasonal rainfall (*Setaria incrassata - Dichanthium annulatum* community) or occur near permanent water with perhaps a shallow water table (*Tribulus terrestris - Senna obtusifolia* community) (authorities for plant species names are according to http://www.theplantlist.org).



Figure 3. Non-metric multidimensional scaling (NMS) ordination of plant communities against soil particle sizes and soil nutrients. This analysis was done on 801 plots. ICOA - Ipomoea chloroneura - Oxygonum alatum; CMJS - Colophospermum mopane - Jasminum stenolobum; EPOP - Eragrostis pallens - Ochna pulchra; CACC - Commiphora angolensis - Combretum collinum; SIDA - Setaria incrassata - Dichanthium annulatum; CVBC - Chloris virgata - Boerhavia coccinea; CCAM - Cenchrus ciliaris - Acacia mellifera; BIRM - Bothriochloa insculpta - Rhynchosia minima; BNCH - Brachiaria nigropedata - Combretum hereroense; TTSO - Tribulus terrestris - Senna obtusifolia; CMSV - Croton megalobotrys - Setaria verticillata; SSGF - Setaria sphacelata - Gomphocarpus fruticosus; JDES - Justicea divaricata - Eragrostis superba; BADG – Boscia albitrunca - Dactyloctenium giganteum; BPBM -Baikiaea plurijuga - Baphia massaiensis.

	Ν	Phosphorus	Potassium	Sodium	Calcium	Magnesium	Sand	Silt	Clay
Community		Mean±SE	Mean±SE	Mean±SE	Mean±SE	Mean±SE	Mean±SE	Mean±SE	Mean±SE
Baikiaea plurijuga - Baphia massaiensis	9	6.5±0.3	412.2±69.3	74.3±4.2	217.5±29.7	135.3±7.8	96.5±0.4	1.4 ± 0.1	2.1±0.2
Ipomoea chloroneura - Oxygonum alatum	16	5.6±0.6	154.9±22.9	66.0±6.7	133.5±19.7	121.3±2.5	97.6±0.2	0.9±0.1	1.4 ± 0.2
Eragrostis pallens - Ochna pulchra	14	6.7±1.2	357.7±68.9	74.2±6.2	321.8±33.5	130.4±10.9	95.6±0.7	2.3±0.5	2.0±0.2
Commiphora angolensis - Combretum collinum	5	4.4±0.2	108.9±21.9	60.2±4.8	156.4±20.5	137.5±5.1	95.3±0.4	0.7±0.3	0.2 ± 0.1
Boscia albitrunca - Dactyloctenium giganteum	20	9.9±4.1	756.6±61.7	75.2±3.0	380.6±56.7	233.3±21.0	95.1±0.4	2.1±0.2	2.8±0.3
Brachiaria nigropedata - Combretum hereroense	8	6.0±0.2	856.4±38.6	70.1±4.9	332.3±18.3	238.8±9.8	93.9±0.5	3.2±0.3	2.8±0.2
Tribulus terrestris - Senna obtusifolia	4	6.8±2.4	226.8±24.9	82.6±5.9	360.2±13.0	130.5±3.9	93.6±1.7	3.1±1.3	2.3±0.4
Colophospermum mopane - Jasminum stenolobum	30	5.1±0.3	662.8±46.3	90.3±4.4	459.7±63.1	169.6±9.7	91.8±0.5	4.5±0.3	3.7±0.3
Setaria sphacelata - Gomphocarpus fruticosus	4	17.7±4.7	2715.8±1322.3	134.1±24.4	5981.0±3017. 5	716.3±260.7	68.7±15.2	11.9±5.5	19.3±9.7
Justicea divaricata - Eragrostis superba	26	10.0±1.8	396.1±58.1	93.7±13.6	875.6±357.2	150.9±14.3	92.7±0.9	4.0±0.6	3.3±0.4
Croton megalobotrys - Setaria verticillata	8	25.4±9.3	777.9±78.1	87.5±5.1	1460.9±172.9	191.1±20.6	89.4±0.7	4.0±0.4	6.5±0.7
Chloris virgata - Boerhavia coccinea	16	18.3±3.7	1683.9±205.8	203.3±60.7	1765.8±446.4	248.2±63.2	79.8±2.9	11.8±1.6	8.4±1.5
Cenchrus ciliaris - Acacia mellifera	10	11.9±3.7	4750.5±378.6	206.7±7.5	6018.2±331.2	329.3±19.4	25.2±6.5	44.2±4.1	30.5±3.7
Bothriochloa insculpta - Rhynchosia minima	8	11.7±2.0	9819.7±191.5	176.5±7.5	5842.1±244.5	488.9±46.7	9.1±1.1	48.4±1.4	42.5±1.1
Setaria incrassata - Dichanthium annulatum	5	8.5±0.9	3862.4±1294.1	101.1±32.8	5892.7±2211.	729.3±260.8	61.3±12.5	19.6±5.9	19.1±6.6

Table 2: Soil texture and nutrients characteristics in the SMLE, northern Botswana

Vegetation on Kalahari sands

The NMS (Figure 3) delineated several vegetation communities in the SMLE that occur on deep Kalahari sands and they appear to be differentiated according to subtle variation in the silt and clay content of the soil (Table 2). In the vegetation/habitat map, we refer to these communities on deep sands as sandveld communities (Figure 2). Although *Baikiaea plurijuga – Baphia massaiensis* is also found on deep sands (Table 2), we refer to it in the map as Baikiaea forest not sandveld (Figure 2).

Baikiaea plurijuga - Baphia massaiensis

This community is associated with high sand and low-clay contents (Table 2). The community is extensive and occurs from northern edge of the beachhead of the MD near Ghoha hills and extends east all the way north east into Zimbabwe (Figure 2). It is also found in small patches near the eastern edge of the Okavango Delta from the Tsam Tsam floodplains to the Vumbura-Motswiri region and in the woodlands west of the Kwando system (Figure 2). Indicator species include *Baikiaea plurijuga*, *Baphia massaiensis*, *Croton gratissimus*, *Hibiscus lobatum*, *Panicum maximum*, *Thunbergia reticulata* and *Combretum apiculatum* (Table 3). Baikiaea forests, while not supporting a high density of herbivores, are critical habitats for rare herbivores such as roan and sable antelope, and thus play a key role in the functional heterogeneity of the region (K. Sianga, personal observation).

Indicator species	Indicator values	P-value
	Baikiaea plurijuga - Baphia massaiensis	
Baikiaea plurijuga	98.7	0.00
Baphia massaiensis	70.2	0.00
Croton gratissimus	65.9	0.00
Hibiscus lobatum	48.8	0.00
Panicum maximum	39.7	0.00
Thunbergia reticulata	38.6	0.00
Combretum apiculatum	34.2	0.00
Vigna stenophylla	22.5	0.00
Dipcadi marlothii	22.2	0.00
Citrullus lanatus	20.8	0.00
Cyperus margaritaceus	14.9	0.01
Merremia pinnata	11.5	0.03
Ledebouria revoluta	10.3	0.03
	Ipomoea chloroneura - Oxygonum alatum	
Ipomoea chloroneura	66.5	0.00
Oxygonum alatum	66	0.00
Hibiscus mastersianus	55.8	0.00
Charmocresta stricta	55.24	0.00
Erlangea misera	54.4	0.00
Pavania senegalensis	45.4	0.00
Charmocresta absus	32.4	0.00
Ceratotheca sesmoides	25.2	0.00
Basananthe pedata	21.4	0.00
Philenoptera nelsii	20.4	0.00
	Eragrostis pallens - Ochna pulchra	
Eragrostis pallens	50	0.00
Ochna pulchra	41.2	0.00
Burkea africana	31.2	0.00
Aristida stipitata	32	0.00
Phyllanthus burchellii	32.8	0.00
Phyllanthus mendesii	29.6	0.00
Digitaria eriantha	18.1	0.00
Dicoma schinzii	18.1	0.01
Euphorbia crotonoides	11.1	0.05
•	Commiphora angolensis - Combretum collinum	
Commiphora angolensis	94.6	0.00
Combretum collinum	80.8	0.00
Acacia ataxacantha	76.1	0.00
Combretum molle	73.7	0.00
comoremant mone	15.1	0.00

Table 3: Indicator species characteristics for 15 class divisions of plant communities in the SMLE (northern Botswana).

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Evolvulus alsinoides	73.4	0.00
Neorautanenia amboensis	73.3	0.00
Xenostegia tridentata	72.1	0.00
Waltheria indica	68.7	0.00
Ochna serrulata	65.4	0.00
Bauhinia petersiana	52	0.00
Duosperma crenatum	48.8	0.00
Acanthosicyos naudinianus	45.4	0.00
Commiphora africana	42.6	0.00
	Boscia albitrunca - Dactyloctenium giganteum	
Boscia albitrunca	44	0.00
Dactyloctenium giganteum	35.6	0.00
Indigofera flavicans	33	0.00
Sida chrysantha	27.4	0.00
Mundulea sericea	21.3	0.00
Ocimum gratissimum	20	0.01
Digitaria ternata	15.5	0.01
Cleome hirta	12.5	0.04
	Brachiaria nigropedata - Combretum hereroense	
Brachiaria nigropedata	85.6	0.00
Combretum hereroense	68	0.00
Lantana angolensis	65	0.00
Andropogon gayanus	63.2	0.00
Dalbergia melanoxylon	55.8	0.00
Schmidtia pappophoroides	46.5	0.00
Polydora poskeana	33.9	0.00
Acacia erioloba	32.7	0.00
Anthephora pubescens	31.2	0.00
Aristida stipoides	24.8	0.00
	Tribulus terrestris - Senna obtusifolia	
Tribulus terrestris	70.5	0.00
Senna obtusifolia	36.7	0.00
Sida cordifolia	33.8	0.00
Commelina benghalensis	23	0.00
Dichrostachys cinerea	22.5	0.02
Zehneria marlothii	17.1	0.01
Gloriosa superba	15.9	0.02
(Colophospermum mopane - Jasminum stenolobum	
Colophospermum mopane	76	0.00
Jasminum stenolobum	54.6	0.00
Tragus berteronianus	50.2	0.00
Zornia glochidiata	46.4	0.00
Kyllinga buchananii	43.5	0.00

Commelina forskaolii	41.7	0.00
Aristida adscensionis	36.9	0.00
Brachiaria deflexa	36	0.00
Ipomoea plebiea	30.3	0.00
Ipomoea coptica	27.8	0.00
Cyperus esculentus	24	0.01
Pycreus macrostachyos	21.6	0.01
Clerodendrum ternatum	18.3	0.02
Ampeloscissus africana	12.8	0.02
Barleria mackenii	12.3	0.03
	Setaria sphacelata - Gomphocarpus fruticosus	
Setaria sphacelata	99	0.00
Gomphocarpus fruticosus	96.2	0.00
Cyperus longus	89.2	0.00
Crotalaria platysepala	83	0.00
Momordica balsamina	80.5	0.00
Sesamum triphyllum	67.8	0.00
Bulbostylis hispidula	66.1	0.00
Cymbopogon caesius	56	0.00
Limeum viscosum	49	0.00
Melinis repens	30.4	0.00
Acrotome inflata	28.6	0.00
Urochloa trichopus	24.4	0.00
	Justicea divaricata - Eragrostis superba	
Justicea divaricata	21.1	0.01
Eragrostis superba	15.8	0.02
Eragrostis trichophora	14.7	0.01
Geigeria schinzii	13.9	0.01
Orthanthera jasminiflora	13	0.04
Justicia betonica	12.7	0.02
Imperata cylindrica	11.7	0.03
Polygonum decipiens	11.7	0.02
	Croton megalobotrys - Setaria verticillata	
Croton megalobotrys	92.6	0.00
Setaria verticillata	76.6	0.00
Diospyros mespiliformis	64.5	0.00
Philenoptera violacea	57.2	0.00
Acacia nigrescens	62.1	0.00
Asystasia gangetica	54.8	0.00
Astripomoea lachnosperma	49.2	0.00
Blainvillea acmella	44.4	0.00
Berchemia discolor	43.7	0.00
Acalypha indica	42.5	0.00

Combretum mossambicense	39.4	0.00
Cocculus hirsutus	37.7	0.00
Hibiscus ovalifolius	37.5	0.00
Blepharis Maderaspatensis	35.9	0.00
	Chloris virgata - Boerhavia coccinea	
Chloris virgata	74.8	0.00
Boerhavia coccinea	52.3	0.00
Acacia tortilis	33.7	0.00
Hermannia kirkii	31.8	0.00
Acacia hebeclada	29.4	0.00
Cucumis anguria	28.2	0.00
Dicoma tomentosa	26.7	0.00
Aerva leucura	26.4	0.00
	Cenchrus ciliaris - Acacia mellifera	
Cenchrus ciliaris	76.5	0.00
Acacia mellifera	67.9	0.00
Indigofera scaberrima	20.8	0.00
Euphorbia polycephala	20.1	0.00
	Bothriochloa insculpta - Rhynchosia minima	
Bothriochloa insculpta	57.6	0.00
Rhynchosia minima	39.4	0.00
Cyathula orthacantha	34	0.00
Leonotis nepetifolia	32.2	0.00
Dinebra retroflexa	30.6	0.00
	Setaria incrassata - Dichanthium annulatum	
Setaria incrassata	99.9	0.00
Dichanthium annulatum	92.3	0.00
Enicostema axillare	70.3	0.00
Panicum coloratum	63.2	0.00
Cynodon dactylon	53.8	0.00
Digitaria milanjiana	34.5	0.00
Aristida scrabrivalvis	28.5	0.00
Indigofera schimperi	28.4	0.00
Aristida hordeacea	20.1	0.00
Bracharia eruciformis	15.4	0.01
Brachiaria retiforms	14.9	0.01

Apart from Baikiaea forest on deep sands, there are six communities which we have collectively mapped as sandveld (Figure 2) and these are discussed below (in order of increasing NMS axis 1 value):

Ipomoea chloroneura - Oxygonum alatum

This is one of the most extensive communities occurring on deep sands, where aeolian sands have infilled ancient river channels among the alluvial soils (supporting mopane) in the extensive woodlands between the Okavango Delta and the Linyanti Swamps (Figure 2). This community is associated with soils of among the highest sand and lowest silt and clay contents, as well as lowest phosphorus, potassium, sodium and magnesium contents (Table 2) and is recognized by the dominance of *Terminalia sericea* in the woody layer. It is one of the most important wet-season habitats for several tall grass grazers because of the abundance of high-quality tall grasses such as *Digitaria eriantha*. Indicator species in this community are *Ipomoea chloroneura*, *Oxygonum alatum*, *Hibiscus mastersianus*, *Chamaecrista stricta*, *Erlangea misera*, *Chamaecrista absus*, *Ceratotheca sesmoides*, *Philenoptera nelsii*, *Pavonia senegalensis* and *Basananthe pedata* (Table 3).

Eragrostis pallens - Ochna pulchra

Similar to the *Ipomoea chloroneura - Oxygonum alatum* community, the *Eragrostis pallens - Ochna pulchra* community is associated with soils among the highest sand and low phosphorus, potassium, sodium and magnesium content (Table 2). Like the previous community, it is recognized by the dominance of *Terminalia sericea* in the woody layer but *Eragrostis pallens*, *Ochna pulchra*, *Burkea africana*, *Aristida stipitata*, *Phyllanthus burchellii*, *Digitaria eriantha*,

Dicoma schinzii, Euphorbia critonoides and *Phyllanthus mendesii* are some of the characteristic species which separate it from the previous community (Table 3).

Commiphora angolensis - Combretum collinum

This community is spatially separated from other sandveld communities being found only south east of the MD and appears to be an extensive Kalahari community, extending towards Nxai Pan and the Central Kalahari Game Reserve (Figure 2). It is associated with the lowest clay contents and highest sand contents, as well as low phosphorus, potassium, sodium and magnesium contents (Table 2) and is characterized by woody species not seen in typical sandveld communities west of the MD, such as Commiphora angolensis, Combretum collinum and Acacia ataxacantha. This communities position in the NMS (Figure 3), however, suggests that its plant composition is more similar to communities with intermediate clay content and we suspect, therefore, that either there is more clay in the subsoil (we only sampled the topsoil) or the sands are not as deep as in the previous two communities. The structure is also different from the other sandveld types, which are relatively tall woodland, whereas Commiphora angolensis -*Combretum collinum* sandveld is more of a shrubland, which may also suggest that the soils are not as deep. Indicator species include Commiphora angolensis, Combretum collinum, Acacia ataxacantha, Combretum molle, Evolvulus alsinoides, Neorautanenia amboensis, Xenostegia tridentata, Waltheria indica, Ochna serrulata, Bauhinia petersiana, Duosperma crenatum, Acanthosicyos naudinianus and Commiphora africana (Table 3). It serves as a key wet season habitat for tall grass grazers such as buffalo, eland and roan antelope, probably because it occurs far from any permanent water sources (Figure 2) and, therefore, has amongst the highest cover of the high-quality grass *Digitaria eriantha*.

Boscia albitrunca - Dactyloctenium giganteum

This community, although still a sandveld community on sandy soils, was associated with higher clay and calcium and phosphorus than other sandveld types (similar to *Brachiaria nigropedata - Combretum hereroense* community in clay content) (Table 2). It is mainly found around the peripheries of Paleolake Mababe (MD) (Figure 2), where there was some moderate deposition of clay and silt by paleolake waters. Indicator species are *Boscia albitrunca*, *Dactyloctenium giganteum*, *Indigofera flavicans*, *Sida chrysantha*, *Mundulea sericea*, *Ocimum gratissimum*, *Digitaria ternata* and *Cleome hirta* (Table 3). There is an abundance of the high-quality grazing grass *Dactyloctenium giganteum* which, together with the important browse provided by *Boscia albitrunca*, results in this community type being a key wet season habitat for herbivores such as buffalo and a dry season habitat for eland and other browsers in the SMLE.

Brachiaria nigropedata - Combretum hereroense

The Brachiaria nigropedata - Combretum hereroense community, like the Boscia albitrunca -Dactyloctenium giganteum community was associated with some moderate degree of ancient sediment deposition in the peripheries of Paleolake Mababe and around the Kwando-Linyanti system, resulting in more clay than in the other sandveld community types (Table 2). It serves as a key wet season habitat for buffalo because of an abundance of one of their most favoured grasses, Brachiaria nigropedata. Indicator species include Brachiaria nigropedata, Combretum hereroense, Lantana angolensis, Andropogon gayanus, Dalbergia melanoxylon, Schmidtia pappophoroides and Polydora poskeana (Table 3).

Tribulus terrestris - Senna obtusifolia

The *Tribulus terrestris* – *Senna obtusifolia* community occurs on deep sands but always adjacent to riparian vegetation (*Croton megalobotrys - Setaria verticillata* and *Justicea divaricata - Eragrostis superba* communities) found near water bodies of the Okavango Delta, Linyanti Swamps, Selinda Spillway and Savuti Channel. Although the sands of this community are deep, they have higher clay content (Table 2), which again is likely associated with ancient sediment deposition from previous water bodies or extreme floods. This community is recognized by the dominance of the woody layer by tall *Philenoptera nelsii* (Kalahari appleleaf) and with very little *Terminalia sericea* occurrence (as opposed to other sandveld communities where *Terminalia sericea* is common), which is likely because of the higher clay content. Indicator species included *Tribulus terrestris*, *Senna obtusifolia*, *Sida cordifolia*, *Dichrostachys cinerea* and *Zehneria marlothii* (Table 3).

Vegetation on alluvial loam soils

These communities occur at intermediate levels of silt and clay (as compared to the lower levels of silt and clay of the sandveld communities) as a result of ancient alluvial deposition of sediments.

Colophospermum mopane - Jasminum stenolobum

This community is recognized by the dominance of the woody layer by *Colophospermum mopane*, which appears to dominate once the clay content of the soil reaches a critical level but not too high where other communities exist (Table 2). This is an extensive community that occurs all over the ecosystem, near and further from permanent water (Figure 2). Seasonal waterholes occur in this community and serve as drinking points for various herbivores during

the wet season and grasses, while sparse are often palatable. Indicator species in mopane woodland include *Colophospermum mopane*, *Jasminum stenolobum*, *Tragus berteronianus*, *Zornia glochidiata*, *Kyllinga buchananii*, *Brachiaria deflexa* and *Aristida adscensionis* (Table 3).

Setaria sphacelata - Gomphocarpus fruticosus

This community was associated with high silt-clay and intermediate sand contents (Table 2) but the key feature driving species composition is that it is seasonally inundated by floodwaters from the major wetland systems of the region. The community is common in moderately-flooded zones within the overall wetland system shown in the map (Figure 2). However, our focus was on the dryland communities and our sampling regime in wetlands was limited and not designed to capture the variation in wetland community composition on flooding depth and duration gradients so this community represents one of many different wetland community types. Characteristic species of this community type included *Setaria sphacelata*, *Gomphocarpus fruticosus*, *Cyperus longus*, *Crotalaria platysepala*, *Momordica balsamina*, *Sesamum triphyllum* and *Bulbostylis hispidula* (Table 3). Wetlands provide critical dry season grazing for herbivores because of their shallow water tables and the ability to provide green forage for herbivores during the dry season.

Justicea divaricata - Eragrostis superba

This is an open grassland community found directly adjacent to floodplains (mapped as dry floodplains in the map) along the major water bodies (Figure 2) and is associated with moderate silt-clay, and but intermediate sand, phosphorus, potassium and calcium contents (Table 2). Although this community is rarely (if ever) subject to flooding, it is probably maintained in a

treeless state by high water tables from the adjacent floodplains. Indicator species include *Justicea divaricata, Eragrostis superba, Eragrostis trichophora, Geigeria schinzii, Orthanthera jasminiflora* and *Justicia betonica* (Table 3).

Croton megalobotrys - Setaria verticillata

This is a riparian woodland community (Figure 2) and it is associated with the highest clay content of the alluvial soil communities (Table 2). Species including *Croton megalobotrys*, *Setaria verticillata*, *Diospyros mespiliformis*, *Philenoptera violacea*, *Acacia nigrescens* and *Asystasia gangetica* characterized this community (Table 3). Riparian woodlands can occur as open or closed woodlands. Open riparian woodlands are structurally characterized by open canopy woodlands dominated by *Philenoptera violacea*, *Acacia nigrescens* and *Combretum imberbe* while closed riparian woodlands are characterized by tall closed canopy woodlands dominated by *Croton megalobotrys*, *Diospyros mespiliformis*, *Philenoptera violacea*, *Acacia nigrescens*, *Acacia nigrescens*, *Acacia nigrescens*, and *Combretum imberbe*. In the map these two riparian woodland communities were mapped as riparian woodlands (Figure 2).

<u>Vegetation on heavy clay lacustrine deposits of the sump of the Mababe Depression (MD)</u>

Chloris virgata - Boerhavia coccinea

The *Chloris virgata – Boerhavia coccinea* community occurs on the more silty, intermediate clay soils on the edge of the sump of the MD (as well as in areas adjacent the Linyanti Swamps and Kwando River) and was associated with high silt, phosphorus and calcium (Table 2). It is included under Acacia grasslands in the vegetation map (Figure 2), which is a widespread community that develops where the clay content reaches higher levels than that found in alluvial

soils. Thus this community type is associated with water bodies that could have deposited those clays such as the Paleo-lake Mababe or the Kwando/Linyanti Swamps (Figure 2). This community was characterized by *Chloris virgata*, *Boerhavia coccinea*, *Acacia tortilis*, *Hermannia kirkii*, *Acacia hebeclada*, *Cucumis anguria*, *Dicoma tomentos*a, and *Aerva leucura* (Table 3). The community is dominated by the highly palatable annual grasses, *Chloris virgata* and *Urochloa trichopus*, and forms a critical wet season grazing resource on the edge of the sump of the MD for migratory zebra, as well as for tsessebe, impala and wildebeest. One of the key functional features of this community for herbivores is that it offers the highest phosphorus levels in soils and grasses of all community types in the ecosystem (Table 2).

As one moves off the silty soils on the edge of the sump of the MD, which support the *Chloris virgata - Boerhavia coccinea* community, towards the centre of the MD, soils become deep, heavy black vertisols dominated by taller grasses such as *Cenchrus ciliaris* and *Bothriochloa insculpta*. The vegetation on these vertisols is mapped as tall open grasslands (Figure 2) and consists of two main communities, (i) the *Cenchrus ciliaris – Acacia mellifera* community and (ii) the *Bothriochloa insculpta – Rhynchosia minima* community:

Cenchrus ciliaris - Acacia mellifera

This open savanna grassland community occurs on deep black-clay soils (Vertisols) deeper into the MD and was associated with among the lowest sand content and highest silt-clay content and importantly had by far the highest soil calcium and potassium content in the SMLE (Table 2). Indicator species are *Cenchrus ciliaris*, *Acacia mellifera*, *Indigofera scaberrima* and *Euphorbia polycephala* (Table 3). The very high soil fertility of the *Cenchrus ciliaris* - *Acacia mellifera* community (Table 2), makes this habitat, together with the *Chloris virgata* – *Boerhavia coccinea* community, which are directly adjacent to each other, an extremely important wet season range for the large migratory zebra population. Thus these two MD vegetation communities make up a critical part of the functional heterogeneity of the region.

Bothriochloa insculpta - Rhynchosia minima

This open savanna grassland community occurs on similar soils to the previous community (Table 2) but it makes up much less area on the MD. *Bothriochloa insculpta, Rhynchosia minima, Cyathula orthacantha, Leonotis nepetifolia,* and *Dinebra retroflexa* characterized this community (Table 3). Dominance by the unpalatable *Bothriochloa insculpta* makes this community type less important for wildlife.

Setaria incrassata - Dichanthium annulatum

This open grassland community also occurs on the MD, being found as vast, extremely open grasslands in the far north eastern part of the MD, and is characterized by seasonal flooding from rainfall. Soils in this community are not as high clay as others in the MD (Table 2) but from a structural point of view the vegetation is mapped as tall open grassland because it is a tall grass community although very different in composition to the other tall grass communities on the MD (Figure 2). *Setaria incrassata, Dichanthium annulatum, Enicostema axillare, Panicum coloratum, Cynodon dactylon, Digitaria milanjiana* and *Aristida scrabrivalvis* are some of the species that characterized this community (Table 3). The community appears to be utilized by many roan antelope over the dry season.

Discussion

Vegetation classification and mapping of the SMLE

The vegetation of the SMLE was clustered into 15 major vegetation communities characterized by different herbaceous and woody species (Figure 3), with the primary axis of variation in plant community composition (NMS1) appearing to be driven by variation in soil texture and fertility (Figure 3; Table 2). The secondary axis of variation in plant community composition (NMS2) appeared to be driven by wetness, although it was not a clear effect as with the texture gradient probably because we focused mainly on dryland communities. The landscape template, which provides the basis of the vegetation heterogeneity of the region, was formed by a variety of processes. The mosaic of sand-filled paleo-river channels among alluvial deposits that support the mopane-sandveld woodland mosaic between the Okavango Delta and the Linyanti Swamps were formed by ancient wetlands similar to the current Delta, with the river channels subsequently becoming infilled by Kalahari sands of aeolian origin (Haddon & McCarthy). Similarly, the deep sands supporting the Baikiaea forests are of aeolian origin (Haddon & McCarthy 2005). The vast 3000 km² MD originates from Paleo-lake Mababe (Teter 2007), which had a central sump of about 70 x 20 km where lacustrine clays and sediments deposited giving rise to the deep vertisols of the MD. Between the beachhead of the lake and the sump zone is a zone of soils where it appears that deposition of lacustrine clays declined with increasing distance from the sump zone. Thus the inner sump has the highest clay content supporting the Bothriochloa insculpta – Rhynchosia minima and Cenchrus ciliaris –Acacia mellifera communities, followed by the edges of the sump with more silty soils supporting the *Chloris virgata – Boerhavia coccinea* community, then a zone of silty sands supporting mopane woodland and between the mopane and the beachhead of the lake are sandy soils but with higher clay and silt than typical aeolian sands, which support the Boscia albitrunca – Dactyloctenium

giganteum and *Brachiaria nigropedata – Combretum hereroense* sandveld communities (Figure 2).

Outside the MD, the typical aeolian sands have the lowest clay and silt content because they received no lacustrine sediment deposition. The extremely-low clay sands support the *Ipomoea chloroneura – Oxygonum alatum, Eragrostis pallens - Ochna pulchra* and *Commiphora angolensis – Combretum collinum* sandveld communities. Species such as *Commiphora angolensis, Combretum collinum, Baikiaea plurijuga, Baphia massaiensis, Philenoptera nelsii, Ochna pulchra, Burkea africana* and *Terminalia sericea* which dominated communities growing on sandy soils in this study were also found as indicator species for sandy regions in other studies (Coetzee *et al.* 1976; Gertenbach & Potgieter 1978; Tedder 2012; Tedder *et al.* 2013).

The mopane community was associated with alluvial soils of slightly higher clay than the sandveld communities (Table 2), as observed elsewhere (Van Voorthuizen 1976; Wolski & Murray-Hudson 2006; Tedder 2012; Tedder *et al.* 2013). The mopane and sandveld communities are widely distributed across the ecosystem forming a woodland mosaic of mopane woodland on alluvial soils alternating with sandveld woodland on paleo-river channels infilled with Kalahari sands (Figure 2). The mopane-sandveld mosaic (as well as *Baikiaea* forest) provides key habitat for herbivore species favouring medium and tall grasses, such as buffalo, roan and sable antelope and elephant (Taolo 2003; Bennitt, Bonyongo & Harris 2014, 2015; Fynn *et al.* 2014; Sianga 2014), because of the abundance of digestible, leafy forage of high-quality grass species dominant in sandveld woodland (e.g. *Digitaria eriantha, Panicum maximum* and *Schmidtia papophoroides*), as well as *Digitaria milanjiana* and *Panicum maximum* in mopane woodland (Sianga *et al.* 2017b). Importantly, these high-quality grasses are most abundant far from permanent water (> 15-20km) (Sianga *et al.* 2017b), which explains why buffalo tend to favour

the woodlands furthest from permanent water during the wet season (Bennitt *et al.* 2014; Sianga 2014; Sianga *et al.* 2017a, 2017b), as do roan and sable antelope (Haveman 2014; Hensman *et al.* 2014). In addition, the numerous ephemeral waterholes of mopane woodland allow herbivores to remain far out from permanent water in these woodlands during the wet season where they are able to avoid high concentrations of predators (Harrington *et al.* 1999). Once the waterholes dry up during the dry season herbivores are forced to move closer to the permanent water sources of the Okavango Delta and Linyanti Swamps, where buffalo forage mainly in the wetlands (Bennitt *et al.* 2014, 2015; Sianga 2014; Sianga *et al.* 2017a) whereas roan and sable antelope visit the wetlands only every three to four days to drink and then return back to the safety of the woodlands far from water (Haveman 2014; Hensman *et al.* 2014). Thus these vast woodland systems provide key functional habitat heterogeneity for provision of high-quality forage far from water during the wet season and low predation risk all year round.

The *Croton megalobotrys - Setaria verticillata* community, a riparian woodland (riverine) community was correlated with silt-clay soils and occurred along edges of watercourses (Witkowski & O'Connor 1996). This community was dominated by species such as *Croton megalobotrys, Philenoptera violacea, Combretum mossambicense, Diospyros mespiliformis* and *Acacia nigrescens*, which are adapted to obtaining soil moisture through lateral ground-water discharge from higher water tables (Ellery *et al.* 1993; Ringrose *et al.* 2007; Hamandawana 2011). The *Setaria sphacelata - Gomphocarpus fruticosus* community, a floodplain grassland type found along watercourses had grass (*Setaria sphacelata*) and sedge (*Cyperus longus*) or forbs (*Gomphocarpus fruticosus*) as indicator species suggesting extensive wetness as these species are mostly abundant in wetlands or swamp margins (Heath & Heath 2009). This community probably experiences periods of dryness over the annual cycle as

indicated by the presence of opportunistic dryland species (Crotalaria platysepala, Momordica balsamina, Sesamum triphyllum and Bulbostylis hispidula). Variation in wetland community composition is driven by gradients of flood depth and duration with Cynodon dactylon often characterizing the parts of the gradient with the lowest depth and duration of flooding, *Panicum* repens and Setaria sphacelata often characterizing areas with intermediate depth and duration of flooding and tall sedges and grasses such as Oryza longistaminata and Vossia cuspidata characterizing areas of the gradient with the largest depth and duration of flooding (Murray-Hudson et al. 2011, 2014; Fynn et al. 2015). This variation in composition and phenology on flooding gradients provides important variation in green forage supply for herbivores from the early to late dry season, owing to variation in availability of soil moisture for growth, allowing for adaptive foraging over the dry season (Fynn et al. 2015). Our sampling focused on the dryland communities and we did not attempt to sample across the flood depth and duration gradient in the wetlands and thus the Setaria sphacelata - Gomphocarpus fruticosus community represents only a small part of the variation in plant community composition that would occur in the region mapped as wetland in figure 2. The spatial location of various wetland community types is not a constant and will shift location within the bounds of the area mapped as wetland (Figure 2) according to variation in flooding regimes over time. From a conservation management perspective, however, it should be recognized that the overall wetland community shown in the map (Figure 2) represents gradients of wetness and composition that provide critically important forage and adaptive foraging options for many herbivore species from the early to late dry season right across Africa (Fynn et al. 2015) and in the SMLE (Bartlam-Brooks et al. 2013; Fynn et al. 2014, Bennitt et al. 2014; Sianga et al. 2017a). Consequently, linkages

between large wetland systems and adjacent dryland systems must be maintained to ensure that functional habitat heterogeneity is maintained (Hopcraft *et al.* 2010; Fynn *et al.* 2015).

Communities on the high-clay soils of the MD, especially the *Chloris virgata - Boerhavia* coccinea, and Cenchrus ciliaris - Acacia mellifera communities, are critical wet season habitats for the large zebra migration in the region, as well as for wildebeest, tsessebe and impala (Joos-Vandewalle 2000; Fynn et al. 2014; Sianga 2014; Sianga et al. 2017a). This is because of the high clay soils and accumulation of a high concentration of minerals in the soil when it was a lake system (Teter 2007). The P-rich soils give rise to high P content in grass leaves (as well as other minerals) (Joos-Vandewalle 2000; Fynn et al. 2014; Sianga 2014). Thus pregnant and lactating herbivores can obtain sufficient intake of nutrients to meet their high demands for nutrients during the wet season, a key functional aspect of wet season ranges for herbivores (Owen-Smith 2004; Hopcraft et al. 2010). In this regard, the Chloris virgata - Boerhavia coccinea community on the edge of the MD appears to be particularly important for P, having the highest soil P levels (Table 2), while the vertisols of the Cenchrus ciliaris - Acacia mellifera communities deeper into the MD have the highest concentrations of K and Ca. This may explain why zebra are observed to switch their foraging bouts between Chloris virgata - Boerhavia coccinea community and the Cenchrus ciliaris - Acacia mellifera community over the day (Sianga 2014), which may be a mechanism to maximize overall intake of key minerals, protein and energy during the wet season (Owen-Smith 2002). Also, the open grasslands of the MD provide better visibility, which reduces predation risk and is thus suitable as a calving ground. In fact, selection for low predation-risk habitat for the calving period may dominate the hierarchy of habitat selection decisions made by ungulates (Rettie & Messier 2000). During the day zebra appeared to make use of short, open grasslands with high visibility (mainly the Chloris virgata -

Boerhavia coccinea community) but at night they moved further into the MD to the *Acacia mellifera* woodlands perhaps as an adaptive strategy to elude predators – reliance on sighting predators during the day and hiding from them at night (Sianga 2014).

Dominance of much of the southern half of the MD by Cenchrus ciliaris is informative as this species is often found in areas with elevated levels of P in soils (Blackmore et al. 1990), which demonstrates why the MD is an important wet season range for herbivores. The Bothriochloa insculpta - Rhynchosia minima community is dominated by Bothriochloa insculpta, which is adapted to seasonally flooded vertisols which form hard surfaces during winter (Cook & Clem 2000). The well-developed root systems of these large perennial grasses (Bothriochloa insculpta and Cenchrus ciliaris) also likely promote access to soil moisture from deeper water tables when surface water dries out during the dry season (Cook & Clem 2000; Hamandawana 2011). The Setaria incrassata - Dichanthium annulatum community was dominated mainly by grass species such as Setaria incrassata, Dichanthium annulatum, Panicum coloratum, Cynodon dactylon and Digitaria milanjiana and occurred on seasonally flooded vertisols, with seasonal flooding maintaining this community as an open grassland with no trees (Cook & Clem 2000). Species such as Setaria incrassata and Dichanthium annulatum are well known dominants of seasonally-flooded heavy clay soils in southern Africa (Cook & Clem 2000). This community type was found only in the north-eastern part of the MD and occurs in one of the most remote and inaccessible areas of northern Botswana, rarely ever accessed by people because there are no roads there and seasonal flooding of the heavy clay soils makes access impossible during the wet season. Our many sightings of roan antelope in this vegetation type while we were sampling suggest that it is regularly used by roan antelope, which is a species

known to favour seasonally flooded grasslands and prefers areas with little disturbance by people.

Conclusion

This study demonstrated that a large heterogeneity of plant communities driven by gradients in soil texture/fertility and wetness plays a key role in providing critical functional resource and habitat heterogeneity that allows (i) herbivores to adapt to seasonal variation in resources and (ii) niche diversity to support a diverse guild of herbivores. Floodplains and seasonally flooded grasslands provide a reliable source of green forage during the dry season for herbivores, while the extensive woodland mosaic of mopane and sandveld on alluvial soils and Kalahari sands provide cover, low predation risk and medium height leafy grasses for rare herbivores all year round and for buffalo and elephant during the wet season. The fertile heavy-clay soils of the MD provide additional functional resource heterogeneity in an ecosystem otherwise largely dominated by sandy soils, where elevated levels of minerals such as Ca and P in grasses on the MD enable pregnant and lactating females to meet their elevated requirements for these resources. Thus the regional-scale separation of large wetland systems (a functional dry season habitat) from large woodland systems and the fertile clay soils of the MD (functional wet season habitats) is an underlying driver of both buffalo (wetlands to woodlands) and zebra (wetlands to paleolake systems) migrations in the SMLE (Naidoo et al. 2014; Bennitt et al. 2014; Sianga 2014).

Certain communities such as the *Boscia albitrunca – Dactyloctenium giganteum* community provide a high density of trees with green leaves of acceptable quality during the dry season (e.g. *Boscia albitrunca*), which provide an important reserve resource for browsers at this

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time of the year (Owen-Smith 2002). Thus the heterogeneous mix of extensive sandveld, mopane and Baikiaea woodlands, open fertile grasslands and extensive wetland systems provides excellent functional habitat and resource heterogeneity in the ecosystems which enables herbivores to adapt to variable resources needs and avoid predation. In addition, this heterogeneity creates niche diversity, which enables coexistence of a high diversity of large mammals (herbivores and carnivores), including one of the largest roan and sable antelope and eland populations in southern Africa. Thus a key point of general significance in our results for conservation science is that protected areas need to incorporate the main large scale regional environmental gradients in a region (e.g. the full texture and wetness gradients in this study region) if they are to provide sufficient habitat heterogeneity needed to provide appropriate seasonal adaptive foraging options for wildlife and to support a diverse guild of herbivores and their associated predators. In addition, this vegetation classification and vegetation map will provide a critical database for wildlife habitat selection studies in the region and will be useful for environmental and conservation policy-makers in the assessment and monitoring of plant communities as well as for developing conservation strategies and management plans for the ecosystem.

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Appendix

Table 1-A1: Multiresponse permutation procedure pairwise comparisons between identified classes for plant communities in the Savuti-Mababe-Linyanti ecosystem (northern Botswana). t, test statistic; A, chance-corrected within group agreement; p, probability of a smaller or equal δ (not corrected for multiple comparisons).

Classes	Τ	A	p
Ipomoea chloroneura – Oxygonum alatum vs.	-70.288	0.146	< 0.0001
Colophospermum mopane – Jasminum stenolobum			
Ipomoea chloroneura – Oxygonum alatum vs. Eragrostis	-25.515	0.073	< 0.0001
pallens – Ochna pulchra			
Ipomoea chloroneura – Oxygonum alatum vs. Justicea	-52.784	0.155	< 0.0001
divaricata – Eragrostis superba			
Ipomoea chloroneura – Oxygonum alatum vs. Tribulus	-34.107	0.188	< 0.0001
terrestris – Senna obtusifolia			
Ipomoea chloroneura – Oxygonum alatum vs. Boscia	-35.861	0.128	< 0.0001
albitrunca – Dactyloctenium giganteum			
Ipomoea chloroneura – Oxygonum alatum vs. Bothriochloa	-32.637	0.176	< 0.0001
insculpta – Rhynchosia minima			
Ipomoea chloroneura – Oxygonum alatum vs. Chloris	-42.954	0.243	< 0.0001
virgata – Boerhavia coccinea			
Ipomoea chloroneura – Oxygonum alatum vs. Cenchrus	-35.628	0.350	< 0.0001
ciliaris – Senegalia mellifera			
Ipomoea chloroneura – Oxygonum alatum vs. Brachiaria	-27.609	0.186	< 0.0001
nigropedata – Combretum hereroense			
Ipomoea chloroneura – Oxygonum alatum vs. Croton	-36.111	0.240	< 0.0001
megalobotrys – Setaria verticillata			
Ipomoea chloroneura – Oxygonum alatum vs. Setaria	-22.085	0.227	< 0.0001
sphacelata – Gomphocarpus fruticosus			
Ipomoea chloroneura – Oxygonum alatum vs. Baikiaea	-30.746	0.216	< 0.0001
plurijuga – Baphia massaiensis			
Ipomoea chloroneura – Oxygonum alatum vs. Commiphora	-29.920	0.192	< 0.0001
angolensis – Combretum collinum			
Ipomoea chloroneura – Oxygonum alatum vs. Setaria	-28.894	0.282	< 0.0001
incrassata – Dichanthium annulatum			
Colophospermum mopane – Jasminum stenolobum vs.	-68.981	0.110	< 0.0001
Eragrostis pallens – Ochna pulchra			
Colophospermum mopane – Jasminum stenolobum vs.	-72.744	0.103	< 0.0001
Justicea divaricata – Eragrostis superba			
Colophospermum mopane – Jasminum stenolobum vs.	-60.097	0.117	< 0.0001
Tribulus terrestris – Senna obtusifolia			
Colophospermum mopane – Jasminum stenolobum vs.	-60.269	0.096	< 0.0001
Boscia albitrunca – Dactyloctenium giganteum			
Colophospermum mopane – Jasminum stenolobum vs.	-44.257	0.078	< 0.0001
Bothriochloa insculpta – Rhynchosia minima			
Colophospermum mopane – Jasminum stenolobum vs.	-69.154	0.136	< 0.0001
Chloris virgata – Boerhavia coccinea			
Colophospermum mopane – Jasminum stenolobum vs.	-67.546	0.171	< 0.0001
Cenchrus ciliaris – Senegalia mellifera			
Colophospermum mopane – Jasminum stenolobum vs.	-40.435	0.081	< 0.0001

Brachiaria nigropedata – Combretum hereroense	57 70 4	0.115	0.0001
Colophospermum mopane – Jasminum stenolobum vs.	-57.794	0.115	<0.0001
Croton megalobotrys – Setaria verticillata	20.104	0.0.00	0.0001
Colophospermum mopane – Jasminum stenolobum vs.	-29.134	0.068	<0.0001
Setaria sphacelata – Gomphocarpus fruticosus	55.254	0.110	0.0001
Colophospermum mopane – Jasminum stenolobum vs.	-55.264	0.119	<0.0001
Baikiaea plurijuga – Baphia massaiensis		0.115	0.0001
Colophospermum mopane – Jasminum stenolobum vs.	-55.555	0.115	<0.0001
Commiphora angolensis – Combretum collinum	4.5.570	0.10.5	0.0001
Colophospermum mopane – Jasminum stenolobum vs.	-46.653	0.106	<0.0001
Setaria incrassata – Dichanthium annulatum	40.250	0.000	0.0001
Eragrostis pallens – Ochna pulchra vs. Justicea divaricata	-49.379	0.098	<0.0001
– Eragrostis superba			
Eragrostis pallens – Ochna pulchra vs. Tribulus terrestris –	-29.657	0.096	< 0.0001
Senna obtusifolia			
Eragrostis pallens – Ochna pulchra vs. Boscia albitrunca –	-31.090	0.071	< 0.0001
Dactyloctenium giganteum			
Eragrostis pallens – Ochna pulchra vs. Bothriochloa	-30.758	0.096	< 0.0001
insculpta – Rhynchosia minima			
Eragrostis pallens – Ochna pulchra vs. Chloris virgata –	-47.404	0.161	< 0.0001
Boerhavia coccinea			
Eragrostis pallens – Ochna pulchra vs. Cenchrus ciliaris –	-43.302	0.226	< 0.0001
Senegalia mellifera			
Eragrostis pallens – Ochna pulchra vs. Brachiaria	-24.656	0.090	< 0.0001
nigropedata – Combretum hereroense			
Eragrostis pallens – Ochna pulchra vs. Croton	-39.310	0.145	< 0.0001
megalobotrys – Setaria verticillata			
Eragrostis pallens – Ochna pulchra vs. Setaria sphacelata –	-20.552	0.105	< 0.0001
Gomphocarpus fruticosus			
Eragrostis pallens – Ochna pulchra vs. Baikiaea plurijuga	-32.165	0.127	< 0.0001
– Baphia massaiensis			
Eragrostis pallens – Ochna pulchra vs. Commiphora	-30.257	0.108	< 0.0001
angolensis –Combretum collinum			
Eragrostis pallens – Ochna pulchra vs. Setaria incrassata –	-32.926	0.161	< 0.0001
Dichanthium annulatum			
Justicea divaricata – Eragrostis superba vs. Tribulus	-36.206	0.091	< 0.0001
terrestris – Senna obtusifolia			
Justicea divaricata – Eragrostis superba vs. Boscia	-38.259	0.074	< 0.0001
albitrunca – Dactyloctenium giganteum			
Justicea divaricata – Eragrostis superba vs. Bothriochloa	-26.907	0.061	< 0.0001
insculpta – Rhynchosia minima			
Justicea divaricata – Eragrostis superba vs. Chloris virgata	-45.638	0.115	< 0.0001
– Boerhavia coccinea			
Justicea divaricata – Eragrostis superba vs. Cenchrus	-47.411	0.186	< 0.0001
ciliaris – Senegalia mellifera			
Justicea divaricata – Eragrostis superba vs. Brachiaria	-26.545	0.077	< 0.0001
nigropedata – Combretum hereroense			
Justicea divaricata – Eragrostis superba vs. Croton	-34.705	0.090	< 0.0001
megalobotrys – Setaria verticillata			
Justicea divaricata – Eragrostis superba vs. Setaria	-22.260	0.080	< 0.0001
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sphacelata – Gomphocarpus fruticosus			
Justicea divaricata – Eragrostis superba vs. Baikiaea	-41.162	0.133	< 0.0001
plurijuga – Baphia massaiensis			
Justicea divaricata – Eragrostis superba vs. Commiphora	-42.738	0.134	< 0.0001
angolensis – Combretum collinum			
Justicea divaricata – Eragrostis superba vs. Setaria	-29.816	0.093	< 0.0001
incrassata – Dichanthium annulatum			
Tribulus terrestris – Senna obtusifolia vs. Boscia albitrunca	-22.155	0.073	< 0.0001
– Dactyloctenium giganteum			
Tribulus terrestris – Senna obtusifolia vs. Bothriochloa	-25.073	0.129	< 0.0001
insculpta – Rhynchosia minima			
Tribulus terrestris – Senna obtusifolia vs. Chloris virgata –	-36.188	0.182	< 0.0001
Boerhavia coccinea			
Tribulus terrestris – Senna obtusifolia vs. Cenchrus ciliaris	-31.904	0.309	< 0.0001
– Senegalia mellifera			
Tribulus terrestris – Senna obtusifolia vs. Brachiaria	-23.736	0.173	< 0.0001
nigropedata – Combretum hereroense			
Tribulus terrestris – Senna obtusifolia vs. Croton	-25.049	0.137	< 0.0001
megalobotrys – Setaria verticillata			
Tribulus terrestris – Senna obtusifolia vs. Setaria	-16.579	0.185	< 0.0001
sphacelata – Gomphocarpus fruticosus			
Tribulus terrestris – Senna obtusifolia vs. Baikiaea	-23.740	0.159	< 0.0001
plurijuga – Baphia massaiensis			
Tribulus terrestris – Senna obtusifolia vs. Commiphora	-28.344	0.204	< 0.0001
angolensis – Combretum collinum			
Tribulus terrestris – Senna obtusifolia vs. Setaria incrassata	-24.258	0.240	< 0.0001
– Dichanthium annulatum			
Boscia albitrunca – Dactyloctenium giganteum vs.	-24.395	0.079	< 0.0001
Bothriochloa insculpta – Rhynchosia minima			
Boscia albitrunca – Dactyloctenium giganteum vs. Chloris	-39.658	0.130	< 0.0001
virgata – Boerhavia coccinea			
Boscia albitrunca – Dactyloctenium giganteum vs.	-38.826	0.216	< 0.0001
Cenchrus ciliaris – Senegalia mellifera			
Boscia albitrunca – Dactyloctenium giganteum vs.	-25.765	0.108	< 0.0001
Brachiaria nigropedata – Combretum hereroense			
Boscia albitrunca – Dactyloctenium giganteum vs. Croton	-30.694	0.115	< 0.0001
megalobotrys – Setaria verticillata			
Boscia albitrunca – Dactyloctenium giganteum vs. Setaria	-17.100	0.099	< 0.0001
sphacelata – Gomphocarpus fruticosus			
Boscia albitrunca – Dactyloctenium giganteum vs. Baikiaea	-30.725	0.135	< 0.0001
plurijuga – Baphia massaiensis			
Boscia albitrunca – Dactyloctenium giganteum vs.	-28.082	0.115	< 0.0001
Commiphora angolensis – Combretum collinum			
Boscia albitrunca – Dactyloctenium giganteum vs. Setaria	-29.545	0.160	< 0.0001
incrassata – Dichanthium annulatum			
Bothriochloa insculpta – Rhynchosia minima vs. Chloris	-23.551	0.100	< 0.0001
virgata – Boerhavia coccinea			
Bothriochloa insculpta – Rhynchosia minima vs. Cenchrus	-24.442	0.200	< 0.0001
ciliaris – Senegalia mellifera			
Bothriochloa insculpta – Rhynchosia minima vs. Brachiaria	-19.987	0.140	< 0.0001

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nigropedata – Combretum hereroense			
Bothriochloa insculpta – Rhynchosia minima vs. Croton	-24.052	0.133	< 0.0001
megalobotrys – Setaria verticillata			
Bothriochloa insculpta – Rhynchosia minima vs. Setaria	-13.788	0.158	< 0.0001
sphacelata – Gomphocarpus fruticosus			
Bothriochloa insculpta – Rhynchosia minima vs. Baikiaea	-23.962	0.179	< 0.0001
plurijuga – Baphia massaiensis			
Bothriochloa insculpta – Rhynchosia minima vs.	-25.536	0.178	< 0.0001
Commiphora angolensis – Combretum collinum			
Bothriochloa insculpta – Rhynchosia minima vs. Setaria	-19.200	0.178	< 0.0001
incrassata – Dichanthium annulatum			
Chloris virgata – Boerhavia coccinea vs. Cenchrus ciliaris	-35.426	0.287	< 0.0001
– Senegalia mellifera			
Chloris virgata – Boerhavia coccinea vs. Brachiaria	-29.563	0.191	< 0.0001
nigropedata – Combretum hereroense			
Chloris virgata – Boerhavia coccinea vs. Croton	-34.587	0.187	< 0.0001
megalobotrys – Setaria verticillata			
Chloris virgata – Boerhavia coccinea vs. Setaria sphacelata	-20.598	0.171	< 0.0001
– Gomphocarpus fruticosus			
Chloris virgata – Boerhavia coccinea vs. Baikiaea plurijuga	-33.380	0.234	< 0.0001
– Baphia massaiensis			
Chloris virgata – Boerhavia coccinea vs. Commiphora	-34.826	0.235	< 0.0001
angolensis – Combretum collinum			
Chloris virgata – Boerhavia coccinea vs. Setaria incrassata	-28.163	0.228	< 0.0001
– Dichanthium annulatum			
Cenchrus ciliaris – Senegalia mellifera vs. Brachiaria	-24.087	0.347	< 0.0001
nigropedata – Combretum hereroense			
Cenchrus ciliaris – Senegalia mellifera vs. Croton	-29.356	0.320	< 0.0001
megalobotrys – Setaria verticillata			
Cenchrus ciliaris – Senegalia mellifera vs. Setaria	-16.892	0.425	< 0.0001
sphacelata – Gomphocarpus fruticosus			
Cenchrus ciliaris – Senegalia mellifera vs. Baikiaea	-26.684	0.386	< 0.0001
plurijuga – Baphia massaiensis			
Cenchrus ciliaris – Senegalia mellifera vs. Commiphora	-27.856	0.382	< 0.0001
angolensis – Combretum collinum			
Cenchrus ciliaris – Senegalia mellifera vs. Setaria	-22.269	0.433	< 0.0001
incrassata – Dichanthium annulatum			
Brachiaria nigropedata – Combretum hereroense vs.	-23.983	0.202	< 0.0001
Croton megalobotrys – Setaria verticillata			
Brachiaria nigropedata – Combretum hereroense vs.	-13.628	0.298	< 0.0001
Setaria sphacelata – Gomphocarpus fruticosus			
Brachiaria nigropedata – Combretum hereroense vs.	-21.706	0.246	< 0.0001
Baikiaea plurijuga – Baphia massaiensis			
Brachiaria nigropedata – Combretum hereroense	-22.341	0.214	< 0.0001
vs.Commiphora angolensis – Combretum collinum			
Brachiaria nigropedata – Combretum hereroense vs	-18.366	0.304	< 0.0001
Setaria incrassata – Dichanthium annulatum	101000	51201	
Croton megalobotrys – Setaria verticillata ys Setaria	-17.090	0.230	< 0.0001
sphacelata – Gomphocarpus fruticosus	11.020	0.200	
Croton megalobotrys – Setaria verticillata vs Raikiaea	-26 743	0.238	< 0.0001
	_010	0.200	

plurijuga – Baphia massaiensis			
Croton megalobotrys – Setaria verticillata vs. Commiphora	-28.762	0.252	< 0.0001
angolensis – Combretum collinum			
Croton megalobotrys – Setaria verticillata vs. Setaria	-22.958	0.266	< 0.0001
incrassata – Dichanthium annulatum			
Setaria sphacelata – Gomphocarpus fruticosus vs. Baikiaea	-15.172	0.313	< 0.0001
plurijuga – Baphia massaiensis			
Setaria sphacelata – Gomphocarpus fruticosus vs.	-16.610	0.300	< 0.0001
Commiphora angolensis – Combretum collinum			
Setaria sphacelata – Gomphocarpus fruticosus vs. Setaria	-11.836	0.457	< 0.0001
incrassata – Dichanthium annulatum			
Baikiaea plurijuga – Baphia massaiensis vs. Commiphora	-24.821	0.258	< 0.0001
angolensis – Combretum collinum			
Baikiaea plurijuga – Baphia massaiensis vs. Setaria	-20.584	0.339	< 0.0001
incrassata – Dichanthium annulatum			
Commiphora angolensis – Combretum collinum vs. Setaria	-21.901	0.334	< 0.0001
incrassata – Dichanthium annulatum			



Figure 1-A1: Cluster analysis showing the 15 plant communities identified in the Savuti-Mababe-Linyanti ecosystem, northern Botswana. BADG, Boscia albitrunca – Dactyloctenium giganteum; BIRM, Bothriochloa insculpta – Rhynchosia minima; BNCH, Brachiaria nigropedata – Combretum hereroense; BPBM, Baikiaea plurijuga – Baphia massaiensis; CACC, Commiphora angolensis – Combretum collinum; CCAM, Cenchrus ciliaris – Senegalia mellifera; CMJS, Colophospermum mopane – Jasminum stenolobum; CMSV, Croton

megalobotrys – Setaria verticillata; CVBC, Chloris virgata – Boerhavia coccinea; EPOP, Eragrostis pallens – Ochna pulchra; ICOA, Ipomoea chloroneura – Oxygonum alatum; JDES, Justicea divaricata – Eragrostis superba; SIDA, Setaria incrassata – Dichanthium annulatum; SSGF, Setaria sphacelata – Gomphocarpus fruticosus; TTSO, Tribulus terrestris – Senna obtusifolia.

Chapter 3

Functional heterogeneity of habitats and dry season forage provision in an Okavango Delta landscape, northern Botswana

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Abstract

The late dry season is a resource-limited period in African savannas that can induce a strong demographic bottleneck in those herbivore populations with limited access to critical resource heterogeneity. We sampled forage characteristics in four habitat types around the distal reaches of the Tsam Tsam floodplains of the Okavango Delta during the late dry season of 2015; the habitat types were mopane and sandveld woodland far from floodplains (two major dryland habitat types), sandveld habitats that receive soil moisture inputs from adjacent floodplains (wet sandveld) and sedgeland habitat within the floodplain. Forage in wet sandveld had by far the highest protein content (~ 16 %) of all habitat types but forage height and biomass were very low, whereas sedgelands had the highest biomass of adequate-quality forage, while dryland

communities had the lowest quantity and quality of forage. Thus foraging between a higherbiomass, adequate-quality reserve resource (sedgeland) and a high-quality but low-quantity bridging resource (wet sandveld) can help to ensure a balanced protein and fibre intake during the late dry season. Our study demonstrates the importance of heterogeneity for meeting intake needs of herbivores during the late dry season and to understand observed buffalo dry season habitat selection in this region.

Key words: Dry season ranges, forage quality, functional, resources, sedgelands, wetlands

Introduction

Forage quantity and quality may become limiting during the dry season in African savannas (Sinclair, 1975; Ellis & Swift, 1988; Owen-Smith, 2008), especially in drier, less productive regions that are favored by herbivores during the wet season (Hopcraft, Olff & Sinclair, 2010; Fynn, Chase & Röder, 2014). As the quality and quantity of forage in their preferred wet season habitats declines through the dry season, herbivores may be forced to migrate away to habitats that provide more reliable water (Redfern *et al.*, 2003) and forage during this resource-limited period (Maddock, 1979; Bartlam-Brooks, Bonyongo & Harris, 2011; Bennitt, Bonyongo & Harris, 2014; Fynn *et al.*, 2014; Sianga, Fynn & Bonyongo, 2017).

A common feature of functional dry season habitats in African savannas is the availability of soil moisture during the dry season to allow growth and the presence of green forage even during the hottest and driest parts of the dry season. Soil moisture may be provided by sufficient dry season rainfall in high rainfall regions (McNaughton & Banyikwa, 1995; Hopcraft *et al.*, 2010; Fynn & Bonyongo, 2011) or by the presence of shallow water tables in poorly-drained regions such as dambos, floodplains and swamps (Hopcraft *et al.*, 2010; Fynn *et al.*, 2015). The ability to provide green forage during the dry season is a key functional aspect of dry season habitats because green forage contains above maintenance levels of energy and protein whereas these resources have dropped below maintenance levels in dry forage (Ellis & Swift, 1988; Owen-Smith, 2008). For example, fires in wet grasslands that provided a green flush during the dry season greatly elevated protein intake of sable antelope (*Hippotragus niger*) relative to years when these wet grasslands were not burned (Parrini & Owen-Smith, 2010). Similarly, buffalo (*Syncerus caffer*) populations in Matusadona National Park (Zimbabwe), which had access to high-quality green forage in lake shore grasslands over the late dry season,

had greater reproductive productivity and population growth rates relative to other savanna populations (Taylor, 1985). In addition, the ability of high-rainfall regions and wetlands to provide a higher standing biomass of forage results in a reserve of forage for the dry season (reserve resource) and critical buffer/key resources during drought periods, which can prevent catastrophic herbivore population collapses (Illius & O'Connor, 2000; Owen-Smith, 2002).

This paper reports on a study of heterogeneity of forage quantity and quality in various habitats of a landscape of the eastern edge of the Okavango Delta, northern Botswana and how this may relate to seasonal herbivore use of these habitats. A variety of large herbivore species are well known for their use of various wetland habitats over the dry season across Africa (Vesey-FitzGerald, 1960; Western, 1973; Tinley, 1977; Taylor, 1985; Prins & Beekman, 1989; Belifuss *et al.*, 2010; Bennitt *et al.*, 2014). From global positioning system (GPS) data, we observe three buffalo herds to focus their late dry season foraging activities in wetlands (floodplains and swamps) in the Savuti-Mababe-Linyanti ecosystem in northern Botswana (Sianga *et al.*, 2017). Typical floodplains are not homogenous vegetation units but have a gradient of increasing depth and duration of flooding, which influences plant productivity, composition and quality, with the deeper parts of floodplains becoming increasingly important for forage provision for herbivores as the dry season progresses because they retain soil moisture later into the dry season (Fynn *et al.*, 2015).

As the depth and duration of flooding increases, seasonal floodplains in the Okavango Delta become increasingly dominated by taller more productive sedges and swamp grasses (Murray-Hudson *et al.*, 2014; Fynn *et al.*, 2015). Thus while the deeper parts of floodplains provide more reliable green forage during the late dry season, their tall fibrous grasses and sedges are expected to be of lower digestibility and quality owing to greater cellulose and lignin content (Wilmshurst, Fryxell & Bergman, 2000). The lower digestibility of wetland plants is further exacerbated by their higher silica content (Mosimane, 2015). Along the Selinda Spillway and the eastern edge of the Okavango Delta we have observed that where plant communities on deep Kalahari sands (sandveld) directly abut the floodplain, without large rises in elevation away from the floodplain, soil moisture from the river channel/floodplain appears to move laterally and permeate these sandy soils, thereby forming a shallow water table that maintains highquality dryland grass species such as Digitaria eriantha and Brachiaria nigropedata (authorities for plant species follows The Herbarium Catalogue, Royal Botanic Gardens, Kew) in a green state during the late dry season (Fig. 1). Thus sandveld communities on deep Kalahari sands can either be termed dryland sandveld (occur far from the river channel and thus do not receive soil moisture inputs from lateral below-ground seepage) or wet sandveld (abut the river channel and thus receive soil moisture inputs from lateral below-ground seepage – but are never inundated by floodwaters). The various channels of the western reaches of the Selinda Spillway (an eastern branch of the Okavango Delta linking to the Linyanti Swamps) have extensive areas of this wet sandveld habitat greening up during the late dry season (Fig. 1), which appears to attract many buffalo herds during this resource-limited time of the year (Naidoo et al., 2014; Sianga et al., 2017).



Figure 1: Wet sandveld showing regrowth of *Brachiaria nigropedata* during the late dry season along the Selinda Spillway (northern Botswana). The taller sedgeland community can be seen in the background, associated with the deeper parts of the floodplain. The photo was taken in the favoured late dry season range of buffalo (see Fig. 2 for location) and the heavy utilization of *B. nigropedata* by buffalo is apparent (photo credit Andrew Zinn).

Our hypothesis was that during the late dry season, the deeper-flooded sedge zone of wetlands would have higher biomass (sedges and grasses) than the adjacent wet sandveld grasses. The other hypothesis was that the wet sandveld grasses would have higher quality owing to their being dryland species with lower silica, cellulose and lignin contents than more productive wetland grasses and sedges (Wilmshurst *et al.*, 2000; Mosimane, 2015).

Materials and methods

Study area

Our study was located in the Tsam Tsam region of the Savuti-Mababe-Linyanti ecosystem (SMLE) of northern Botswana between the Okavango Delta and the Linyanti Swamps (Fig. 2). Detailed descriptions of the hydrology, ecology and vegetation of the ecosystem can be found in Fynn et al. (2014) and Sianga and Fynn (2017). One key feature of relevance to this study is the Selinda Spillway - a channel connecting the Okavango Delta and the Linyanti Swamps (Fig. 2). The floodplains of the western section of the Selinda Spillway have areas of wet sandveld communities adjacent to the various channels of the Spillway (Fig. 1). Similarly, the nearby Tsam Tsam floodplains on the eastern edge of the Okavango Delta extend out into the woodlands (Fig. 2) and thus intersect with sandveld communities, thereby giving rise to wet sandveld. Thus both the Selinda Spillway and the Tsam Tsam were preferred by several collared buffalo herds during the dry season, which moved between these areas (Naidoo et al., 2014; Sianga *et al.*, 2017). Owing to their greater accessibility than the western region of the Selinda Spillway we used the Tsam Tsam floodplains as our study area (Fig. 2). The climate is semi-arid with rainfall around 500 mm per annum (Botswana Meteorological Services). Seasons may be divided into a wet season (December-April), cool early dry season (or flooding season) and hot late dry season (September-November), where maximum daily temperatures range between 35 and 40 °C (Botswana Meteorological Services). Another key feature of the region is the long time taken for the flood pulse to reach the Okavango Delta from the distant high-rainfall Angolan highlands, resulting in the flood levels peaking during the early dry season (hence the term flooding season) and receding over the late dry season (Mendelsohn et al., 2010). This

exposes the floodplains during the late dry season and provides sufficient soil moisture input to support green forage production during this resource-limited period (Fynn *et al.*, 2014).



Figure 2: A map of the study area within the Savuti-Mababe-Linyanti ecosystem, northern Botswana (adapted from Sianga & Fynn, 2017).

Comparison of forage quality and quantity between habitats

We selected four habitat (plant community) types around the distal reaches of the Tsam Tsam floodplains of the Okavango Delta for the study (Fig. 2): sandveld woodland on deep Kalahari sands and mopane woodlands on alluvial soils, both far from floodplains (two major dryland habitat types of the region), a wet sandveld community on deep Kalahari sands abutting the floodplains and a sedgeland community within the parts of the floodplain flooded at intermediate depth and duration (4-6 months, Murray-Hudson *et al.*, 2014).

Sampling was conducted in 2015 during the late dry season (September and October) because this is the time of the year when forage quantity and quality is most limiting to herbivores in African savannas (Sinclair, 1975; Ellis & Swift, 1988; Owen-Smith, 2008) and thus when the functional nature of dry season habitats is most relevant to herbivores (green forage production during the most resource limited time of the year). Within walking distance (< 2km) to the only access road to the distal end of the Tsam Tsam floodplains we located four different sites where deep Kalahari sands intersected the floodplains, thus providing four spatially-blocked replicates as sampling sites for wet sandveld and adjacent sedgeland habitats (Fig. 2). The dryland communities (mopane and sandveld) were sampled at four sites along the access road where it passed through the dryland woodlands between the main edge of the Okavango Delta (between Splash and Kwara) and the distal reaches of the Tsam Tsam floodplains where they extend out into the woodlands (Fig. 2). These dryland woodlands consist of alternating patches of sandveld communities on deep Kalahari sands and mopane communities on alluvial soils enabling us to select four patches of sandveld and four patches of mopane as spatially-blocked sampling sites. At each of the four sampling sites per habitat type a 40 m tape measure was laid down subjectively to ensure that it passed through a representative section of the habitat in question. Thus we sampled four 40 m transects per habitat type (wet sandveld and sedgelands) on the Tsam Tsam floodplains and 4 transects per habitat type in the dryland woodlands (sandveld and mopane) yielding a total of 16 transects.

Forage (grasses and sedges) greenness, height and biomass were sampled at every five metre mark on the tape measure (transect) using a one x one metre quadrat (five quadrats per transect). Forage height was determined by measuring the leaf table height of grasses and sedges at the centre of the quadrat using a 30 cm measuring ruler. Greenness of forage was estimated as

percentage cover of green grasses and sedges rooted within the quadrat, while forage biomass was estimated by clipping all grasses and sedges at ground surface level in the quadrat. The clipped samples were air-dried in the field and then oven dried for 48 hours at 60 degrees centigrade at the Okavango Research Institute laboratory (Maun, Botswana), followed by weighing on an electric balance for biomass. We also collected leaves (no stems) from sedges and grasses in each habitat type. The *Cyperus esculentus* was observed in the sedgeland while *D. eriantha*, *B. nigropedata*, *Schmidtia pappophoroides* and *Eragrostis* spp were in sandveld (wet and dry) and *Heteropogon contortus*, *Eragrostis rigidior* and *Digitaria milanjiana* were in mopane. These samples were oven dried, milled (Okavango Research Institute, Maun, Botswana) and analysed for total nitrogen (TN) following Kjeldahl procedures at Bernlab (Western Cape, South Africa). Crude protein content was calculated as % TN x 6.25 (Crampton & Harris, 1969).

Data analysis

Data of grass greenness, height, biomass and protein were analyzed using a Kruskal-Wallis test ('kruskalmc' function in the pgirmess package) after failing assumptions of normality (Shapiro-Wilk Test) or homogeneity of variance (Levene Statistic) in R (RCore-Team, 2013).

Results

The sedgeland habitat and the wet sandveld woodlands had plants of higher greenness, height and protein content than dryland habitats far from floodplains (mopane and sandveld woodland). The wet sandveld woodland had the highest protein content (~16 %) of all habitat types (P < 0.05, Fig. 3; Table 1). Despite their high protein content during the dry season, plant height and biomass in wet sandveld woodland was much less than that in sedgelands (P < 0.05, Fig. 3; Table 1) but similar to that of sandveld and mopane woodland (P > 0.05, Fig. 3; Table 1). Clearly then, forage of dryland sandveld and mopane woodland is strongly limiting to herbivores during the late dry season in terms of both quantity and quality while wet sandveld provides the highest quality and sedgeland the highest quantity of forage (of intermediate quality) during this season (Fig. 3).



Figure 3: Forage characteristics across the four habitats sampled in the Savuti-Mababe-Linyanti ecosystem, northern Botswana (S - sedgelands, WS - wet sandveld, SV – dryland sandveld and M – dryland mopane). Sedgeland habitat and the wet sandveld woodlands had plants of higher greenness, height and protein content than dryland habitats far from floodplains (mopane and sandveld woodland).

Habitat characteristics	Habitat	Habitat	Test statistic	P value
Grass greenness (%)	Mopane	Sedgelands	-48.98	0.00*
	Mopane	Wet sandveld	-34.75	0.00*
	Mopane	Sandveld	-6.58	1
	Wet sandveld	Sedgelands	14.23	0.29
	Sandveld	Sedgelands	42.4	0.00*
	Sandveld	Wet sandveld	28.18	0.00*
Grass height (cm)	Mopane	Sedgelands	-37.2	0.00*
	Mopane	Wet sandveld	-14.95	0.23
	Mopane	Sandveld	5.15	1
	Wet sandveld	Sedgelands	22.25	0.01*
	Sandveld	Sedgelands	42.35	0.00*
	Sandveld	Wet sandveld	20.1	0.03*
Grass biomass (g/m ²)	Mopane	Sedgelands	-52.95	0.00*
	Mopane	Wet sandveld	-23.9	0.00*
	Mopane	Sandveld	-19.95	0.03*
	Wet sandveld	Sedgelands	29.05	0.00*
	Sandveld	Sedgelands	33	0.00*
	Sandveld	Wet sandveld	3.95	1
Protein (%)	Mopane	Sedgelands	-48.98	0
	Mopane	Wet sandveld	-34.75	0
	Mopane	Sandveld	-6.57	1
	Wet sandveld	Sedgelands	14.23	0.29
	Sandveld	Sedgelands	42.4	0
	Sandveld	Wet sandveld	-28.17	0.00

 Table 1: Kruskal Wallis Multiple Comparison Test (*. Significant difference at the 0.05 level) on forage characteristics in the SMLE.

Discussion

High-quality grasses such as *D. eriantha* and *B. nigropedata*, which are found in both wet and dry sandveld woodlands had high leaf protein levels (~16 %) during the late dry season in the wet sandveld habitat were soil moisture inputs from adjacent floodplains appeared to enable these grasses to produce green leaves at a time when grasses and sedges in dryland habitats have

dried out. This is a key functional trait of a dry season habitat (Fynn et al., 2016) and indicates that wet sandveld woodland is likely important for dry season nutrition for buffalo and other herbivores in the region. This interpretation, however, needs to be tempered by the fact that grass height and biomass in this habitat type was low and no better than that in dryland habitats (Fig. 3), which is probably because of heavy grazing pressure (Blackmore & Vitousek, 2000) on this protein-rich resource. Buffalo generally avoid short grass because of their large body size combined with a tongue sweep strategy for maximizing bite size (e.g. Bhola et al., 2012) and, therefore, their intake rates on short grass are likely to be strongly constrained whereas smallerbodied short grass grazers such as gazelles, impala and wildebeest are able to meet their intake requirements on short grasses (Illius & Gordon, 1987; Wilmshurst et al., 2000). Thus the highquality but short nature of grasses in the wet sandveld woodland suggests that they are a restricted intake resource (high quality but intake limited by quantity – high digestibility, high energy and protein concentrations but requiring a small bite size) for taller grass grazers such as buffalo and a high-quality resource (both quality nor quantity are not limiting intake - high digestibility, high energy and protein concentrations and adequate bite size) for short-grass grazers such as gazelles, impala and wildebeest (Owen-Smith, 2002).

A restricted intake resource can help to balance intake of protein versus fibre for herbivores if used in combination with a higher biomass, adequate-quality resource. For example, Prins & Beekman (1989) showed that buffalo were able to achieve sufficient protein intake as well as overall bulk (fibre) intake by foraging adaptively between short, high-quality *Cynodon dactylon* lawns around Lake Manyara and taller sedgelands within the lake (Prins & Beekman, 1989), very similar to what we found with buffalo foraging between the short grasses of wet sandveld woodland and the taller sedgelands in the Selinda-Okavango region. In contrast to a restricted intake resource, which merely helps to balance intake of energy and protein, a high-quality resource helps to maximize intake rates of protein and energy to meet the elevated intake requirements for growth and reproduction because neither quality nor quantity is limiting intake rate (Owen-Smith, 2002). The presence of a high-quality green forage resource in wet sandveld during the most resource-limited time of the year could also be referred to as a bridging resource because wet sandveld provides a bridge of high-quality forage between the previous and next wet season (Owen-Smith, 2002). Modeling has demonstrated that a bridging resource formed by emergence of fresh green leaves of certain tree species during the late dry season plays a disproportionately-large role in maintaining kudu population densities in Kruger National Park, South Africa (Owen-Smith, 2002). Classification as a high-quality resource is traditionally reserved for a resource that meets the elevated intake requirements of pregnant and lactating females during the wet season period of growth and reproduction and is often dry or depleted by the dry season (Murray, 1995; Owen-Smith, 2002; Hopcraft et al., 2010), whereas a bridging resource, while also of relatively high quality, acts to prevent loss of body condition over the resource-limited late dry season, while its high quality likely also contributes to foetus development over the late dry season (Taylor, 1985; Owen-Smith, 2002). The sedgeland could be referred to as a reserve resource or key resource as it provides adequate-quality forage to prevent large declines in body condition or even mortality over the late dry season but its lower quality will not be ideal for optimal foetus development (Illius & O'Conner, 2000; Owen-Smith, 2002).

Thus adaptive foraging between the wet sandveld (high quality but low quantity) and sedgelands (moderate quality but high quantity) is likely to result in better protein and bulk intake for buffalo in the region than foraging solely in any one habitat type, suggesting that bridging resources and reserve/key resources are most effective when they act in combination rather than individually (see Prins & Beekman, 1989; Owen-Smith, 2002). This may explain why buffalo herds concentrate on the western end of the Selinda Spillway during the late dry season (Naidoo *et al.*, 2014; Sianga *et al.*, 2017; Fig. 2) because wet sandveld habitats appear to be more extensive in this region of the Selinda Spillway than elsewhere in the ecosystem, allowing buffalo to forage adaptively between these wet sandveld areas and adjacent sedgelands (Fig. 1). In addition, apart from the consistent water source for drinking (Redfern *et al.*, 2003), the higher quality and quantity offered by the various habitats in and adjacent wetlands than in drylands during the dry season explains why buffalo and other herbivores switch from dryland woodland habitats during the wet season to wetland habitats during the dry season (Taylor, 1985; Fynn *et al.*, 2014; Sianga, 2014; Sianga *et al.*, 2017).

In conclusion, our study demonstrated that it is the heterogeneity of forage height and nutrient content created by different degrees of flood depth/duration and its effects on habitat productivity that created adaptive foraging options between high-quality but lower quantity resources (restricted intake/bridging resource) and moderate quality but higher quantity resources (reserve/key resource). This likely enables herbivores to better balance their overall nutritional requirements than if they had access to only one structural/ nutrient content - as has been demonstrated elsewhere (Prins & Beekman, 1989; Owen-Smith, 2004). Structural and nutrient content heterogeneity is, therefore, likely to be a key factor determining population productivity and stability in herbivore populations (Owen-Smith, 2002, 2004; Hopcraft *et al.*, 2010).

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Data accessibility

Data (forage characteristics) used in this paper will be freely available on the Okavango Delta Information System (ODIS) at the Okavango Research Institute (ORI), Maun Botswana.

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Chapter 4

Spatial refuges buffer landscapes against homogenization and degradation by large herbivore populations and facilitate vegetation heterogeneity

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ABSTRACT

Environmental heterogeneity across savanna landscapes, including different seasonal resources at different distances from water, may play a critical role in maintaining the size and diversity of wildlife populations and the sustainability of their resource base. We investigated whether extensive landscapes with functionally-diverse seasonal resources and large waterless regions, can mediate the effect of herbivory on plant composition, structure and diversity. Vegetation composition, structure and richness in two different vegetation types (Mopane and Sandveld woodland) at three distance zones (0-5, 10-15 and > 20 km) from the permanent water of the Okavango Delta and Linyanti Swamps were surveyed. We investigated vegetation response of the most abundant species to herbivory in relation to distance from permanent water, and included fire frequency as a covariate. Trees favoured by elephants during the dry season occurred typically as shrublands, pollarded populations within 5 km of permanent water sources while mature tall populations of these species were found far from water (> 10-15 km). Similarly, short high-quality grazing grasses were more abundant within 5 km of permanent water whereas taller high-quality perennial grasses were abundant beyond 20 km from permanent water. Trends in herbaceous richness with distance from water were contingent upon vegetation type, while tree richness did not change with distance from water. Spatial refuges in waterless regions of landscapes in the Savuti-Mababe-Linyanti ecosystem (SMLE), facilitate the creation of heterogeneity of vegetation structure, composition and richness by large herds of mammalian herbivores. Therefore, the extension of herbivore dry season foraging range by, for example, the creation of artificial water points in backcountry woodlands, could undermine the resilience of landscapes to herbivory by reducing the availability of spatial refuges. Consequently, it could reduce the resilience of herbivore and predator populations that depend on

these spatial refuges. We strongly advise that future scientific work, and management and policy actions should be focused on the identification and sustaining of these spatial refuges in wildlife areas.

Key words: Elephant effects, forage resources, herbivores, plant diversity, water availability

INTRODUCTION

Environmental heterogeneity across savanna landscapes (spatial heterogeneity) may play a key role in determining plant (MacFayden *et al.* 2016), large mammal and bird diversity (Mills & Gorman 1997; Harrington *et al.* 1999; Fuhlendorf *et al.* 2006; Krook *et al.* 2007). This heterogeneity also determines the strength of density-dependent feedbacks on large herbivore population growth (Wang *et al.* 2006; Hobbs *et al.* 2008) and the viability of their populations (Illius & O'Connor 2000; Owen-Smith 2004; Hobbs *et al.* 2008; Hopcraft *et al.* 2010). Spatial heterogeneity is determined by spatial variation in abiotic factors such as physical, chemical, topographic, hydrological, climatic and biotic factors (Owen-Smith 2004; Hobbs *et al.* 2008; Hopcraft *et al.* 2010; Fynn 2012).

Distance to water during the dry season, which affects herbivore foraging intensity, habitat structure and niche diversity, is another form of spatial heterogeneity. Plant species favoured by large herbivores may be spared from excessive herbivore impact in regions of landscapes far from permanent water (O'Connor *et al.* 2007). Sable (*Hippotragus niger*) and roan (*H. equinus*) antelope depend upon waterless, backcountry parts of landscapes to avoid higher concentrations of predators and other herbivore species closer to permanent water (Harrington *et al.* 1999; Hensman *et al.* 2014; Haveman 2014). These species have specialized narrow mouths adapted to foraging on taller grasses in these low herbivore density backcountry habitats (Codron *et al.* 2008; Fynn *et al.* 2016). Similarly, meso-carnivores, such as African wild dog (*Lycaon pictus*), may also be forced by competition with larger carnivores to focus their hunting in regions of landscapes with lower abundances of their favoured prey (Mills & Gorman 1997). Thus, large distances from water during the dry season are a key characteristic of landscapes in African savannas, creating spatial refuges for various plant and animal species. For
example, in the Kruger National Park, where artificial water provision from boreholes in waterless, backcountry parts of landscapes removed these spatial refuges, which may have resulted in a collapse of rare herbivore populations (Harrington *et al.* 1999).

Fragmentation of ecosystems and landscapes by anthropogenic activities poses a threat to the viability of wildlife populations due to restricted access to spatially heterogeneous landscapes, and by degrading resources caused by an increase in the strength of coupling of herbivores to their resources (Hopcraft *et al.* 2010; Fynn 2012). Herbivores become increasingly coupled to their resources as the opportunity for adaptive foraging declines with greater restrictions on movement and with decreasing heterogeneity (Hobbs *et al.* 2008; Hopcraft *et al.* 2010; Fynn 2012). Thus, extensive heterogeneous landscapes, where herbivores are able to move seasonally between functionally-different habitats and avoid heavily-utilized areas and where large distances from permanent water exist, are likely to be more resilient to the impacts of large herbivore populations but this resilience is likely declining with increasing modification of ecosystems by agriculture, fencing and artificial water provision (AWP).

The African elephant (*Loxodonta africana*) is notorious for its effects on woody vegetation (O'Connor *et al.* 2007) and there is much concern that growing elephant populations may negatively influence ecosystem functioning and diversity in protected areas (Cumming *et al.* 1997). Elephants have induced dramatic changes in ecosystems by transforming woodlands into open savanna or grasslands (Laws 1970; Spinage 1994), effects that may be compounded by interactions with fire (O'Connor *et al.* 2007). Elephants can kill large trees and shrubs through pollarding, ring-barking and young plants through uprooting (Vesey-FitzGerald 1973; O'Connor *et al.* 2007) reducing the density and structure of woody vegetation (Glover 1963; Cumming *et al.* 1997; Ben-Shahar 1998; Teren & Owen-Smith 2010; Asner & Levick 2012).

However, the ability of elephants to access food is strongly constrained by water availability, with bulls and breeding herds generally limited to foraging within 15 and 5 km of water, respectively (O'Connor et al. 2007; Young & Van Aarde 2010). Thus, areas further from water than the viable foraging range of elephants (> 15 km) are likely to represent a spatial refuge from elephant impact, for vegetation and herbivores which depend on these spatial refuges (O'Connor et al. 2007). The diet of elephants varies seasonally, with green grass and herbs being favoured during the wet season, browse during the early dry season and tree roots and bark by the late dry season (O'Connor et al. 2007). Certain woody species appear to be particularly favoured during the dry season, and it is expected that these species will be heavily impacted in areas within 5 km of water during the dry season (maximum foraging range of breeding herds) with little impact beyond 15 km from permanent water (maximum foraging range of bulls). We refer to this as the distance from water spatial refuge hypothesis (DWSR hypothesis) (O'Connor et al. 2007). The DWSR hypothesis is also applicable to large populations of other grazers whose year-round grazing effects may eliminate high-quality tufted perennial grasses that require long periods of recovery from grazing (Fynn 2012). Thus, one may expect to find a higher abundance of high-quality, tufted perennial grasses within habitat types beyond the maximum foraging range of herbivores from water during the dry season and a higher abundance of more grazing-tolerant shorter grasses closer to available water. This suggests that herbivory gradients across unmodified landscapes facilitate greater compositional and structural heterogeneity than in landscapes where distance to dry season water has been greatly modified by AWP.

Against this background, AWP is increasingly used in protected areas in African savannas, with the consequence that landscapes are losing spatial refuges from year-round

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herbivory for plants and animals, even in very large protected areas (e.g. Redfern et al. 2003). Owing to the potential for AWP to disrupt spatial refuges for plants and animals it is becoming increasingly urgent to study the effects of herbivory on vegetation and animals in extensive, unfragmented landscapes that still have large areas without AWP and with large distances away from permanent water. The northern conservation area of Botswana is one of the few remaining open, wildlife systems in Africa (about 100 000 km² on the Botswana side and extending into protected areas in Namibia and Zimbabwe), supporting the largest African elephant population globally at around 130 000 (Chase 2011; Chase et al. 2016). This Savuti-Mababe-Linyanti ecosystem (SMLE) is a relatively pristine region of the northern conservation area containing extensive savanna woodlands sandwiched between the permanent water sources of the Okavango Delta and Linyanti Swamps, where large areas of woodland may occur > 20 km from permanent water sources, well beyond the maximum movement distance of the more mobile bull elephants during the dry season. Thus the extensive unmodified landscapes of the SMLE with their large distances from available water during the dry season (> 20 km), their lack of anthropogenicallyinduced barriers to herbivore movement, and their large populations of elephant, buffalo (Syncerus caffer) and zebra (Equus quagga) provide an ideal study site to gain insights into landscape-mediated herbivore controls of vegetation composition, structure and diversity.

Considering that a large proportion of the landscapes of the SMLE occur beyond the reach of large herbivores during the dry season (spatial refuge), we hypothesized that greater year-round herbivore density within five km of permanent water will negatively affect woody structure, grass cover and plant richness in this zone but have little effect in zones further from permanent water. Thus at a landscape scale herbivores are likely to create spatial heterogeneity

in plant composition, diversity and structure, as opposed to homogenization of plant composition and structure and a decline of species richness in less resilient landscapes.

METHODS

Study area

This study was conducted over the 2014 wet season in the northern conservation area of Botswana, in the extensive open woodland landscapes between the Okavango Delta in the south west and the Linyanti Swamps in the north east (Fig. 1). Rainfall in the area averages between 500 and 600 mm in the Okavango region (western boundary of the SMLE) and Chobe Enclave region (eastern boundary of the SMLE), respectively (Fynn et al. 2014). Rainfall is received between November and April (Botswana Meteorological Services), with maximum daily temperatures between 35 and 40 °C (Fynn et al. 2014). The Kwando River that feeds into the Linyanti Swamps and the Okavango River that feeds into the Okavango Delta are the primary sources of permanent water in the ecosystem (Fig. 1). One artificial water point at Hyena Pan (~ 11 km from water), near one of our large transects (T3), has been pumped consistently since 2013, about a year prior to our sampling, and as such unlikely to have affected the vegetation at that time. The major vegetation of the woodlands between the Okavango Delta and Linyanti Swamps is a mosaic of mopane woodland on alluvial soils and sandveld woodland on deep Kalahari sands, which have filled old river channels (Mendelsohn et al. 2010). Mopane woodland is dominated by *Colophospermum mopane* in the tree layer and *Jasminum stenolobum*, Zornia glochdiata, Kyllinga buchananii, Commelina forskaolii, Aristida adscensionis, Aristida scrabrivalvis and Urochloa trichopus in the herbaceous layer, while sandveld woodland is dominated by Terminalia sericea and Philenoptera nelsii in the tree layer and Ipomea

chloroneura, *Oxygonum alatum*, *Hibiscus mastersianus*, *Chaemacrista stricta*, *Aristida stipitata*, *Digitaria eriantha* and *Panicum maximum* in the herbaceous layer (Sianga & Fynn 2017).



Figure 1: A map of the study area in the woodlands between the Okavango Delta and the Linyanti Swamps showing the locations of the large (T1-4) and small transects.

Vegetation sampling

Four large transects (about 27 km each) perpendicular to permanent water sources of the Linyanti Swamps and Okavango Delta (Fig. 1) were sampled during the wet season (from January to end of March 2014) along easy access routes such as cutlines extending out from the two wetland systems and, therefore, across the major axis of the landscape (Fig. 1). Each transect

was divided into three distance zones: near zone (0-5 km), intermediate zone (10-15 km) and a far zone (> 20 km; up to 27 km) from permanent water. Thus, our four large transects represent landscapes with > 40 % of their total area being beyond the maximum movement distance of elephant from water during the dry season. We controlled for environmental effects by selecting only mopane and sandveld woodland because these are dryland plant communities that occur in all three distance zones. Thus, we avoided the confounding effects of soil type and soil moisture by keeping vegetation and soil types constant along the large transects (we avoided moist riverine communities directly adjacent to floodplains). The mopane-sandveld mosaic makes up over 90 % of the total surface area of the dryland vegetation and so provides the greater bulk of the forage resources outside of the wetlands (Fig. 1). This study aimed to assess the integrated effect of herbivory on vegetation in both the wet and dry season, which is manifest in wet season growth. Additionally, dry season sampling is difficult, since all species senesce and most herbaceous species disappear completely, making it inaccurate (and spurious) to determine composition and richness during this time of year. Therefore, vegetation sampling was done during the wet season, starting in January for easier identification of species (i.e. presence of flowers or inflorescence).

In each distance zone along the large transects, we laid down 6 - 7 small transects in each of the two vegetation types (mopane and sandveld). The position of small transects was identified by using two random number of meters between 20 and 100, with the first random number taken along an access route (cutline) and the second perpendicular from the cutline into the vegetation. A transect was set at a point where the second number fell. Each small transect was 100 m long and orientated perpendicular to the access road. Small transects were at least 500 m apart if in the same patch of woodland but we generally chose a new patch of sandveld or

mopane woodland for each transect (the mopane and sandveld communities consists of a mosaic of patches, each generally several hundred meters wide, determined by patches of alluvial soils alternating with sand filled paleo-river channels).

Plant species richness

For plant species richness, all forb, grass and woody species were enumerated in one 40 m x 20 m releve plot per transect laid down over the first 40 m of each small transect. On large transect 3 (T3) in the > 20 km zone in mopane woodland, only three releve plots were used in the analysis instead of seven, owing to an error in plot sizes (50 m x 20 m instead of 40 m x 20 m) for four releve plots, which we discarded.

Woody vegetation

Woody vegetation structure was assessed at three points on the small transects (0 m, 50 m and 100 m) according to an adaptation of the Point-Centred Quarter method (PCQ; Mitchell 2010), whereby we added height classes of woody vegetation (0-1 m, 1-2 m, 2-4 m and > 4 m). Per centre point, the area to be sampled was divided into quarters by imagining a line perpendicular to the transect line. For every quarter (hereafter sample point) the closest tree was identified in every height class. To avoid overlap between the sample points, a maximum sampling distance of 25 m to the nearest tree of a specific height class was chosen. For the sampled trees, distance from sampling point to centre of tree trunk (with use of a rangefinder) and height (with use of a measuring pole) (Mitchell 2010) was recorded. While plotless methods such as the point-centre quarter method may not be suitable for estimating the density of rare species, we restricted our

analyses to the three most abundant species and our probability estimates are expected to be robust.

Grasses

Grasses were sampled at five points on the small transects (0 m, 25 m, 50 m, 75 m and 100 m) in 1 m^2 quadrats (hereafter sample point). All grass species rooted within each quadrat were listed and their cover estimated (to within 5 % accuracy if cover >10% (Koerner *et al.* 2014), and to within 1% accuracy if cover <10%, as not to overestimate the abundance of rare species). Grasses that could not be identified to the species level, mainly due to the absence of inflorescence or small growth stage of the plant in young grasses, were if possible identified to the genus level or else marked as 'unidentified'.

Unknown plants were pressed in the field and brought to the Peter Smith Herbarium (PSUB) collection at the Okavango Research Institute (Maun, Botswana) for identification. All vegetation nomenclature followed Germishuizen *et al.* (2006).

Herbivore density estimates

Herbivore dung was used to estimate herbivore density in our study area. Elephant and other herbivore dung heaps were counted within 2 m of each side of each small transect. Dung counts of elephants are a reliable index of elephant density (Barnes 2001), which is also true for the other mammalian herbivores (Cromsigt *et al.* 2009). Owing to the long lasting nature of elephant dung, dung counts represent current wet season deposits as well as carry over from the previous

dry season. Identification of herbivore species based on dung found in our study area was based on Walker (1996) and the expertise of Dr. Richard Fynn.

Fire

To test the effects of fire we used Moderate Resolution Imaging Spectroradiometer (MODIS) Normalised Difference Vegetation Index (NDVI) time-series to map fire events over the last 15 years. These data were used to determine the burn frequency of each small transect, which was used as a co-variate in our statistical models.

Statistical analysis

Data from the two vegetation types (mopane and sandveld) were analysed separately. We analysed the relationships between each of the three response variables, (1) species richness of grasses, forbs and trees, (2) woody species structure (height class) and (3) grass cover in mopane and sandveld woodland, and four predictor variables: (a) distance zone from permanent water, (b) elephant dung count, (c) herbivore dung count, and (d) fire frequency, and added one or two (see motivation below) random effects: (r1) small transect and (r2) sample point, using Bayesian Generalized Linear Mixed Models (BGLMM) with Markov Chain Monte Carlo estimation (MCMC) using the MCMCglmm package (Hadfield 2010) in R, version 3.2.3 (RCore-Team 2013). We tested our hypothesis that greater elephant density closer to permanent water would negatively affect woody structure, grass cover and plant richness using two approaches: (i) a model that considered distance zone from permanent water and fire frequency and their interaction as fixed effects, where the 0-5 km zone was thought to be subject to year-round elephant occupancy in greater numbers, but occupancy and abundance would decline further

from permanent water, especially beyond 20 km during the dry season (O'Connor *et al.* 2007; Young & Van Aarde 2010); (ii) a model that considered elephant dung count (or herbivore dung count) and fire frequency and their interaction as fixed effects (as elephant dung count strongly differed between distance zone and could cause collinearity in the model). We included fire frequency as a covariate because fire is considered to be a critical variable affecting the composition and structure of woody vegetation (Mudongo *et al.* 2015). Furthermore, previous studies indicate that fire frequency interacts with herbivory in its effect on plant richness (Collins *et al.* 1998; Koerner *et al.* 2014).

Random effects were included in the models based on the rules of thumb: > 5-6 levels per random effect and > 10-20 samples per treatment level or experimental unit (Bolker *et al.* 2008). Thus, none of our models included the large transects (4 levels) in the random effect structure. The models for grass cover and species richness included only small transect (7 levels) in the random effect structure, while for woody species we also included sample point as a random effect (12 levels), nested within small transect.

For species richness a Poisson distribution with a log-link (family "poisson") was specified for both models. Initial models started with an inverse Wishart prior for both the residual and random effect (co)variances (R and G-structures: $Pr(\sigma 2) \sim IW (V = 1, nu = 0.002)$). For the response variables woody structure and grass cover, binomial distributions with logit-links (families "categorical" and "multinomial2", respectively) were specified. Initial models started with a prior residual variance component fixed to 1 (R-structure: $Pr(\sigma 2) \sim IW(V = 1, fix = 1)$) and an inverse Wishart prior for the random effect (co)variances (G-structure: $Pr(\sigma 2) \sim IW(V = 1, nu = 0.002)$).

We ran all initial models with 500 000 iterations, a burn-in period of 100 000, and a thinning interval of 100 iterations to allow us to store 4 000 samples. We examined sampling efficiency and convergence of each initial model through their mixing properties, using trace plots and calculated autocorrelation within and between all fixed and random effects. We only accepted models if the autocorrelation < 0.1 (Hadfield 2015).

If model sampling efficiency and convergence was unsatisfactory we used a stepwise process to improve the model's performance: first, by adding a redundant non-identified parameter to the G-structure of the initial prior (parameter expanded priors: alpha.mu = 0 and alpha.V = 1 000); then, by using the slice sampling method of (Damien *et al.* 1999) in combination with both the initial and parameter expanded priors; and, when previous adjustments did not improve mixing properties of the models to a satisfying level, we improved mixing by varying the residual variance from 1 to a maximum of 10. These adjustments may improve mixing properties of the chain and lead to quicker model convergence (Hadfield 2015). If this still did not result in an acceptable level of autocorrelation we increased the total number of iterations with steps of 500 000 iterations until it did, which required also increasing the thinning and burn-in proportionally (thin = 0.0002 and burnin = 0.2 of total number of iterations) to maintain the total number of stored samples at 4000. Our final models are specified in supplementary material under Table S1. We validated our models by running each final model three times and calculate their average autocorrelation and check model convergence using the Gelman and Rubin's convergence diagnostic (Gelman & Rubin 1992), which compares within and between chain variance. Models had converged if the potential scale reduction factor PSR <1.1. For woody structural and grass cover responses, we here present only species that were abundant enough to be analyzed, e.g. to give an adequate model convergence. Hence, hereafter we discuss only three tree species (*C. mopane*, *P. nelsii* and *T. sericea*) and twelve grass species (*Aristida adscensionis, Aristida scrabrivalvis, Aristida stipitata, Dactyloctenium giganteum, Digitaria eriantha, Digitaria milanjiana, Eragrostis rigidior, Eragrostis trichophora, Panicum maximum, Pogonarthria fleckii, Schmidtia pappophoroides and Urochloa trichopus).*

RESULTS

We observed a total of 38 tree, 191 forb and 66 grass species. Unidentified grass species (including grasses that were identified only to the genus level) accounted for < 1% cover in both mopane and sandveld woodland.

Plant species richness

Grasses

Species richness of grasses, forbs and trees responded differently to distance zone, elephant dung counts and fire frequency and between vegetation types (Table 1, Figs. 2 and 3). In mopane woodland, grass richness was not significantly related to distance zone, elephant or herbivore dung count or fire, but in sandveld woodland the far zone (> 20 km) had significantly lower grass richness than the near zone (< 5 km) (pMCMC = 0.01) (Table 1 and Fig. 2). Similar to distance zone, grass richness was greater in sites with higher elephant dung counts (but not herbivore dung counts) in sandveld woodland (pMCMC = 0.03), suggesting that higher richness in the near zone in sandveld is related to greater elephant impact in this zone (Table 1 and Fig. 3). Similarly, fire frequency was positively related to grass richness in sandveld woodland (pMCMC = 0.01) (Table 1).

Table 1: MCMC analyses (Hadfield 2010) of grass, forb and tree richness data in sandveld and mopane woodland in different distance zones from permanent water (zone) and gradients of elephant density (elephant dung count). Significant variables (P < 0.05) in bold font. E.Dung = Elephant dung count; H.Dung = Herbivore dung count

Grasses	Mopane	T			Sandveld			
Variable	Post. Mean	Lower CI	Unner CI	nMCMC	Post Mean	Lower CI	Upper CI	pMCMC
Intercept	2.22	2.04	2.40	<3e-04	1.88	1.64	2.11	<3e-04
Zone 2	-0.07	-0.34	0.22	0.63	-0.15	-0.52	0.23	0.44
Zone 3	-0.03	-0.33	0.24	0.80	-0.50	-0.89	-0.11	0.01
Fire	0.03	-0.10	0.15	0.66	0.06	-0.09	0.21	0.41
Zone 2:Fire	0.10	-0.09	0.27	0.28	0.00	-0.21	0.23	1.00
Zone 3:Fire	0.04	-0.14	0.19	0.61	0.19	-0.01	0.40	0.06
Intercept	2.20	2.06	2.34	<3e-04	1.55	1.35	1.77	<3e-04
E.Dung	0.00	-0.01	0.01	0.92	0.01	0.00	0.02	0.03
Fire	0.08	-0.01	0.16	0.07	0.16	0.04	0.27	0.01
E.Dung:Fire	0.00	-0.01	0.00	0.69	0.00	-0.01	0.00	0.35
Intercept	2.21	2.08	2.33	<3e-04	1.65	1.48	1.84	<3e-04
H.Dung	-0.01	-0.07	0.05	0.75	0.02	-0.03	0.07	0.36
Fire	0.07	0.00	0.15	0.05	0.14	0.05	0.22	0.00
H.Dung:Fire	0.00	-0.03	0.03	0.95	-0.01	-0.06	0.04	0.66
Forbs								
Intercept	3.55	3.44	3.65	<3e-04	3.70	3.60	3.80	<3e-04
Zone 2	0.03	-0.14	0.19	0.77	-0.09	-0.25	0.07	0.28
Zone 3	0.25	0.08	0.40	0.00	-0.23	-0.38	-0.05	0.01
Fire	-0.06	-0.14	0.02	0.11	0.01	-0.06	0.07	0.84
Zone 2:Fire	0.07	-0.04	0.18	0.24	0.03	-0.06	0.13	0.48
Zone 3:Fire	0.06	-0.03	0.17	0.21	0.07	-0.02	0.16	0.13
Intercept	3.63	3.54	3.73	<3e-04	3.54	3.45	3.63	<3e-04
E.Dung	0.00	-0.01	0.00	0.46	0.01	0.00	0.01	0.01
Fire	0.04	-0.01	0.10	0.11	0.06	0.01	0.11	0.01
E.Dung:Fire	-0.01	-0.01	0.00	0.01	0.00	0.00	0.00	0.09
Intercept	3.61	3.51	3.70	<3e-04	3.57	3.50	3.65	<3e-04
H.Dung	0.01	-0.03	0.05	0.74	0.03	0.01	0.05	0.01
Fire	0.01	-0.04	0.07	0.61	0.05	0.01	0.08	0.02
H.Dung:Fire	0.00	-0.02	0.02	0.98	-0.01	-0.04	0.01	0.18

Trees								
Intercept	1.87	1.66	2.08	<3e-04	1.88	1.63	2.11	<3e-04
Zone 2	0.00	-0.37	0.35	1.00	-0.41	-0.83	0.01	0.06
Zone 3	-0.05	-0.40	0.29	0.79	-0.28	-0.66	0.12	0.16
Fire	-0.10	-0.26	0.06	0.22	-0.10	-0.27	0.06	0.23
Zone 2:Fire	0.01	-0.24	0.26	0.94	0.13	-0.11	0.39	0.30
Zone 3:Fire	0.10	-0.12	0.31	0.38	0.14	-0.08	0.37	0.22
Intercept	1.84	1.66	2.02	<3e-04	1.62	1.41	1.84	<3e-04
E.Dung	0.00	-0.01	0.01	0.97	0.01	0.00	0.01	0.26
Fire	-0.02	-0.14	0.08	0.67	-0.06	-0.18	0.07	0.37
E.Dung:Fire	0.00	-0.01	0.00	0.37	0.00	0.00	0.01	0.48
Intercept	1.84	1.67	1.99	<3e-04	1.64	1.44	1.83	<3e-04
H.Dung	0.01	-0.06	0.08	0.80	0.04	-0.01	0.09	0.12
Fire	-0.04	-0.14	0.06	0.45	0.00	-0.10	0.10	0.96
H.Dung:Fire	-0.01	-0.06	0.03	0.51	-0.05	-0.11	0.01	0.09



Figure 2: The relationship between species richness in mopane woodland and distance zone from permanent water or elephant dung count.



Figure 3: The relationship between species richness in sandveld woodland and distance zone from permanent water or elephant dung count.

Forbs

Forb richness showed similar responses to grasses being higher in the near zone of sandveld woodland (pMCMC = 0.01) and increasing with increasing elephant dung count (pMCMC = 0.01) (Table 1 and Fig. 3) but showed the opposite response in mopane woodland, being lower in the near than the far zone (pMCMC = 0.00) (Table 1 and Figs. 2-3). While there was no significant relationship between grass richness and herbivore dung count, for forb richness there was a significant positive relationship in sandveld woodland (pMCMC = 0.01), similar to the relationship with elephant dung count (Table 1 and Figs. 3). Thus there appears to be a general trend of forb and grass richness being affected positively by disturbances from elephants (and to

a lesser extent herbivores) in sandveld woodland, but with the opposite trend in mopane woodland.

Trees

In contrast to grasses and forbs, fire, elephant and herbivore dung count and distance zone were not significantly related to tree richness in sandveld or mopane woodland (Table 1).

Woody species structural responses

For *C. mopane*, there was a significant zone x height class 4 interaction where the > 20 km zone (posterior mean = 2.80, pMCMC = 0.01) had a significantly higher probability of finding individuals of C. mopane in the > 4 m height class (Table S2; Fig. 4). This was also reflected in the elephant dung count x height class interaction where the probability of finding individuals of C. mopane of the > 4 m height class was lower with higher elephant dung count (posterior mean= - 0.06, pMCMC= 0.03) (Table S2; Fig. 4). However, these effects were small relative to those on T. sericea. Fire frequency was negatively related to the probability of observing C. *mopane*, especially in the taller height classes as shown by the fire frequency x height class interaction (Table S2). For *P. nelsii*, there was also a significant zone x height class 4 interaction but in the opposite direction to T. sericea, where the 10-15 km zone (posterior mean = -2.35, pMCMC = 0.02) and the > 20 km zone (posterior mean = -4.12, pMCMC = 0.00) had significantly lower probability of containing individuals of *P. nelsii* > 4 m height class (Table S2; Fig. 4). In other words, taller trees of *P. nelsii* were more common in the 0-5 km zone (Fig. 4). There was a lower probability of finding individuals of P. nelsii > 4 m tall where fire frequency was greater (posterior mean = -0.93, pMCMC = 0.01) (Table S2).



Figure 4: The relationship between the height structure of the three most dominant tree species of the study area and distance zone from permanent water. HC = Height class (1: 0-1 m, 2: 1-2 m, 3: 2-4 m and 4: > 4 m), *C. mopane* = *Colophospermum mopane*, *P. Nelsii* = *Philenoptera nelsii* and *T. sericea* = *Terminalia sericea*.

For *T. sericea*, there was a significant zone x height class 4 interaction, whereby the 10-15 km zone (posterior mean = 6.48, pMCMC = 0.00) and the > 20 km zone (posterior mean = 6.38, pMCMC = 0.00) had significantly higher probability of containing individuals of *T. sericea* in the > 4 m height class (Table S2; Fig. 4). This was also reflected in the elephant dung count x height class interaction where the probability of finding individuals of *T. sericea* of the > 4m height class was lower with higher elephant dung count (posterior mean = -0.10, pMCMC = 0.01) (Table S2; Fig. 4).

Grass cover responses

Distance from permanent water

Digitaria eriantha, a high-quality medium/tall perennial grass, was not different across the three distance zones (0-5 km: posterior mean = -14.08, pMCMC = 0.00, 10-15 km: posterior mean = 2.56, pMCMC = 0.37and > 20 km: posterior mean = 0.97, pMCMC = 0.76) in mopane woodland (Fig. 5; Table S3). However, in its preferred habitat, sandveld, where it is more abundant, D. eriantha had lower cover in the near zone (0-5 km) than the intermediate (10-15 km) (posterior mean = 2.02, pMCMC = 0.03) and far zones (> 20 km) (posterior mean = 2.23, pMCMC =0.01) (Table S3; Fig. 5) but for *Panicum maximum*, another high-quality tall perennial grass, cover in the 10-15 km (posterior mean = 0.50, pMCMC = 0.70) and > 20 km (posterior mean = -0.56, pMCMC =0.68) zones did not differ from the 0-5 km zone in sandveld woodland (Fig. 5; Table S3). Urochloa trichopus, a high-quality short annual grass, had much greater cover in the 0-5 km zone than the 10-15 km (posterior mean = -6.86, pMCMC = 0.00) and > 20 km (posterior mean = -4.46, pMCMC = 0.01) zones in sandveld woodland, while in mopane woodland only the 10-15 km (posterior mean = -4.05, pMCMC = 0.02) and not the > 20 km (posterior mean = -1.65, pMCMC = 0.27) zone was significantly lower than the 0-5 km zone (Fig. 5; Table S3). For poor-quality grazing grasses, such as Aristida adscensionis, the cover of the 10-15 km (posterior mean = 0.79, pMCMC = 0.29) and > 20 km (posterior mean = 0.31, pMCMC = 0.68) zones in mopane woodland did not differ from the 0-5 km zone (Fig. 5; Table S3) as was the case with Aristida stipitata in sandveld woodland, where its cover in the 10-15 km (posterior mean = -0.63, pMCMC = 0.60) and far > 20 km (posterior mean = 0.21, pMCMC = 0.88) zones did not differ from the 0-5 km zone (Fig. 5; Table S3). However, cover of the poor quality *Pogonarthria fleckii* was greater in the 0-5 km zone in both sandveld (posterior mean = -7.72, pMCMC = 3e-04) and mopane woodlands (posterior mean = -6.04, pMCMC = 0.00) (Fig. 5; Table S3).



Figure 5: The relationship between the cover of the major grasses of the study area and distance zone from permanent water. Uro.trich = Urochloa trichopus, Sch.papp = Schmidtia pappophoroides, Pog.flec = Pogonarthria fleckii, Pan. Maxi = Panicum maximum, Era.tric = Eragrostis trichophora, Era.regi = Eragrostis rigidior, Dig.mila = Digitaria milanjiana, Dig.eria = Digitaria eriantha, Dac.giga = Dactyloctenium giganteum, Ari.stipi = Aristida stipitata, Ari.scab = Aristida scrabrivalvis, Ari.adsc = Aristida adscensionis

Elephant dung count

Cover of poor-quality grazing grass such as *P. fleckii* increased with increasing elephant dung count in mopane (posterior mean= 0.20, pMCMC= 0.00) and sandveld woodlands (posterior mean= 0.26, pMCMC=

0.00), respectively but that of *A. adscensionis* and *Eragrostis trichophora* decreased with increasing elephant dung count in mopane woodland (posterior mean= -0.05, pMCMC= 0.01, posterior mean= -0.56, pMCMC= 0.00) respectively (Table S3). The high-quality annual grass *Dactyloctenium giganteum* also decreased with increasing elephant dung count in sandveld woodland (posterior mean=-0.09, pMCMC= 0.02) (Fig. 5; Table S3).

Herbivore dung count

A. adscensionis, E. rigidior, E. trichophora and *S. pappophoroides* (all in mopane woodland) decreased with herbivore dung respectively (posterior mean= -0.31, pMCMC= 0.03, posterior mean= -1.25, pMCMC= 0.03, posterior mean= -1.60, pMCMC= 0.01, posterior mean= -3.03, pMCMC= 0.00 (Table S3) while that of *U. trichopus* in sandveld woodland increased with herbivore dung (posterior mean = 0.53, pMCMC= 0.03) (Table S3).

Fire

Fire had no effect on *A. adscensionis*, *U. trichopus*, *E. rigidior*, *E. trichophora*, *P. maximum*, *P. fleckii* in mopane woodland and *D. giganteum*, *D. eriantha*, *P. maximum*, *U. trichopus* and *P. fleckii* (all in sandveld) respectively (Table S3). Grasses such as *D. eriantha* and *S. pappophoroides* increased with fire in mopane woodland (Table S3).

DISCUSSION

Our study demonstrated that spatial refuges far from permanent water in the relatively unmodified landscapes of our study area provided a buffering effect against homogenization of vegetation composition, structure and diversity across the landscape by a large elephant population and large populations of buffalo and other large herbivores. This supported our hypothesis that landscapes that have a large proportion of their area beyond the maximum foraging distance from water during the dry season for most large herbivores (>15 km) would be resilient to the impacts of large herbivore populations. There is great concern that growing populations of elephant may eventually reach levels that will negatively affect ecosystem

function and diversity, and thereby populations of other herbivore species (Cumming *et al.* 1997). Northern Botswana has by far the largest population of elephants in Africa at approximately 130 000 (Chase 2011; Chase *et al.* 2016) and there is therefore potential for elephant to homogenize vegetation structure and reduce diversity across landscapes (e.g. Asner & Levick 2012). However, in the landscapes of our study area, which extend to at least 25 km from available water during the dry season, we did not observe homogenization of vegetation composition, structure or richness but rather heterogeneity in these variables. For example, woody species favoured over the dry season such as *T. sericea* (Ben-shahar 1993), occurred as immature populations of short, pollarded shrubs within 5 km of water but tall mature populations of these species were typical of the landscape beyond 20 km from permanent water but even as little as 10 km (Fig. 4; Fig.6).



Figure 6: Structure of *Terminalia sericea* with increasing distance from water. Within 5 km of water most individuals of *T. sericea* have been severely pollarded (A) and kept in a shrubland structural state (B). However, greater than 10 km from water individuals of *T. sericea* > 4 m in height are common (C). Photo credit – Jip Vrooman.

By contrast, elephants are impacting favoured woody species right across landscapes in the Kruger National Park (Asner & Levick 2012), where artificial water points have reduced the average distance to available water in the dry season to around six kilometres (Redfern *et al.* 2003), well under our proposed distance of 15 km, thereby eliminating spatial refuges in the landscape for favoured woody species. Similarly, elephants

are impacting trees up to 60 km from the Chobe River (Fullman & Child 2013) because of many artificial water points in those distant back country woodlands, enabling elephant to spend all year in the backcountry areas (no spatial refuge available).

In addition, there was no change in woody species richness in sandveld and mopane woodland with distance from water or with elephant dung count (Table 1), suggesting that in these extensive landscapes most woody species populations are not extirpated under high elephant impact but rather survive in a shorter structural state. Thus, in accordance with our hypothesis, it appears that in extensive, heterogeneous landscapes without fences restricting movement, where elephant are able to move seasonally between functionally-different habitats and shift their foraging away from over-utilized areas, woody plants are able to persist under a large elephant population (albeit in a shorter state), such that woody diversity is not negatively impacted (sensu Fynn 2012). By contrast, richness of woody species was found to be significantly lower in the elephant impacted zone (< 10 km) of the Chobe River Front (Fullman & Child 2013) and inside the southern buffalo fence of the Okavango Delta (Cassidy et al. 2013). The much greater effect of elephants on tree richness in sandveld and mopane woodlands (the same communities examined in our study) along the southern buffalo fence than in our study could possibly have been caused by elephant movement ranges in these woodlands being constrained to a relatively narrow band of woodland between the floodplains of the Okavango Delta and the southern buffalo fence, hence no spatial refuges are possible and the southern buffalo fence is likely to further concentrate elephant foraging. Thus in these extensive, relatively unfragmented woodland landscapes, where large parts of the landscape occur greater than 15 km from permanent water (spatial refuges), elephants have not homogenised woody vegetation structure or reduced diversity but rather have created structural heterogeneity across the landscape, as predicted for large unmodified landscapes (Du Toit et al. 2014).

The contrasting responses of forb and grass richness to herbivory and distance from permanent water in mopane and sandveld woodlands appear to be related to well known interactions of herbivory and habitat productivity on grass and forb richness, with richness generally being decreased by herbivory in less productive habitats and increased by herbivory in more productive habitats, observed globally (Proulx & Mazumder 1998; Osem *et al.* 2002; Bakker *et al.* 2006) and in African savannas (Burkepile *et al.* 2017). This is because in more productive habitats herbivory reduces competition from dominant herbaceous species while in unproductive habitats dominants are not productive enough to exclude other species but instead herbivory increases stress on many species (Burkepile *et al.* 2017). Sandveld woodland generally has a taller and denser grass layer than mopane woodland, which has a lot of bare ground. For example, during the wet season, the total cover of grasses in the > 20 km zone of sandveld woodland was 83.4 ± 29.3 %, whereas in mopane woodland total grass cover was 56.9 ± 12.9 %. Thus it appears that insufficient fire or herbivory in sandveld woodland results in large dominant herbaceous species excluding small grasses and forbs (e.g. Koerner *et al.* 2014). Thus overall, richness does not appear to have undergone catastrophic declines under foraging and trampling impacts of a large herbivore biomass, but rather responds to herbivory positively or negatively depending upon habitat productivity and the potential for competitive exclusion (Proulx & Mazumder 1998; Osem *et al.* 2002; Bakker *et al.* 2006; Burkepile *et al.* 2017).

Similarly to patterns of woody vegetation structure with distance from water, we found that taller tufted high-quality perennial grasses such as D. eriantha were more abundant far from water (> 20 km) but that shorter, high quality grasses such as U. trichopus were most abundant within 5 km of water (Fig. 5) demonstrating that gradients of herbivory and trampling by elephant and other large herbivores with increasing distance from permanent water created both compositional and structural heterogeneity in the grass layer. Had there been significant numbers of artificial water points in the backcountry parts of these landscapes, however, we would predict that elephant and other large herbivores would have homogenized the structure of favoured woody species as well as composition and structure of grasses right across the landscape. A decline in the abundance of high-quality tall grasses with year-round grazing in the backcountry woodlands would be expected to negatively impact tall grass grazers such as buffalo, sable and roan antelope (Fynn et al. 2016). This might have had negative knock on effects on other biota such as various birds, bats, insects, etc. that rely on mature woodland or taller grasses as optimal habitat (e.g. Cumming et al. 1997). Creation of heterogeneity in woodland structure (zones of short, immature and tall, mature woodland) and in grass composition and structure may be expected to maximize niches for various biota, some of which may favour different structural and compositional states of woodland and grassland, as observed for birds with woodland structural heterogeneity (Bradbury et al. 2005) and for birds and insects with grassland structural heterogeneity (Chambers & Samways 1998; Fuhlendorf *et al.* 2006; Krook *et al.* 2007).

In addition, creation of heterogeneity in grassland structure facilitates adaptive foraging options and more stable and productive herbivore populations (Owen-Smith 2002, 2004; Hopcraft et al. 2010). Grassland structural heterogeneity also facilitates niche diversity for medium and tall-grass grazers such as roan and sable antelope and buffalo, having a spatial refuge far from water and short-grass grazers such as wildebeest and impala having a special niche closer to water (Fynn et al. 2016). Several studies in this landscape have shown that roan and sable antelope prefer these backcountry areas far from water in both wet and dry seasons, though they will walk to water every three or four days to drink during the dry season (Hensman et al. 2014; Haveman 2014). In addition, it has been observed that immediately once the rains arrive African buffalo leave the floodplains and move far out from water, presumably to benefit from the higher abundance of *D. eriantha* far from water (Sianga et al. 2017). These effects of herbivores on composition and structural heterogeneity across these landscapes are likely to be further enhanced by the observation that herbivory also increased heterogeneity in grass and forb richness across the landscape (Table 1). Richness may be important for adaptive foraging options for herbivores in the form of diet breadth expansion (Owen-Smith 2002). Owing to the spatial refuges for tall grasses in our study area, roan and sable populations are indeed maintained here at healthy numbers (Chase 2011; Hensman et al. 2014; Haveman 2014) but have collapsed in Kruger National Park where spatial refuges in landscapes have been eliminated by artificial water provision (Harrington et al. 1999).

CONCLUSION

It is clear that herbivory on the large distance gradients away from permanent water (>20 km) in the SMLE has created key diversity, compositional and structural heterogeneity in grass, forb and woody species that is likely to result in greater niche diversity and adaptive foraging options that will enhance biodiversity and herbivore population stability and productivity. In this regard, our findings show that spatial refuges for both grass and woody species operated beyond 15 km from permanent water with the implication that managers should avoid artificial water provision in backcountry woodlands, because water points will reduce the

distance to available water during the dry season and consequently eliminate spatial refuges for plants and animals. If artificial water provision cannot be avoided, for whatever reason, then artificial water points should be spaced at least 50 km apart to ensure a 25 km distance away from dry season water providing for large proportion (around 40 %) of the landscape area as a spatial refuge from herbivory during the dry season (15-25 km = 40 % of the landscape). Consequently, too many artificial water points in backcountry woodlands could seriously undermine the resilience of landscapes to herbivory by reducing the proportion of landscapes beyond 15 km from permanent water (reduced area of spatial refuges), which will reduce the resilience of plant, herbivore and predator populations that depend on these spatial refuges. We strongly advise that future scientific work, and management and policy actions should be focused on the identification and sustaining of these spatial refuges in wildlife areas.

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Appendix

Table S1: Details of model specifications for the MCMCglmm analyses of grass, forb and tree richness, structural responses of various tree species and cover of various grass species.

Species / Functional group	Vegetation	Response	Fixed	Random	Nitt	Burnin	Thin	Error distr	link	Slice	Prior
Trees	Mopane	SR	Zone * Fire.freq	LT:Zone:ST	1e+06	2e+05	200	Poisson ("poisson")	Log	True	R-structure: $Pr(\sigma 2) \sim IW(V=3, nu=0.002)$ G-structure: $Pr(\sigma 2) \sim IW(V=1, nu=0.002, alpha.mu=0, alpha.V=1 000)$
Trees	Mopane	SR	E.Dung * Fire.freq	LT:Zone:ST	1.5e+06	3e+05	300	Poisson ("poisson")	Log	True	R-structure: $Pr(\sigma 2) \sim IW(V=3, nu=0.002)$ G-structure: $Pr(\sigma 2) \sim IW(V=1, nu=0.002, alpha.mu=0, alpha.V=1 000)$
Trees	Mopane	SR	H.Dung * Fire.Freq	LT:Zone:ST	1.5e+06	3e+05	300	Poisson ("poisson")	Log	True	R-structure: $Pr(\sigma 2) \sim IW(V=3, nu=0.002)$ G-structure: $Pr(\sigma 2) \sim IW(V=1, nu=0.002, alpha.mu=0, alpha.V=1 000)$
Grasses	Mopane	SR	Zone * Fire.freq	LT:Zone:ST	1e+06	2e+05	200	Poisson ("poisson")	Log	True	R-structure: $Pr(\sigma 2) \sim IW(V=3)$ nu=0.002) G-structure: $Pr(\sigma 2) \sim IW(V=1)$ nu=0.002, $alpha.mu=0alpha.V=1\ 000)$
Grasses	Mopane	SR	E.Dung *	LT:Zone:ST	1e+06	2e+05	200	Poisson ("poisson")	Log	True	R-structure: $Pr(\sigma 2) \sim IW(V=3)$

			Fire.freq								nu=0.002)
											G-structure: $Pr(\sigma 2) \sim IW(V=1,$
											nu=0.002, alpha.mu=0,
											alpha.V=1 000)
											R-structure: $Pr(\sigma 2) \sim IW(V=3,$
			H Dung *								nu=0.002)
Grasses	Mopane	SR	Fire freq	LT:Zone:ST	1e+06	2e+05	200	Poisson ("poisson")	Log	True	G-structure: $Pr(\sigma 2) \sim IW(V=1,$
			The.neq								nu=0.002, alpha.mu=0,
											alpha.V=1 000)
											R-structure: $Pr(\sigma 2) \sim IW(V=3,$
			Zone *								nu=0.002)
Forbs	Mopane	SR	Fire freq	LT:Zone:ST	5e+05	1e+05	100	Poisson ("poisson")	Log	True	G-structure: $Pr(\sigma 2) \sim IW(V=1,$
			Themeq								nu=0.002, alpha.mu=0,
											alpha.V=1 000)
											R-structure: $Pr(\sigma 2) \sim IW(V=3,$
			E Dung *								nu=0.002)
Forbs	Mopane	SR	Fire freq	LT:Zone:ST	1e+06	2e+05	200	Poisson ("poisson")	Log	True	G-structure: $Pr(\sigma 2) \sim IW(V=4,$
			1								nu=0.002, alpha.mu=0,
											alpha.V=1 000)
											R-structure: $Pr(\sigma 2) \sim IW(V=3,$
			H.Dung *								nu=0.002)
Forbs	Mopane	SR	Fire.frea	LT:Zone:ST	5e+05	1e+05	100	Poisson ("poisson")	Log	True	G-structure: $Pr(\sigma 2) \sim IW(V=1,$
											nu=0.002, alpha.mu=0,
											alpha.V=1 000)
											R-structure: $Pr(\sigma 2) \sim IW(V=3,$
Trees	Sandveld	eld SR	Zone * Fire.freq	LT:Zone:ST	1e+06	2e+05	200	Poisson ("poisson")	Log	True	nu=0.002)
											G-structure: $Pr(\sigma 2) \sim IW(V=4,$
											nu=0.002, alpha.mu=0,

											alpha.V=1 000)
Trees	Sandveld	SR	E.Dung * Fire.freq	LT:Zone:ST	1e+06	2e+05	200	Poisson ("poisson")	Log	True	R-structure: $Pr(\sigma 2) \sim IW(V=3, nu=0.002)$ G-structure: $Pr(\sigma 2) \sim IW(V=4, nu=0.002, alpha.mu=0, alpha.V=1 000)$
Trees	Sandveld	SR	H.Dung * Fire.freq	LT:Zone:ST	1.5e+06	3e+05	300	Poisson ("poisson")	Log	True	R-structure: $Pr(\sigma 2) \sim IW(V=3, nu=0.002)$ G-structure: $Pr(\sigma 2) \sim IW(V=1, nu=0.002, alpha.mu=0, alpha.W=1 000)$
Grasses	Sandveld	SR	Zone * Fire.freq	LT:Zone:ST	1e+06	2e+05	200	Poisson ("poisson")	Log	True	R-structure: $Pr(\sigma 2) \sim IW(V=3, nu=0.002)$ G-structure: $Pr(\sigma 2) \sim IW(V=1, nu=0.002, alpha.mu=0, alpha.W=1 000)$
Grasses	Sandveld	SR	E.Dung * Fire.freq	LT:Zone:ST	1e+06	2e+05	200	Poisson ("poisson")	Log	True	R-structure: $Pr(\sigma 2) \sim IW(V=3, nu=0.002)$ G-structure: $Pr(\sigma 2) \sim IW(V=1, nu=0.002, alpha.mu=0, alpha.V=1 000)$
Grasses	Sandveld	SR	E.Dung * Fire.freq	LT:Zone:ST	1e+06	2e+05	200	Poisson ("poisson")	Log	True	R-structure: $Pr(\sigma 2) \sim IW(V=3, nu=0.002)$ G-structure: $Pr(\sigma 2) \sim IW(V=1, nu=0.002, alpha.mu=0, alpha.W=1 000)$
Forbs	Sandveld	SR	Zone * Fire.freq	LT:Zone:ST	5e+05	1e+05	100	Poisson ("poisson")	Log	True	R-structure: $Pr(\sigma 2) \sim IW(V=3, nu=0.002)$

											G-structure: $Pr(\sigma 2) \sim IW(V=1,$
											nu=0.002, alpha.mu=0,
											alpha.V=1 000)
											R-structure: $Pr(\sigma 2) \sim IW(V=3,$
			E Dung *								nu=0.002)
Forbs	Sandveld	SR	E.Dung	LT:Zone:ST	5e+05	1e+05	100	Poisson ("poisson")	Log	True	G-structure: $Pr(\sigma 2) \sim IW(V=8,$
			Themeq								nu=0.002, alpha.mu=0,
											alpha.V=1 000)
											R-structure: $Pr(\sigma 2) \sim IW(V=3,$
			U Dung *								nu=0.002)
Forbs	Sandveld	SR	Fire freq	LT:Zone:ST	5e+05	1e+05	100	Poisson ("poisson")	Log	True	G-structure: $Pr(\sigma 2) \sim IW(V=1,$
			Pile.neq								nu=0.002, alpha.mu=0,
											alpha.V=1 000)
											R-structure: $Pr(\sigma 2) \sim IW(V=10,$
	Mopane	Count	Zone * HC * Fire.freq	LT:Zone:ST + LT:Zone:ST:S_Point	5e+05	1e+05	100	Binary ("categorical")			fix=1)
C. mopane									logit	True	G-structure: $Pr(\sigma 2) \sim IW(V=1,$
											nu=0.002, alpha.mu=0,
											alpha.V=1 000)
											R-structure: $Pr(\sigma 2) \sim IW(V=10,$
			E.Dung *	I T. Zone ST +				Binary			fix=1)
C. mopane	Mopane	Count	HC *	LT:Zone:ST:S Point	5e+05	1e+05	100	("categorical")	logit	True	G-structure: $Pr(\sigma 2) \sim IW(V=1,$
			Fire.freq	L1.2010.51.5_1011t				(categorical)			nu=0.002, alpha.mu=0,
											alpha.V=1 000)
											R-structure: $Pr(\sigma 2) \sim IW(V=10,$
T. sericea		Count	Zone *	I T'Zone'ST +	1e+06	2e+05		Binary			fix=1)
	Sandveld		HC * Fire.freq	LT:Zone:ST:S_Point +			200	("categorical")	logit	True	G-structure: $Pr(\sigma 2) \sim IW(V=1,$
											nu=0.002, alpha.mu=0,
											alpha.V=1 000)

T. sericea	Sandveld	Count	E.Dung * HC * Fire.freq	LT:Zone:ST + LT:Zone:ST:S_Point	1e+06	2e+05	200	Binary ("categorical")	logit	True	R-structure: $Pr(\sigma 2) \sim IW(V=10, fix=1)$ G-structure: $Pr(\sigma 2) \sim IW(V=1, nu=0.002, alpha.mu=0, alpha.V=1 000)$
P. nelsii	Sandveld	Count	Zone * HC * Fire.freq	LT:Zone:ST + LT:Zone:ST:S_Point	1e+06	2e+05	200	Binary ("categorical")	logit	True	R-structure: $Pr(\sigma 2) \sim IW(V=10, fix=1)$ G-structure: $Pr(\sigma 2) \sim IW(V=1, nu=0.002, alpha.mu=0, alpha.W=1 000)$
P. nelsii	Sandveld	Count	E.Dung * HC * Fire.freq	LT:Zone:ST + LT:Zone:ST:S_Point	5e+05	1e+05	100	Binary ("categorical")	logit	True	R-structure: $Pr(\sigma 2) \sim IW(V=10, fix=1)$ G-structure: $Pr(\sigma 2) \sim IW(V=1, nu=0.002, alpha.mu=0, alpha.Mu=0, lipha.W=1 000)$
A. adscensionis	Mopane	% Cover	Zone * Fire.freq	LT:Zone:ST	5e+05	1e+05	100	Binomial ("multinomial2")	logit	False	R-structure: $Pr(\sigma 2) \sim IW(V=1, fix=1)$ G-structure: $Pr(\sigma 2) \sim IW(V=1, nu=0.002)$
A. adscensionis	Mopane	% Cover	E.Dung * Fire.freq	LT:Zone:ST	5e+05	1e+05	100	Binomial ("multinomial2")	logit	False	R-structure: $Pr(\sigma 2) \sim IW(V=1, fix=1)$ G-structure: $Pr(\sigma 2) \sim IW(V=1, nu=0.002)$
A. scabrivalvis	Mopane	% Cover	Zone * Fire.freq	LT:Zone:ST	4e+06	8e+05	800	Binomial ("multinomial2")	logit	True	R-structure: $Pr(\sigma 2) \sim IW(V=10, fix=1)$ G-structure: $Pr(\sigma 2) \sim IW(V=1, nu=0.002, alpha.mu=0, alpha.W=1 000)$
A. scabrivalvis	Mopane	% Cover	E.Dung * Fire.freq	LT:Zone:ST	4e+06	8e+05	800	Binomial ("multinomial2")	logit	True	R-structure: $Pr(\sigma 2) \sim IW(V=10, fix=1)$ G-structure: $Pr(\sigma 2) \sim IW(V=1, nu=0.002, alpha.mu=0, alpha.V=1 000)$
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A. stipitata	Sandveld	% Cover	Zone * Fire.freq	LT:Zone:ST	5e+05	1e+05	100	Binomial ("multinomial2")	logit	True	R-structure: $Pr(\sigma 2) \sim IW(V=5, fix=1)$ G-structure: $Pr(\sigma 2) \sim IW(V=1, nu=0.002)$
A. stipitata	Sandveld	% Cover	E.Dung * Fire.freq	LT:Zone:ST	5e+05	1e+05	100	Binomial ("multinomial2")	logit	True	R-structure: $Pr(\sigma 2) \sim IW(V=5, fix=1)$ G-structure: $Pr(\sigma 2) \sim IW(V=1, nu=0.002)$
D. giganteum	Sandveld	% Cover	Zone * Fire.freq	LT:Zone:ST	5e+05	1e+05	100	Binomial ("multinomial2")	logit	True	R-structure: $Pr(\sigma 2) \sim IW(V=5, fix=1)$ G-structure: $Pr(\sigma 2) \sim IW(V=1, nu=0.002, alpha.mu=0, alpha.W=1 000)$
D. giganteum	Sandveld	% Cover	E.Dung * Fire.freq	LT:Zone:ST	5e+05	1e+05	100	Binomial ("multinomial2")	logit	True	R-structure: $Pr(\sigma 2) \sim IW(V=5, fix=1)$ G-structure: $Pr(\sigma 2) \sim IW(V=1, nu=0.002, alpha.mu=0, alpha.V=1 000)$
D. eriantha	Sandveld	% Cover	Zone * Fire.freq	LT:Zone:ST	5e+05	1e+05	100	Binomial ("multinomial2")	logit	False	R-structure: $Pr(\sigma 2) \sim IW(V=1, fix=1)$ G-structure: $Pr(\sigma 2) \sim IW(V=1, nu=0.002)$
D. eriantha	Sandveld	% Cover	E.Dung *	LT:Zone:ST	5e+05	1e+05	100	Binomial	logit	False	R-structure: $Pr(\sigma 2) \sim IW(V=1,$

			Fire.freq					("multinomial2")			fix=1) G-structure: $Pr(\sigma 2) \sim IW(V=1, nu=0.002)$
D. milanjiana	Mopane	% Cover	Zone * Fire.freq	LT:Zone:ST	2e+07	4e+06	4 000	Binomial ("multinomial2")	logit	False	$R=structure: Pr(\sigma 2) \sim IW(V=10, fix=1)$ G-structure: $Pr(\sigma 2) \sim IW(V=1, nu=0.002, alpha.mu=0, alpha.V=1 000)$
D. milanjiana	Mopane	% Cover	E.Dung * Fire.freq	LT:Zone:ST	2e+07	4e+06	4 000	Binomial ("multinomial2")	logit	False	R-structure: $Pr(\sigma 2) \sim IW(V=10, fix=1)$ G-structure: $Pr(\sigma 2) \sim IW(V=1, nu=0.002, alpha.mu=0, alpha.V=1000)$
E. regidior	Mopane	% Cover	Zone * Fire.freq	LT:Zone:ST	1e+06	2e+05	200	Binomial ("multinomial2")	logit	False	R-structure: $Pr(\sigma 2) \sim IW(V=10, fix=1)$ G-structure: $Pr(\sigma 2) \sim IW(V=1, nu=0.002, alpha.mu=0, alpha.V=1 000)$
E. regidior	Mopane	% Cover	E.Dung * Fire.freq	LT:Zone:ST	1.5e+06	3e+05	300	Binomial ("multinomial2")	logit	False	R-structure: $Pr(\sigma 2) \sim IW(V=10, fix=1)$ G-structure: $Pr(\sigma 2) \sim IW(V=1, nu=0.002, alpha.mu=0, alpha.V=1000)$
E. trichophora	Mopane	% Cover	Zone * Fire.freq	LT:Zone:ST	1.5e+06	3e+05	300	Binomial ("multinomial2")	logit	False	R-structure: $Pr(\sigma 2) \sim IW(V=10, fix=1)$ G-structure: $Pr(\sigma 2) \sim IW(V=1, nu=0.002)$
E. trichophora	Mopane	% Cover	E.Dung *	LT:Zone:ST	1e+07	2e+06	2 000	Binomial	logit	False	R-structure: $Pr(\sigma 2) \sim IW(V=10,$

			Fire.freq					("multinomial2")			fix=1) G-structure: $Pr(\sigma 2) \sim IW(V=1,$
P. maximum	Mopane	% Cover	Zone * Fire.freq	LT:Zone:ST	5e+06	1e+06	1 000	Binomial ("multinomial2")	logit	False	nu=0.002) R-structure: $Pr(\sigma 2) \sim IW(V=10, fix=1)$ G-structure: $Pr(\sigma 2) \sim IW(V=1, nu=0.002, alpha.mu=0, alpha.mu=0, alpha.V=1000)$
P. maximum	Mopane	% Cover	E.Dung * Fire.freq	LT:Zone:ST	4e+06	8e+05	800	Binomial ("multinomial2")	logit	False	R-structure: $Pr(\sigma 2) \sim IW(V=10, fix=1)$ G-structure: $Pr(\sigma 2) \sim IW(V=1, nu=0.002, alpha.mu=0, alpha.V=1000)$
P. maximum	Sandveld	% Cover	Zone * Fire.freq	LT:Zone:ST	5e+05	1e+05	100	Binomial ("multinomial2")	logit	False	R-structure: $Pr(\sigma 2) \sim IW(V=5, fix=1)$ G-structure: $Pr(\sigma 2) \sim IW(V=1, nu=0.002)$
P. maximum	Sandveld	% Cover	E.Dung * Fire.freq	LT:Zone:ST	5e+05	1e+05	100	Binomial ("multinomial2")	logit	False	R-structure: $Pr(\sigma 2) \sim IW(V=5, fix=1)$ G-structure: $Pr(\sigma 2) \sim IW(V=1, nu=0.002)$
P. fleckii	Mopane	% Cover	Zone * Fire.freq	LT:Zone:ST	3e+06	6e+05	600	Binomial ("multinomial2")	logit	True	R-structure: $Pr(\sigma 2) \sim IW(V=10, fix=1)$ G-structure: $Pr(\sigma 2) \sim IW(V=1, nu=0.002, alpha.mu=0, alpha.V=1 000)$
P. fleckii	Mopane	% Cover	E.Dung * Fire.freq	LT:Zone:ST	2.5e+06	5e+05	500	Binomial ("multinomial2")	logit	True	R-structure: $Pr(\sigma 2) \sim IW(V=10, fix=1)$

											G-structure: $Pr(\sigma 2) \sim IW(V=1,$
											nu=0.002, alpha.mu=0,
											alpha.V=1 000)
											R-structure: $Pr(\sigma 2) \sim IW(V=10,$
P. fleckii	Sandveld	% Cover	Zone *	LT:Zone:ST	4e+07	8e+06	8 000	Binomial	logit	False	fix=1)
1. jieenii	Sund (Cita	70 00 00	Fire.freq		10107	00100	0 000	("multinomial2")	logit	i uise	G-structure: $Pr(\sigma 2) \sim IW(V=1,$
											nu=0.002)
											R-structure: $Pr(\sigma 2) \sim IW(V=10,$
P flackij	Sandveld	% Cover	E.Dung *	I T.Zone.ST	3e±07	6e±06	6.000	Binomial	logit	False	fix=1)
1. јісски	Sanavera	70 COVCI	Fire.freq		50107	00100	0.000	("multinomial2")	logit	1 alse	G-structure: $Pr(\sigma 2) \sim IW(V=1,$
											nu=0.002)
											R-structure: $Pr(\sigma 2) \sim IW(V=10,$
<i>S</i> .	Monana	% Cover	Zone *	I T.Zone.ST	20+06	<u>4e+05</u>	400	Binomial	logit	Falsa	fix=1)
pappophoroides	Wopane	70 COVCI	Fire.freq	L1.Zone.S1	20+00	40+05	400	("multinomial2")	logit	raise	G-structure: $Pr(\sigma 2) \sim IW(V=1,$
											nu=0.002)
											R-structure: $Pr(\sigma 2) \sim IW(V=10,$
<i>S</i> .	Monane	% Cover	E.Dung *	I T.Zone.ST	3 5e±06	7e±05	700	Binomial	logit	False	fix=1)
pappophoroides	Wopane	70 COVCI	Fire.freq	L1.Zone.S1	5.50+00	70+05	700	("multinomial2")	logit	raise	G-structure: $Pr(\sigma 2) \sim IW(V=1,$
											nu=0.002)
											R-structure: $Pr(\sigma 2) \sim IW(V=5,$
			Zono *					Dinomial			fix=1)
U. trichopus	Mopane	% Cover	Lone T	LT:Zone:ST	5e+05	1e+05	100	Dinomial ("multinomial?")	logit	True	G-structure: $Pr(\sigma 2) \sim IW(V=1,$
			rne.neq					(mutinoimaiz)			nu=0.002, alpha.mu=0,
											alpha.V=1 000)
							1				R-structure: $Pr(\sigma 2) \sim IW(V=10,$
TT , • 1	M		E.Dung *		505	105	100	Binomial	1	T	fix=1)
0. tricnopus	wopane	% Cover	Fire.freq	L1:Zone:51	3e+05	10+05	100	("multinomial2")	logit	True	G-structure: $Pr(\sigma 2) \sim IW(V=1,$
											nu=0.002, alpha.mu=0,
	1	1			1		1		1		1

											alpha.V=1 000)
U. trichopus	Sandveld	% Cover	Zone * Fire.freq	LT:Zone:ST	5e+05	1e+05	100	Binomial ("multinomial2")	logit	False	R-structure: $Pr(\sigma 2) \sim IW(V=10)$ fix=1) G-structure: $Pr(\sigma 2) \sim IW(V=1)$ nu=0.002, alpha.mu=0 alpha.V=1 000)
U. trichopus	Sandveld	% Cover	E.Dung * Fire.freq	LT:Zone:ST	5e+05	1e+05	100	Binomial ("multinomial2")	logit	False	R-structure: $Pr(\sigma 2) \sim IW(V=10)$ fix=1)G-structure: $Pr(\sigma 2) \sim IW(V=1)$ nu=0.002,alpha.W=1 000)

 Table S2: MCMC analyses (Hadfield 2010) of the relationship between the height structure of the three most dominant tree species of the study area and distance zone from permanent water. Posterior means, 95% confidence intervals and p-values (<0.05 in bold).</th>

	C. mopane								T. sericea			
X7	Posterior	Lower	Upper		Posterior	Lower	Upper		Posterior	Lower	Upper	
variable	mean	95% CI	95% CI	pMCMC	mean	95% CI	95% CI	pMCMC	mean	95% CI	95% CI	pMCMC
Zone*HC*Fire												
(Intercept)	2.23	0.62	3.79	0.01	-2.36	-3.86	-0.82	0.00	-6.93	-9.04	-4.91	<3e-04
Zone10-15	-0.30	-2.78	2.35	0.82	1.74	-0.56	4.33	0.17	4.31	1.62	7.33	0.00
Zone>20	-1.26	-3.69	1.18	0.32	2.00	-0.50	4.30	0.11	4.34	1.52	7.21	0.00
HC2	1.67	0.45	2.81	0.00	1.64	0.49	2.71	0.00	1.65	-0.23	3.43	0.08
HC3	2.84	1.54	4.11	<3e-04	1.48	0.31	2.59	0.01	0.82	-1.18	2.65	0.40
HC4	2.88	1.63	4.20	<3e-04	0.43	-0.70	1.52	0.46	-4.33	-8.32	-0.52	0.02
Fire	-0.14	-1.23	1.03	0.81	0.25	-0.76	1.27	0.63	1.68	0.34	2.97	0.01
Zone10-15:HC2	1.10	-0.67	3.06	0.26	0.48	-1.41	2.24	0.61	-1.06	-3.40	1.23	0.39
Zone>20:HC2	1.30	-0.56	3.26	0.19	0.13	-1.61	1.78	0.88	-1.48	-3.91	0.80	0.23

Zone10-15:HC3	0.19	-1.67	2.21	0.85	-0.91	-2.61	0.96	0.32	0.96	-1.48	3.40	0.43
Zone>20:HC3	0.95	-0.86	2.99	0.35	-0.38	-2.01	1.42	0.67	-0.44	-2.61	2.16	0.72
Zone10-15:HC4	0.71	-1.19	2.65	0.46	-2.35	-4.20	-0.47	0.02	6.48	2.40	10.75	0.00
Zone>20:HC4	2.80	0.66	4.88	0.01	-4.12	-6.07	-2.35	<3e-04	6.38	2.18	10.39	0.00
Zone10-15:Fire	-0.37	-2.19	1.19	0.67	-0.38	-1.96	1.03	0.62	-1.25	-2.95	0.49	0.16
Zone>20:Fire	0.59	-0.95	2.05	0.46	0.05	-1.30	1.40	0.94	-2.10	-3.71	-0.49	0.01
HC2:Fire	0.98	0.10	1.79	0.02	-0.02	-0.82	0.72	0.96	0.06	-1.07	1.20	0.93
HC3:Fire	1.08	0.17	2.12	0.03	0.04	-0.75	0.86	0.93	-0.85	-2.10	0.36	0.17
HC4:Fire	2.43	1.07	3.83	<3e-04	-0.93	-1.76	-0.21	0.01	-1.07	-3.89	1.77	0.46
Zone10-15:HC2:Fire	-0.89	-2.09	0.39	0.16	-0.68	-1.84	0.43	0.24	0.15	-1.28	1.49	0.83
Zone>20:HC2:Fire	-0.61	-1.75	0.72	0.32	-0.41	-1.42	0.54	0.41	0.24	-1.24	1.42	0.71
Zone10-15:HC3:Fire	-1.50	-2.85	-0.26	0.03	-0.78	-1.89	0.38	0.18	1.09	-0.40	2.48	0.15
Zone>20:HC3:Fire	-1.65	-2.84	-0.35	0.01	-0.99	-1.98	0.06	0.06	1.97	0.57	3.41	0.01
Zone10-15:HC4:Fire	-3.67	-5.35	-2.13	<3e-04	-0.44	-1.75	0.78	0.51	1.10	-1.79	4.10	0.47
Zone>20:HC4:Fire	-3.68	-5.26	-2.07	<3e-04	0.47	-0.55	1.52	0.40	2.40	-0.34	5.52	0.09
E.Dung*Fire												
(Intercept)	1.61	0.32	2.85	0.01	-0.73	-2.07	0.56	0.26	-3.88	-5.55	-2.07	<3e-04
E.Dung	0.00	-0.07	0.07	0.88	-0.05	-0.12	0.01	0.09	-0.03	-0.11	0.05	0.46
HC2	2.83	1.84	3.85	<3e-04	1.77	0.74	2.66	<3e-04	-0.69	-1.87	0.49	0.26
HC3	2.76	1.73	3.88	<3e-04	0.80	-0.20	1.73	0.11	-0.38	-1.53	0.82	0.54
HC4	4.60	3.62	5.68	<3e-04	-1.53	-2.54	-0.52	0.00	1.46	0.18	2.72	0.02
Fire	0.38	-0.41	1.21	0.35	0.32	-0.39	1.11	0.41	0.85	-0.19	1.75	0.08
E.Dung:HC2	-0.04	-0.09	0.01	0.16	0.01	-0.04	0.06	0.77	0.10	0.04	0.16	0.00
E.Dung:HC3	0.06	-0.01	0.14	0.11	0.04	-0.01	0.08	0.14	0.07	0.01	0.13	0.02
E.Dung:HC4	-0.06	-0.11	-0.01	0.03	0.03	-0.01	0.08	0.18	-0.10	-0.18	-0.03	0.01
E.Dung:Fire	-0.06	-0.11	0.00	0.06	0.01	-0.03	0.04	0.69	-0.02	-0.06	0.03	0.46

HC2:Fire	0.00	-0.60	0.66	0.99	-0.68	-1.23	-0.11	0.02	0.46	-0.20	1.13	0.19
HC3:Fire	-0.49	-1.12	0.16	0.13	-1.18	-1.75	-0.62	0.00	0.83	0.16	1.50	0.01
HC4:Fire	-1.55	-2.17	-0.92	<3e-04	-2.00	-2.62	-1.38	<3e-04	0.74	0.05	1.47	0.04
E.Dung:HC2:Fire	0.05	0.01	0.10	0.01	0.02	-0.01	0.04	0.24	-0.02	-0.06	0.02	0.26
E.Dung:HC3:Fire	0.05	0.00	0.10	0.04	0.02	-0.01	0.05	0.13	-0.01	-0.05	0.02	0.44
E.Dung:HC4:Fire	0.13	0.07	0.17	<3e-04	0.04	0.01	0.07	0.00	0.02	-0.02	0.06	0.35
H.Dung:HC:Fire												
(Intercept)	1.53	0.36	2.65	0.01	-1.19	-2.22	-0.05	0.03	-3.79	-5.09	-2.40	<3e-04
H.Dung	0.21	-0.29	0.69	0.40	0.04	-0.28	0.39	0.82	-0.43	-0.93	0.05	0.09
HC2	2.66	1.83	3.56	<3e-04	1.45	0.66	2.28	0.00	1.10	0.13	2.00	0.02
HC3	2.98	2.10	3.88	<3e-04	0.57	-0.24	1.40	0.18	1.52	0.58	2.50	0.00
HC4	4.15	3.19	5.04	<3e-04	-2.14	-2.99	-1.26	<3e-04	1.84	0.87	2.81	<3e-04
HC4 Fire	4.15 0.05	3.19 -0.66	5.04 0.71	<3e-04 0.88	-2.14 0.39	-2.99 -0.19	-1.26 0.96	<3e-04 0.18	1.84 0.30	0.87 -0.36	2.81 0.99	<3e-04 0.39
HC4 Fire H.Dung:HC2	4.15 0.05 -0.33	3.19 -0.66 -0.68	5.04 0.71 0.02	<3e-04 0.88 0.06	-2.14 0.39 0.13	-2.99 -0.19 -0.13	-1.26 0.96 0.37	< 3e-04 0.18 0.31	1.84 0.30 -0.94	0.87 -0.36 -1.60	2.81 0.99 -0.25	<3e-04 0.39 0.00
HC4 Fire H.Dung:HC2 H.Dung:HC3	4.15 0.05 -0.33 0.11	3.19 -0.66 -0.68 -0.26	5.04 0.71 0.02 0.51	< 3e-04 0.88 0.06 0.59	-2.14 0.39 0.13 0.41	-2.99 -0.19 -0.13 0.14	-1.26 0.96 0.37 0.69	<3e-04 0.18 0.31 0.00	1.84 0.30 -0.94 -0.84	0.87 -0.36 -1.60 -1.68	2.81 0.99 -0.25 -0.03	<3e-04 0.39 0.00 0.03
HC4 Fire H.Dung:HC2 H.Dung:HC3 H.Dung:HC4	4.15 0.05 -0.33 0.11 -0.36	3.19 -0.66 -0.68 -0.26 -0.72	5.04 0.71 0.02 0.51 -0.01	<3e-04 0.88 0.06 0.59 0.04	-2.14 0.39 0.13 0.41 0.58	-2.99 -0.19 -0.13 0.14 0.30	-1.26 0.96 0.37 0.69 0.83	<3e-04	1.84 0.30 -0.94 -0.84 -0.53	0.87 -0.36 -1.60 -1.68 -1.35	2.81 0.99 -0.25 -0.03 0.24	<3e-04 0.39 0.00 0.03 0.15
HC4 Fire H.Dung:HC2 H.Dung:HC3 H.Dung:HC4 H.Dung:Fire	4.15 0.05 -0.33 0.11 -0.36 -0.11	3.19 -0.66 -0.68 -0.26 -0.72 -0.40	5.04 0.71 0.02 0.51 -0.01 0.17	<3e-04 0.88 0.06 0.59 0.04 0.46	-2.14 0.39 0.13 0.41 0.58 -0.33	-2.99 -0.19 -0.13 0.14 0.30 -0.67	-1.26 0.96 0.37 0.69 0.83 0.00	<3e-04	1.84 0.30 -0.94 -0.84 -0.53 0.45	0.87 -0.36 -1.60 -1.68 -1.35 0.04	2.81 0.99 -0.25 -0.03 0.24 0.89	<3e-04 0.39 0.00 0.03 0.15 0.04
HC4 Fire H.Dung:HC2 H.Dung:HC3 H.Dung:HC4 H.Dung:Fire HC2:Fire	4.15 0.05 -0.33 0.11 -0.36 -0.11 0.39	3.19 -0.66 -0.68 -0.26 -0.72 -0.40 -0.19	5.04 0.71 0.02 0.51 -0.01 0.17 0.89	<3e-04 0.88 0.06 0.59 0.04 0.46 0.17	-2.14 0.39 0.13 0.41 0.58 -0.33 -0.32	-2.99 -0.19 -0.13 0.14 0.30 -0.67 -0.76	-1.26 0.96 0.37 0.69 0.83 0.00 0.09	<3e-04	1.84 0.30 -0.94 -0.84 -0.53 0.45 -0.02	0.87 -0.36 -1.60 -1.68 -1.35 0.04 -0.49	2.81 0.99 -0.25 -0.03 0.24 0.89 0.47	<3e-04 0.39 0.00 0.03 0.15 0.04 0.94
HC4 Fire H.Dung:HC2 H.Dung:HC3 H.Dung:HC4 H.Dung:Fire HC2:Fire HC3:Fire	4.15 0.05 -0.33 0.11 -0.36 -0.11 0.39 0.11	3.19 -0.66 -0.68 -0.26 -0.72 -0.40 -0.19 -0.43	5.04 0.71 0.02 0.51 -0.01 0.17 0.89 0.64	<3e-04	-2.14 0.39 0.13 0.41 0.58 -0.33 -0.32 -0.56	-2.99 -0.19 -0.13 0.14 0.30 -0.67 -0.76 -0.98	-1.26 0.96 0.37 0.69 0.83 0.00 0.09 -0.13	<3e-04	1.84 0.30 -0.94 -0.84 -0.53 0.45 -0.02 0.41	0.87 -0.36 -1.60 -1.68 -1.35 0.04 -0.49 -0.04	2.81 0.99 -0.25 -0.03 0.24 0.89 0.47 0.91	<3e-04 0.39 0.00 0.03 0.15 0.04 0.94 0.09
HC4 Fire H.Dung:HC2 H.Dung:HC3 H.Dung:HC4 H.Dung:Fire HC2:Fire HC3:Fire HC4:Fire	4.15 0.05 -0.33 0.11 -0.36 -0.11 0.39 0.11 -0.61	3.19 -0.66 -0.68 -0.26 -0.72 -0.40 -0.19 -0.43 -1.19	5.04 0.71 0.02 0.51 -0.01 0.17 0.89 0.64 -0.11	<3e-04 0.88 0.06 0.59 0.04 0.46 0.17 0.68 0.03	-2.14 0.39 0.13 0.41 0.58 -0.33 -0.32 -0.56 -0.83	-2.99 -0.19 -0.13 0.14 0.30 -0.67 -0.76 -0.98 -1.30	-1.26 0.96 0.37 0.69 0.83 0.00 0.09 -0.13 -0.35	<3e-04	1.84 0.30 -0.94 -0.84 -0.53 0.45 -0.02 0.41 0.62	0.87 -0.36 -1.60 -1.68 -1.35 0.04 -0.49 -0.04 0.13	2.81 0.99 -0.25 -0.03 0.24 0.89 0.47 0.91 1.09	<3e-04 0.39 0.00 0.03 0.15 0.04 0.94 0.09 0.01
HC4 Fire H.Dung:HC2 H.Dung:HC3 H.Dung:HC4 H.Dung:Fire HC2:Fire HC3:Fire HC4:Fire H.Dung:HC2:Fire	4.15 0.05 -0.33 0.11 -0.36 -0.11 0.39 0.11 -0.61 0.13	3.19 -0.66 -0.68 -0.26 -0.72 -0.40 -0.19 -0.43 -1.19 -0.09	5.04 0.71 0.02 0.51 -0.01 0.17 0.89 0.64 -0.11 0.35	<3e-04	-2.14 0.39 0.13 0.41 0.58 -0.33 -0.32 -0.56 -0.83 0.11	-2.99 -0.19 -0.13 0.14 0.30 -0.67 -0.76 -0.98 -1.30 -0.14	-1.26 0.96 0.37 0.69 0.83 0.00 0.09 -0.13 -0.35 0.37	<3e-04	1.84 0.30 -0.94 -0.84 -0.53 0.45 -0.02 0.41 0.62 0.76	0.87 -0.36 -1.60 -1.68 -1.35 0.04 -0.49 -0.04 0.13 0.23	2.81 0.99 -0.25 -0.03 0.24 0.89 0.47 0.91 1.09 1.24	<3e-04 0.39 0.00 0.03 0.15 0.04 0.94 0.09 0.01 0.01 0.00
HC4 Fire H.Dung:HC2 H.Dung:HC3 H.Dung:HC4 H.Dung:Fire HC2:Fire HC3:Fire HC4:Fire H.Dung:HC2:Fire H.Dung:HC2:Fire	4.15 0.05 -0.33 0.11 -0.36 -0.11 0.39 0.11 -0.61 0.13 -0.18	3.19 -0.66 -0.68 -0.26 -0.72 -0.40 -0.19 -0.43 -1.19 -0.09 -0.39	5.04 0.71 0.02 0.51 -0.01 0.17 0.89 0.64 -0.11 0.35 0.02	<3e-04	-2.14 0.39 0.13 0.41 0.58 -0.33 -0.32 -0.56 -0.83 0.11 -0.10	-2.99 -0.19 -0.13 0.14 0.30 -0.67 -0.76 -0.98 -1.30 -0.14 -0.42	-1.26 0.96 0.37 0.69 0.83 0.00 0.09 -0.13 -0.35 0.37 0.16	<3e-04	1.84 0.30 -0.94 -0.84 -0.53 0.45 -0.02 0.41 0.62 0.76 0.02	0.87 -0.36 -1.60 -1.68 -1.35 0.04 -0.49 -0.04 0.13 0.23 -0.53	2.81 0.99 -0.25 -0.03 0.24 0.89 0.47 0.91 1.09 1.24 0.53	<3e-04 0.39 0.00 0.03 0.15 0.04 0.94 0.09 0.01 0.00 0.01 0.00 0.98

	Mopane										
Variable	Posterior	Lower 95% CI	Upper 95% CI	рМСМС	Posterior	Lower 95%	Upper 95%	pMCMC	Posterior	Lower	Up
variable	mean		opper 55% er	pineme	mean	CI	CI	pineme	mean	95% CI	CI
Zone*Fire	A. adscension	nis			A. scabriva	lvis			D. milanjiar	а	
Intercept	-1.26	-8.86	0.14	<2e-16	-2.25	-15.64	0.14	<2e-16	-14.86	-20.26	-10
Zone10-15	0.35	0.22	1.57	0.12	-0.64	-3.17	0.20	0.00	2.48	-4.13	8.8
Zone>20	0.12	0.22	0.57	0.57	-0.44	-2.20	0.20	0.03	-1.94	-8.88	5.2
Fire	-0.05	-0.48	0.10	0.63	0.01	0.09	0.15	0.88	2.07	-0.75	5.1
Zone10-15:Fire	-0.11	-0.73	0.14	0.46	0.56	0.13	4.16	0.00	0.27	-3.67	4.3
Zone>20:Fire	0.01	0.08	0.13	0.94	0.12	0.12	1.01	0.31	1.01	-2.69	4.9
E.Dung*Fire											
Intercept	-14.58	-10.53	-19.08	<3e-04	-14.58	-19.08	-10.53	<3e-04	-15.37	-19.63	-11
E.Dung	0.12	-0.05	0.30	0.16	0.12	-0.05	0.30	0.16	0.09	-0.10	0.2
Fire	2.82	0.70	5.10	0.01	2.82	0.70	5.10	0.01	2.96	1.05	5.0
E.Dung:Fire	-0.08	-0.23	0.07	0.30	-0.08	-0.23	0.07	0.30	-0.05	-0.18	0.1
H.Dung*Fire											
Intercept	-1.65	-2.27	-1.06	<3e-04	-13.55	-17.47	-9.73	<3e-04	-13.99	-17.66	-10
H.Dung	-0.31	-0.58	-0.02	0.03	0.38	-1.07	1.83	0.59	-0.50	-2.14	1.1
Fire	-0.27	-0.66	0.11	0.17	2.47	0.52	4.46	0.01	2.32	0.73	4.2
H.Dung:Fire	0.12	-0.04	0.28	0.15	-0.58	-1.59	0.34	0.22	0.17	-0.55	0.9
	-1.26	-8.86	0.14	<2e-16	-2.25	-15.64	0.14	<2e-16	-14.86	-20.26	-10
Zone*Fire	E. rigidior				E. trichoph	ora			P. maximun	1	

 Table S3: Grass cover responses. Posterior means, 95% confidence intervals and p-values (<0.05 in bold).</th>

Intercept	-10.59	-13.52	-8.06	<3e-04	-10.07	-13.18	-6.74	<3e-04	-13.20	-17.19	-9.5
Zone10-15	2.11	-1.62	5.51	0.26	2.03	-2.72	6.73	0.38	4.45	-1.35	9.8
Zone>20	2.77	-0.86	6.94	0.16	2.08	-2.63	6.56	0.37	5.80	0.05	11.
Fire	-1.55	-3.83	0.85	0.17	0.48	-1.60	2.48	0.61	0.08	-2.18	2.6
Zone10-15:Fire	1.88	-1.08	4.61	0.17	-1.61	-4.82	1.49	0.32	-2.32	-6.01	1.8
Zone>20:Fire	0.43	-2.53	3.19	0.77	-1.06	-4.02	1.64	0.45	-3.62	-8.08	0.2
E.Dung*Fire											
Intercept	-7.88	-10.15	-5.81	<3e-04	-5.13	-8.22	-2.30	0.00	-9.14	-11.93	-6.4
E.Dung	-0.16	-0.36	0.02	0.06	-0.56	-1.01	-0.12	0.00	-0.06	-0.21	0.0
Fire	-0.63	-1.95	0.74	0.34	-1.22	-2.86	0.49	0.14	-2.86	-5.25	-0.7
E.Dung:Fire	0.02	-0.11	0.15	0.78	0.12	-0.10	0.34	0.24	0.12	0.01	0.2
H.Dung*Fire											
Intercept	-8.31	-10.00	-6.58	<3e-04	-7.70	-9.91	-5.61	<3e-04	-10.59	-13.05	-8.3
H.Dung	-1.27	-2.51	0.02	0.02	-1.61	-3.27	-0.19	0.02	0.56	-0.34	1.4
Fire	-0.70	-1.81	0.34	0.20	-0.81	-2.06	0.42	0.20	-1.21	-2.76	0.2
H.Dung:Fire	0.44	-0.15	1.05	0.14	0.64	0.00	1.34	0.04	-0.18	-0.97	0.4
Zone*Fire	P. fleckii				S. pappoph	oroides			U. trichopu	\$	
Intercept	-6.04	-9.40	-2.92	0.00	-9.83	-12.70	-7.31	<3e-04	-3.73	-5.44	-1.8
Zone10-15	-8.43	-14.90	-2.77	0.00	-2.25	-6.37	1.58	0.26	-4.05	-7.54	-0.9
Zone>20	-7.47	-13.99	-2.03	0.01	-2.97	-7.25	1.61	0.17	-1.65	-4.71	1.3
Fire	-2.42	-5.14	0.33	0.06	-2.64	-5.34	0.05	0.04	-0.03	-1.23	1.2
Zone10-15:Fire	5.30	1.45	9.35	0.00	4.97	1.85	8.31	0.00	0.07	-2.13	2.2

Zone>20:Fire	2.56	-1.17	6.23	0.17	3.81	0.65	7.06	0.02	-1.98	-4.00	-0.0
E.Dung*Fire											
Intercept	-12.28	-15.49	-9.31	<3e-04	-10.61	-13.54	-7.76	<3e-04	-6.66	-8.75	-4.8
E.Dung	0.20	0.07	0.34	0.00	-0.18	-0.47	0.06	0.14	0.08	-0.03	0.18
Fire	0.59	-1.19	2.26	0.50	0.50	-1.15	1.97	0.53	-1.11	-2.44	0.18
E.Dung:Fire	-0.06	-0.17	0.07	0.36	0.04	-0.10	0.20	0.55	0.01	-0.08	0.0
H.Dung*Fire											
Intercept	-10.55	-13.60	-7.83	<3e-04	-10.04	-12.41	-7.77	<3e-04	-6.20	-8.06	-4.3
H.Dung	0.36	-0.72	1.49	0.50	-3.02	-5.71	-0.50	0.00	0.62	-0.35	1.64
Fire	-0.25	-1.99	1.35	0.77	-0.02	-1.23	1.15	0.99	-0.75	-1.91	0.4
H.Dung:Fire	-0.06	-0.70	0.53	0.84	1.24	0.33	2.19	0.00	-0.85	-1.79	0.0
	Sandveld										
Variable	Sandveld Posterior	Lower 95% CI	Upper 95% CI	pMCMC	Posterior	Lower 95%	Upper 95%	nMCMC	Posterior	Lower	Upj
Variable	Sandveld Posterior mean	Lower 95% CI	Upper 95% CI	рМСМС	Posterior mean	Lower 95% CI	Upper 95% CI	рМСМС	Posterior mean	Lower 95% CI	Upj CI
Variable	Sandveld Posterior mean	Lower 95% CI	Upper 95% CI	рМСМС	Posterior mean	Lower 95% CI	Upper 95% CI	рМСМС	Posterior mean	Lower 95% CI	Up _l CI
Variable <u>Zone*Fire</u>	Sandveld Posterior mean A. stipitata	Lower 95% CI	Upper 95% CI	рМСМС	Posterior mean D. giganteum	Lower 95% CI n	Upper 95% CI	рМСМС	Posterior mean D. eriantha	Lower 95% CI	Upl CI
Variable <u>Zone*Fire</u> Intercept	Sandveld Posterior mean <i>A. stipitata</i> -4.13	Lower 95% CI -5.61	Upper 95% CI -2.73	pMCMC <3e-04	Posterior mean <i>D. giganteun</i> -6.72	Lower 95% CI <i>n</i> -8.43	Upper 95% CI -5.02	pMCMC <3e-04	Posterior mean <i>D. eriantha</i> -4.49	Lower 95% CI -5.64	Uрј СІ -3.3
Variable <u>Zone*Fire</u> Intercept Zone10-15	Sandveld Posterior mean <i>A. stipitata</i> -4.13 -0.66	Lower 95% CI -5.61 -3.05	Upper 95% CI -2.73 1.74	pMCMC <3e-04 0.59	Posterior mean <i>D. giganteun</i> -6.72 -0.24	Lower 95% CI <i>n</i> -8.43 -3.10	Upper 95% CI -5.02 2.72	pMCMC <3e-04 0.87	Posterior mean <i>D. eriantha</i> -4.49 2.01	Lower 95% CI -5.64 0.33	Upj CI -3.3 3.88
Variable <u>Zone*Fire</u> Intercept Zone10-15 Zone>20	Sandveld Posterior mean A. stipitata -4.13 -0.66 0.19	Lower 95% CI -5.61 -3.05 -1.95	Upper 95% CI -2.73 1.74 2.52	pMCMC <3e-04 0.59 0.86	Posterior mean D. giganteun -6.72 -0.24 0.28	Lower 95% CI n -8.43 -3.10 -2.78	Upper 95% CI -5.02 2.72 3.04	pMCMC <3e-04 0.87 0.86	Posterior mean D. eriantha -4.49 2.01 2.30	Lower 95% CI -5.64 0.33 0.65	Upj CI -3.3 3.88 4.10
Variable <u>Zone*Fire</u> Intercept Zone10-15 Zone>20 Fire	Sandveld Posterior mean <i>A. stipitata</i> -4.13 -0.66 0.19 -0.29	Lower 95% CI -5.61 -3.05 -1.95 -1.32	Upper 95% CI -2.73 1.74 2.52 0.62	pMCMC <3e-04 0.59 0.86 0.57	Posterior mean D. giganteun -6.72 -0.24 0.28 0.66	Lower 95% CI n -8.43 -3.10 -2.78 -0.55	Upper 95% CI -5.02 2.72 3.04 1.77	pMCMC <3e-04 0.87 0.86 0.25	Posterior mean D. eriantha -4.49 2.01 2.30 0.47	Lower 95% CI -5.64 0.33 0.65 -0.27	Upj CI -3.3 3.83 4.10 1.22
Variable <u>Zone*Fire</u> Intercept Zone10-15 Zone>20 Fire Zone10-15:Fire	Sandveld Posterior mean <i>A. stipitata</i> -4.13 -0.66 0.19 -0.29 0.01	Lower 95% CI -5.61 -3.05 -1.95 -1.32 -1.47	Upper 95% CI -2.73 1.74 2.52 0.62 1.38	pMCMC <3e-04 0.59 0.86 0.57 0.97	Posterior mean -6.72 -0.24 0.28 0.66 -0.91	Lower 95% CI * -8.43 -3.10 -2.78 -0.55 -2.74	Upper 95% CI -5.02 2.72 3.04 1.77 0.82	pMCMC <3e-04 0.87 0.86 0.25 0.29	Posterior mean <i>D. eriantha</i> -4.49 2.01 2.30 0.47 -0.34	Lower 95% CI -5.64 0.33 0.65 -0.27 -1.43	Upp CI -3.3 3.84 4.10 1.22 0.75

E.Dung*Fire

Intercept	-5.40	-6.57	-4.17	<3e-04	-5.41	-6.94	-3.90	<3e-04	-2.89	-4.02	-1.9
E.Dung	0.07	0.02	0.12	0.01	-0.09	-0.17	-0.02	0.02	-0.03	-0.08	0.0
Fire	0.19	-0.49	0.87	0.61	-0.55	-1.43	0.32	0.21	0.20	-0.35	0.7
E.Dung:Fire	-0.03	-0.06	0.00	0.04	0.03	-0.01	0.07	0.17	0.01	-0.01	0.04
H.Dung*Fire											
Intercept	-4.23	-5.32	-3.20	<3e-04					-3.22	-4.14	-2.2
H.Dung	-0.07	-0.42	0.23	0.67					-0.30	-0.60	0.0
Fire	-0.35	-0.89	0.22	0.22					0.32	-0.16	0.8
H.Dung:Fire	0.10	-0.22	0.39	0.53					-0.25	-0.57	0.0
	-4.13	-5.61	-2.73	<3e-04	-6.72	-8.43	-5.02	<3e-04	-4.49	-5.64	-3.3
Zone*Fire	P. maximum				P. fleckii				U. trichop	us	
Intercept	-5.71	-7.27	-4.03	<3e-04	-7.72	-11.57	-4.30	<3e-04	-5.62	-7.51	-3.7
Zone10-15	0.50	-2.09	3.02	0.70	-6.92	-13.44	-0.62	0.03	-6.86	-11.03	-3.1
Zone>20	-0.56	-3.16	1.92	0.68	-26.10	-47.63	-8.39	<3e-04	-4.46	-7.87	-0.9
Fire	-0.78	-1.88	0.32	0.17	-0.05	-2.52	2.51	0.96	0.05	-1.11	1.4
Zone10-15:Fire	0.40	-1.17	1.92	0.63	2.53	-1.06	6.30	0.17	0.74	-1.52	2.8
Zone>20:Fire	0.99	-0.51	2.36	0.18	8.10	1.91	15.97	0.00	0.56	-1.27	2.3
E.Dung*Fire											
Intercept	-5.46	-6.85	-4.11	<3e-04	-16.76	-21.54	-12.54	<3e-04	-8.21	-10.53	-5.8
E.Dung	-0.03	-0.08	0.04	0.43	0.26	0.12	0.42	0.00	-0.02	-0.12	0.0
Fire	-0.29	-1.04	0.51	0.45	2.87	0.90	4.98	0.00	-0.07	-1.32	1.2
E.Dung:Fire	0.01	-0.02	0.04	0.57	-0.09	-0.18	0.00	0.03	0.00	-0.05	0.0
H.Dung*Fire											
Intercept	-5.80	-6.96	-4.72	<3e-04	-14.06	-17.94	-10.50	< 3e-04	-9.48	-11.30	-7.3

H.Dung	0.21	-0.12	0.53	0.21	0.55	-0.28	1.44	0.19	0.53	-0.01	1.02
Fire	-0.04	-0.58	0.56	0.90	1.71	0.04	3.30	0.03	0.30	-0.72	1.23
H.Dung:Fire	-0.46	-0.83	-0.13	0.01	0.39	-0.38	1.14	0.31	-0.07	-0.54	0.43

Chapter 5

Seasonal habitat selection by African buffalo *Syncerus caffer* in the Savuti-Mababe-Linyanti ecosystem of northern Botswana

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ABSTRACT

This study aimed to establish seasonal movement and habitat selection patterns of African buffalo *Syncerus caffer* in relation to a detailed habitat map and according to seasonal changes in forage quality and quantity in the Savuti-Mababe-Linyanti ecosystem (Botswana). Two cows were collared in November 2011 and another in October 2012. All three buffalo had greater activities in the mopane-sandveld woodland mosaic during the wet season, which provided high-quality leafy grasses and ephemeral water for drinking, but moved to permanent water and

reliable forage of various wetlands (swamps and floodplains) and riverine woodlands during the dry season. Wetlands had higher grass greenness, height and biomass than woodlands, respectively during the dry season. Buffalo had similar wet season concentration areas in the 2011-2012 and 2012-2013 wet season and similar dry season concentration areas over 2012 and 2013 dry seasons. However, their dry season location of collaring in 2011 differed dramatically from their 2012 and 2013 dry season concentration areas possibly because of the exceptionally high flood levels in 2011, which reduced accessibility to their usual dry season concentration areas. The study demonstrates that extremely large and heterogeneous landscapes are needed to conserve buffalo in sandy, dystrophic ecosystems with variable rainfall.

Conservation Implications: This study emphasizes the importance of spatial scale available for movement, which enables adaptation to changing conditions between years and seasons.

Key words: Adaptive foraging, floodplains, forage dynamics, key resources, migration

INTRODUCTION

African buffalo (*Syncerus caffer*) have a large distributional range across the savannas of Africa. Their habitat selection and foraging ecology has been relatively well studied (Sinclair 1979; Taylor 1985; Landman & Kerley 2001; Macandza *et al.* 2004). Due to their large body size and large groups, buffalo are able to fend off predators (Sinclair *et al.* 2003), thereby enabling them to forage in wooded vegetation with relatively low visibility and high predation risk. The large absolute food demands of buffalo, which is a function of their large body size (Illius & Gordon 1987; Wilmshurst *et al.* 2000), combined with their inability to efficiently crop short grass (use of tongue to increase bite size cannot work on short grass) constrains them to foraging in vegetation with sufficient height and biomass of forage (Illius & Gordon 1987; Codron *et al.* 2008). Buffalo generally avoid heavily-grazed regions of short grassland (Jarman & Sinclair 1979; Traill & Bigalke 2007; Bhola *et al.* 2012), preferring woodlands dominated by tufted and leafy perennial grasses during the wet season and often relying on more productive riverine vegetation during the dry season (Bell 1970; Sinclair 1979; Macandza *et al.* 2012; Bennitt *et al.* 2014; Fynn *et al.* 2014).

While drylands often support less productive but higher-quality forage than wetlands over the wet-season (Taylor 1985; Fynn *et al.* 2014), their moisture-limited position in the landscape results in forage drying out and declining in forage quality and quantity over the dry season (Taylor 1985; Ellis & Swift 1988; Owen-Smith 2008). Thus wetlands, where permanent water is easily accessible and perennial grasses continue to produce green forage over the dry season, would be expected to be favoured by many herbivores at this time with drylands being favoured over the wet season (Bell 1970; Maddock 1979; Taylor 1985; Fynn *et al.* 2014).

In contrast to more mobile species such as zebra (*Equus burchelli*) and wildebeest (*Connochaetes taurinus*), which often migrate between distinct wet- and dry-season ranges (Maddock 1979; Bartlam-Brooks *et al.* 2011), most buffalo studies have found strong overlap between wet- and dry-season ranges (Ryan 2006; Ryan *et al.* 2006; Venter & Watson 2008; Macandza *et al.* 2012). Many studies, however, were conducted in small reserves (Landman & Kerley 2001; Ryan *et al.* 2006; Tshabalala *et al.* 2009) where opportunity for large seasonal movements are limited or in larger reserves where functional heterogeneity of resources may be well developed at the landscape (catena) scale (Bell 1970; Sinclair 1979; Perrin & Brereton-Stiles 1999; Macandza *et al.* 2012) thereby reducing the need for large seasonal movements (Hopcraft *et al.* 2010). However, in large, relatively unfragmented ecosystems and where landscape scale functional heterogeneity may be poorly developed relative to regional scale heterogeneity (Fynn *et al.* 2014), larger buffalo movements may be expected (Skarpe *et al.* 2004; Naidoo *et al.* 2012).

The Savuti-Mababe-Linyanti ecosystem (SMLE) is part of the > 80 000 km² northern conservation area of Botswana, one of the largest relatively unfragmented wildlife regions in Africa (Fynn & Bonyongo 2011). Despite several studies on buffalo in the SMLE (Patterson 1972; Fynn *et al.* 2014), detailed seasonal movement and habitat selection patterns of buffalo in the region have not been fully identified and established, especially seeing that no detailed habitat map has been available until this year (2016). Considering their non-specialized mouth anatomy and their large body size-mediated demands for absolute food intake we expected buffalo in the SMLE to favour vegetation where tufted, leafy grasses provided sufficient height and biomass of grass to enable food intake requirements to be satisfied (Illius & Gordon 1987; Wilmshurst *et al.* 2000) (Hypothesis 1 - H1). The strongly developed regional-scale distribution (rather than landscape scale) of functional heterogeneity of wet- and dry-season vegetation types in the SMLE (Fynn *et al.* 2014) is likely to promote extension of buffalo home ranges beyond the landscape scale (Hopcraft *et al.* 2010). Consequently we expected seasonal movement patterns of buffalo in the SMLE to match the scale at which functional seasonal vegetation types are distributed in the ecosystem, which is strongly regional (Fynn *et al.* 2014) (Hypothesis 2 - H2). The objectives of this study were to (i) To examine seasonal movements and habitat selection of buffalo in the SMLE of northern Botswana, and (ii) To link seasonal movements to the quality and quantity (grass greenness, height and biomass) of vegetation in favoured seasonal regions of the landscape.

METHODS

Study area

This study was conducted in the SMLE (northern Botswana, Fig. 1).



Figure 1. Savuti-Mababe-Linyanti ecosystem (SMLE) vegetation (adapted from Sianga & Fynn 2017).

Climate in the study area is described as semi-arid with mean annual rainfall ranging from around 500 mm in the Okavango region (western boundary of the SMLE) to over 600 mm in the Chobe Enclave (eastern boundary of the SMLE), most of which is received between November and April (Botswana Meteorological Services). Seasons may be functionally separated into a wet season (December-April), a cool early dry season (May-August) and a hot late dry season (September-November), where daily maximum temperatures are between 35 to 40 °C (Fig. 2, adapted from Fynn *et al.* 2014).



Figure 2. Rainfall and temperature patterns between 2010 and 2013 (adapted from Fynn et al. 2014).

The SMLE is defined by a variety of vegetation types from swamps, floodplains and riverine in wetter areas to vast dryland woodland systems away from permanent water comprising a mosaic of mopane woodland on alluvial soils and sandveld woodland on Kalahari sands (Fig. 1) (Wolski & Murray-Hudson 2006; Sianga & Fynn 2017). In addition, very heavy clay soils formed under sedimentation in a paleolake system known as the Mababe Depression (Teter 2007) give rise to open grassland and sparse savanna in the eastern section of the SMLE (Fig. 1). Another key

feature are the dambo grasslands of the Chobe Enclave, which are seasonally-flooded shallow, linear depressions (flooded by runoff from upslope regions) supporting tall grassland.

Buffalo habitat use

Cows in three buffalo herds were fitted with satellite collars (Africa Wildlife Tracking, Pretoria, South Africa). Buffalo 1 (BH1) and Buffalo 2 (BH2) were collared in the Savuti Channel floodplains and near the Savuti Marsh respectively at the end of the late dry season in November 2011. Buffalo 3 (BH3) was collared in the Savuti Marsh in the late dry season (October 2012). Anaesthetic M3080 Xylazine was used to immobilize cows during capturing and later reversed using *Naltrexone* after fitting collars. Collars were programmed to take a GPS position of the animal every four hours. Every fix obtained by the satellite collars was downloaded and plotted in ArcGIS 10.1 (ESRI 2010) for various analyses. For analyses relating to seasonal differences in movement patterns and habitat selection, we defined six seasonal periods to which each GPS fix could be allocated. The seasonal periods were early wet season (mid November to end of December), mid wet season (January and February), late wet season (March and April), early dry season (May and June), mid dry season (July and August) and late dry season (September to mid November). For visual presentation of seasonal movements and locations for each buffalo we plotted the home-ranges of each buffalo (colour coded for each of the six seasonal periods) in local Convex Hull (a-LoCoH, 95 % isopleths) (Getz et al. 2007) in R (RCore Team 2013) and later displayed as a shapefile on a habitat map of the region. The habitat map was developed from a detailed vegetation classification and mapping study of the SMLE funded by SASSCAL; a detailed account of the vegetation communities and habitat map can be seen in an accompanying paper in this special issue on Botswana (Sianga & Fynn 2017). LoCoH has been found to be an appropriate tool in GPS studies (Getz *et al.* 2007).

Ethics statement

A veterinarian registered with the government of Botswana conducted all darting operations with the research permit (EWT 8/36/4 XVII (31) and the supplementary collaring permit (EWT 8/36/4 XVII (41)) issued by the Ministry of Environment, Wildlife and Tourism and The Department of Wildlife and National Parks (Gaborone, Botswana). Darting operations or removing collars from cows were done from a vehicle and helicopter respectively. Collars were removed successfully after two successive years.

Vegetation sampling

GPS data from satellite collars was used to locate sites where buffalo have been during the wet and dry seasons. Sampling of buffalo wet season vegetation types were conducted in 2012-2013 wet season while their dry season vegetation types were sampled in the 2012 dry season. A total of 124 samples (grass greenness, height and biomass) were collected from sites where the buffalo have been. Seventy-five samples (20 and 55) were collected for BH1 during the early and late dry season of 2012 while 20 samples were collected for BH2 in the late dry season of 2012. At each site five 0.25 m² quadrats were set-up at the GPS position obtained from the collar. The first quadrat was set at the zero meter position on the hand held GPS (Garmin GPS Map 62s) and the other four quadrats 5 m each side of the first (central) quadrat. Greenness was estimated visually as the percentage of green tissue of grasses and sedges rooted within the quadrat. Grass height was measured by lowering a brown paper sample bag at the centre of each quadrat and the height above the soil surface was measured. All grasses rooted within the quadrats were clipped at ground surface level and air-dried during the field exercise. The air-dried grasses were ovendried at 60 degrees centigrade for 48 hours and weighed for biomass at the Okavango Research Institute laboratory (Maun, Botswana). In addition, to determine the vegetation type, we noted grasses and trees common within approximately a 10 m radius around the central quadrat.

Statistical analyses

Home ranges and habitat selection

For analysis of habitat selection, we determined seasonal Minimum Convex Polygons (MCPs) in ArcGIS 10.1 (ESRI 2010) and local convex hulls in R (RCore-Team 2013; Getz et al. 2007) using seasonal location data of each collared buffalo. Seasonal habitat selection indices of each buffalo were determined by dividing the proportion use of each habitat by the proportion of availability of each habitat following Jacobs Index (J.I) = (r - p)/(r + p - 2rp), where (r = r - p)/(r + p - 2rp)proportion of habitat used, p = proportion of habitat available) (Jacobs 1974). J.I ranges between -1 (selected against) to +1 (selected for). To consider the effects of scale on resource availability (Gustine et al. 2006), we calculated habitat selection at second and third order. Second order selection (Johnson 1980) was determined by comparing the availability of various habitat types in the individual buffalo MCPs against availability in the overall population MCP (Thomas & Taylor 1990), while third order selection (Johnson 1980) was determined by comparing the availability of various habitat types in the individual buffalo local convex hulls to availability in the respective individual buffalo MCPs (Thomas & Taylor 1990). Owing to having only three collared individual buffalo, there was insufficient replication to effectively statistically test habitat selection. Thus the J.I merely provides a guide to readers on potential habitat selection.

To determine home-range overlaps between seasons, we used Intersect Tool (Universal Transverse Mercator, ESRI 2010) to estimate area percentage overlaps, where; % overlaps = area overlap of two seasons/ (area of season 1+ season 2) x 100. To examine how buffalo moved in relation to distance from perennial water sources differed seasonally, we determined the distance to the nearest perennial water source of every GPS location of all buffalo throughout the study period using Near Tool in ArcGIS 10.1 (Universal Transverse Mercator, ESRI 2010).

Vegetation data

Data of grass greenness, height and biomass were subjected to Shapiro-Wilk Test (Test of normality) and Levene Statistic (Test of homogeneity of variance) in R version 2.15.2 (RCore-Team 2013). Data sets that failed assumptions of normality or homogeneity of variance were natural log transformed and failure to meet these assumptions after transformation led to the use of non-parametric tests (Kruskal-Wallis Test). Multiple comparison tests (kruskalmc' function) in 'pgirmess' package in R (RCore-Team 2013) was used to analyze data sets.

RESULTS

All three buffalo had much greater activities in sandveld and mopane woodland during the wet season and various wetland systems during the dry season (Fig. 3).



Figure 3. Percentage of various vegetation types observed in the follow ups of GPS collar locations during the wet season and late dry season.

BH1 and BH2 had greater separation of their wet and dry season concentration areas than BH3 (quantified by percentage overlap of their wet and dry season 95 % local convex hull isopleths – Table 1; also see Fig. 4 vs. Fig. 5). BH1 and BH2 demonstrated distinct wet and dry season concentration areas, returning to these respective seasonal locations in successive years (Table 1; Fig. 6).

Season	%	%	% overlap**	
	overlap*	overlap*	(BH3)	
	(BH1)	(BH2)		
Early wet-Mid wet	12.2	0	13.6	
Early wet-Late wet	9.8	0	29.7	
Early wet-Early dry	1.4	0	12.9	
Early wet-Mid dry	0	0	18.4	
Early wet-Late dry	0	0		
Mid wet-Late wet	22.3	15.5	22	
Mid wet-Early dry	11.1	0	1.9	
Mid wet-Mid dry	0.6	0	1.8	
Mid wet-Late dry	0.6	0.9		
Late wet-Early dry	17.9	6.5	14.1	
Late wet-Mid dry	11.1	2.5	19.8	
Late wet-Late dry	11.1	13.2	32.6	
Early dry-Mid dry	26.6	23.3		
Early dry-Late dry	26.6	21.1		
Mid dry-Late dry	0.5	8.8		
Mid wet-Mid wet***	23.4	6.6		
Mid dry-Mid dry***	4.5	0		

Table 1. Percentage overlaps of home-ranges by buffalo in different seasons over the 2012 and 2013.

*= year 2012

**= year 2013

***= year 2012 and 2013



Figure 4. Movement patterns of buffalo 1 (BH1) and buffalo 2 (BH2) over the 2011/2012 annual cycle, in relation to vegetation (Sianga & Fynn 2017).



Figure 5. Movement patterns of buffalo 3 (BH3) over the 2012/2013 annual cycle, in relation to vegetation (Sianga & Fynn 2017).



Figure 6. Movement patterns of buffalo 1 (BH1) and 2 (BH2) in the mid wet and mid dry season of 2012 and 2013, in relation to vegetation (Sianga & Fynn 2017).

For second order habitat selection, the buffalo selected mopane and sandveld woodlands over the wet season while riverine and wetland habitats were selected over the dry season (Table 2), while third order habitat selection also suggested the buffalo selected for mopane woodlands over the wet season and acacia grasslands, riverine and wetland habitats over the dry season (Table 3).

					Mean±SE	Mean±SE		
	Mean±SE	Mean±SE	Mean±SE	Mean±SE	(Annual	(Annual	Mean±SE	Mean±SE
	(Annual MCP	(Annual MCP	(Annual MCP	(Annual MCP	MCP vs	MCP vs	(Annual MCP	(Annual MCP
	vs Herds	vs Herds	vs Herds	vs Herds	Herds	Herds	vs Herds	vs Herds
	MCP_W)	MCP_D)	MCP_EW)	MCP_MW)	MCP_LW)	MCP_ED)	MCP_MD)	MCP_LD)
Acacia grasslands	-0.12±0.29	-0.07 ± 0.14	-0.06 ± 0.28	-0.27 ± 0.40	-0.19±0.30	-0.11±0.15	-0.07 ± 0.16	-0.01±0.14
Baikiaea forests	-0.65 ± 0.19	-0.78 ± 0.20	-0.67 ± 0.20	-0.99 ± 0.01	-0.94 ± 0.04	-0.77±0.21	-0.72 ± 0.26	-0.97 ± 0.01
Dry floodplains	-0.46±0.23	-0.33±0.36	-0.41 ± 0.27	-0.50±0.37	-0.44±0.28	-0.44±0.33	-0.38±0.38	-0.27 ± 0.61
Mopane	0.10 ± 0.22	0.00 ± 0.11	0.07 ± 0.22	0.32±0.17	0.12±0.25	0.04±0.13	-0.13±0.16	-0.14 ± 0.03
Riverine	-0.01 ± 0.21	0.12 ± 0.05	0.02 ± 0.21	-0.27 ± 0.30	-0.01±0.24	0.08 ± 0.08	0.18 ± 0.06	0.28 ± 0.06
Sandveld	0.03 ± 0.11	0.03±0.15	0.02 ± 0.11	-0.15±0.25	-0.03±0.14	0.05 ± 0.15	0.11±0.18	-0.29 ± 0.05
Tall open								
grasslands	-0.09 ± 0.42	-0.53 ± 0.25	-0.09 ± 0.42	-0.24 ± 0.39	-0.41±0.45	-0.50±0.23	-0.47±0.26	-0.83±0.16
Wetland	-0.64±0.01	-0.29±0.20	-0.62±0.08	-0.91±0.04	-0.54 ± 0.04	-0.38±0.15	-0.28 ± 0.21	0.35±0.01

 Table 2. 2nd order habitat selection (annual MCP vs wet or dry seasons MCPs) by three buffalo in the Savuti-Mababe-Linyanti ecosystem (northern Botswana). W- wet season, D- Dry season, EW-Early wet, MW-Mid wet, LW-Late wet, ED-Early dry, MD-Mid dry and LD-Late dry seasons.

	Mean ± SE (Annual MCP vs Herds LoCoH- EW)	Mean ± SE (Annual MCP vs Herds LoCoH- MW)	Mean ± SE (Annual MCP vs Herds LoCoH- LW)	Mean ± SE (Annual MCP vs Herds LoCoH- ED)	Mean ± SE (Annual MCP vs Herds LoCoH- MD)	Mean ± SE (Annual MCP vs Herds LoCoH- LD)
Acacia grasslands	-0.05 ± 0.44	-0.22 ± 0.44	-0.04 ± 0.19	0.06 ± 0.65	0.28 ± 0.22	0.19 ± 0.31
Baikiaea forests	$\textbf{-0.93} \pm 0.07$	$\textbf{-0.99} \pm 0.04$	$\textbf{-0.99} \pm 0.006$	-0.95 ± 0.06	$\textbf{-0.99} \pm 0.006$	$\textbf{-0.99} \pm 0.00$
Dry floodplains	-0.64 ± 0.30	-0.35 ± 0.41	-0.38 ± 0.31	-0.24 ± 0.88	-0.25 ± 0.51	0.01 ± 0.70
Mopane	-0.05 ± 0.37	0.31 ± 0.20	0.07 ± 0.22	-0.22 ± 0.43	-0.35 ± 0.19	-0.64 ± 0.19
Riverine	0.11 ± 0.28	-0.35 ± 0.23	0.07 ± 0.25	0.45 ± 0.098	0.56 ± 0.01	0.48 ± 0.09
Sandveld Tall open	-0.05 ± 0.05	-0.14 ± 0.29	-0.16 ± 0.19	-0.25 ± 0.11	-0.31 ± 0.03	-0.64 ± 0.14
grasslands	0.04 ± 0.52	-0.34 ± 0.33	-0.45 ± 0.37	-0.81 ± 0.17	-0.81 ± 0.14	$\textbf{-0.99} \pm 0.009$
Wetlands	-0.63 ± 0.14	-0.95 ± 0.02	-0.31 ± 0.23	-0.29 ± 0.57	-0.24 ± 0.16	0.49 ± 0.33

Table 3. 3rd order habitat selection (annual MCP vs wet or dry season TLoCoH) by three buffalo in the SMLE (northern Botswana). EW-Early wet,

MW-Mid wet, LW-Late wet, ED-Early dry, MD-Mid dry and LD-Late dry seasons.

For more detail of the plant species composition and classification of these plant communities and for details of the habitat map development see a parallel paper in this special issue (Sianga & Fynn 2017). Over both dry seasons, BH1 concentration areas were in wetland and adjacent woodlands where it focused on the Linyanti Swamp in increasing proportions (and regularly across the international border with Namibia) as the dry season progressed (Fig. 4). The concentrations of BH2 were in the Selinda Spillway and Kwando River wetland (floodplains) and adjacent woodlands in the 2012 and 2013 dry seasons (Fig. 4 & 6). Interestingly, BH2 concentrated its activities in the Tsam Tsam wetlands (floodplains) of the Okavango Delta in the late wet season of April 2013 (which it did not do in 2012) before moving to the Selinda Spillway later in the dry season (Fig. 6). BH3 had the wetland habitats of the Savuti Channel and Savuti Marsh at the core of its range, which it focused on during the dry season, and utilized adjacent woodlands on the peripheries of the home range during the wet season (Fig. 5).

During the early and late dry season of 2012, wetland habitats (floodplain not sampled in the early dry season) had higher grass greenness, height and biomass than mopane, sandveld and riverine habitats respectively (P < 0.05) (Fig. 7), while mopane, sandveld and riverine habitats were not significantly different in grass greenness, height and biomass respectively (P > 0.05) (Fig. 7).



Figure 7. Grass greenness (a), height (b) and biomass (c) of Mopane woodland, Sandveld, riverine and wetland used by buffalo herds during the early and late dry season. Error bars shows standard error of the mean. Different letters shows significant difference according to Kruskal-Wallis Test at α =0.05.

DISCUSSION

Buffalo shifted their seasonal concentration areas between wetlands and woodlands (Figs 3 & 4) as an adaptive strategy to seasonal forage dynamics and water availability over the annual cycle,

with BH1 and BH2 having a migratory strategy with little overlap between wet and dry season concentration areas. However, the distance moved from perennial water sources over the wet season varied significantly across the buffalo, with BH3 being more sedentary. Bennitt *et al.* (2014) and Taolo (2003) reported similar results, noting that buffalo selected contrasting seasonal vegetation types, using woodlands far from permanent water during the rainy season and seasonally-flooded vegetation close to permanent water during the early and late flood seasons. As with our findings, several other studies in the region have also found a mix of strategies (migratory vs. sedentary) between buffalo (Naidoo *et al.* 2012; Bennitt *et al.* 2014; Naidoo *et al.* 2014, Bennitt *et al.* 2015). Cornélis *et al.* (2011) also noted similar findings where buffalo were observed to range between woodlands and riverine habitats during the wet and dry season respectively.

A key factor that may influence buffalo concentration patterns during the wet season appears to be the availability of higher-quality, soft-leaved grasses (such as *Digitaria eriantha*) in back-country woodlands than in wetlands (floodplains), which in contrast support tougher-leaved grasses adapted to shading and litter accumulation under the more productive conditions of wetlands (Fynn *et al.* 2011), and where greater biomass dilutes nutrient concentrations (Jarrell & Beverly 1981), while greater silica contents of wetland vs. dryland grasses further reduce digestibility (Mosimane 2015). One of the most favoured grasses by buffalo, *D. eriantha*, peaks in abundance beyond 10 km from the permanent water of the Okavango Delta and Linyanti Swamps, whereas shorter grazing- lawn forming grasses such as *Urochloa trichopus* peaked in abundance with 5 km of these extensive wetland systems (Sianga *et al.* 2017). The medium to tall, leafy high quality *D. eriantha* would be expected to be optimal in height and digestibility for maximizing protein and energy intake rates in buffalo, which explains why buffalo focused their

wet season foraging beyond 10 km from wetland systems (Fig. 4). By contrast, wildebeest and impala, which favour shorter grasses, focused within 5 km of these wetland systems (Fynn et al. 2014). This suggests short and tall grass grazers in the SMLE have distinct spatial niche separation during the wet season driven by distance to wetland systems. Similar observations have been made in the Masai-Mara, where buffalo favour the taller grass areas within the reserve and wildebeest and gazelles the shorter grass areas outside the reserve (Bhola et al. 2012). Thus a high conception rate of buffalo during the wet season is probably due the availability of high quality green forage of optimal height and biomass (Ryan et al. 2007). Thus concentration during the wet season by the three buffalo in vegetation types (sandveld and mopane) where tufted, softleaved grasses are more abundant supports our first hypothesis (H1). Drying up of ephemeral pans over the dry season forced buffalo to move away from favoured wet season ranges towards permanent water sources (Figs 3 & 4), which included floodplains and swamps (wetlands) and adjacent woodlands within the study area. It is this forced movement away from favoured wet season ranges towards permanent water that likely contributes to reduced grazing pressure in favoured wet season ranges and, therefore, higher abundances of favoured grasses such as D. eriantha far from permanent water. This indicates that artificial water provision in back country woodlands far from permanent water may be an unwise management option that could reduce niche diversity in the system leading to declines in taller grass grazers such as buffalo, as well as roan and sable antelope.

These floodplain and swamp (wetlands) systems provided buffalo not only with reliable drinking water during the dry season but also with forage significantly greener than that found in woodlands, as observed in other studies in the region (Taolo 2003; Bennitt *et al.* 2014; Fynn *et al.* 2014). More productive wetland areas are likely to provide a critical reserve and critical

buffer resources (Owen-Smith 2002) for the late dry season, or elsewhere referred to as key resources (Illius & O'Connor 2000), especially during drought years when more preferred resources have been depleted (Owen-Smith 2002). The ability of wetlands to provide taller green forage with higher energy and protein levels relative to drylands during the late dry season has been shown to greatly elevate buffalo population productivity (Taylor 1985). The taller grass of wetlands is likely to be especially critical for buffalo which are highly vulnerable to competition for forage (Bhola *et al.* 2012), owing to their tongue sweep foraging strategy, which cannot deal with short grass.

Thus our findings of increasing use of swamp, marsh and floodplains (wetlands) as the dry season progressed by our three buffalo together with similar observations in other studies (Vesey-FitzGerald 1960; Western 1973; Tinley 1977; Taylor 1985; Prins & Beekman 1989), demonstrates the importance of wetland systems as dry-season key-resource habitat for buffalo, as is the case for cattle and other wild herbivores across Africa (Fynn *et al.* 2015).

Our collared buffalo migrated at an intermediate scale from wetlands to woodlands rather than from wetlands to the high quality Mababe Depression grasslands, favoured by a migratory zebra population over the wet season (Sianga 2014) and thus our second hypothesis (H2) that buffalo seasonal movements would match the regional-scale distribution of functional seasonal vegetation types was not supported. Though this finding does not support our H2, it does not rule out the possibility of buffalo migrating into the depression during the wet season because not all buffalo herds in the ecosystem were fitted with collars to determine their movements. Also aerial surveys conducted by Fynn *et al.* (2014) did not observe any buffalo in the Mababe Depression at that time suggesting that buffalo probably do not favour the Mababe Depression during the wet season unlike the zebra population (Sianga 2014). However, the buffalo appear to show adaptive variation in seasonal presence to changing environmental conditions in different years. For instance, in 2011 BH1 and BH2 avoided floodplains and swamps (wetlands) in their usual dry season concentration areas of the Linyanti Swamps and Selinda Spillway (2012 and 2013) due to the exceptionally high floods of 2011, being forced to use the more elevated floodplains of the Savuti Channel. This shift in location of different dry season concentration areas emphasizes the importance of having a large spatial scale available for movement (Fynn *et al.* 2014), which enables adaptation to changing conditions between years. Finally, the finding of cross border movements by BH1, together with those of Naidoo *et al.* (2014) and Patterson (1972), demonstrates the importance of Transfrontier Conservation Areas such as this one (Kavango Zambezi Transfrontier Conservation Area, KAZA), which transcends the borders of Angola, Namibia, Botswana, Zimbabwe and Zambia allowing adaptive foraging to a variety of different functional seasonal resources.

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Chapter 6

Seasonal habitat selection by migrating plains zebra *Equus quagga* in an unfragmented landscape in northern Botswana.

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Abstract

Seasonal herbivore migrations are declining globally due to various anthropogenic factors, increasing the need to study and conserve migrations, particularly those in the few remaining relatively unfragmented ecosystems that are likely to support higher levels of resilience. We studied seasonal movements and habitat selection by plains zebra *Equus quagga* in the Savuti-

Mababe-Linyanti ecosystem of northern Botswana. Six female zebra were fitted with GPS collars and their movements monitored for a full annual cycle. Zebra displayed 2nd order habitat selection by migrating between distinct seasonal ranges but no significant 3rd order habitat selection was detected within their seasonal ranges. Wet and dry season ranges were characterized by open grasslands on high clay content, fertile soils, and woodland systems adjacent to the Linyanti Swamps respectively, which provided reliable water and some floodplain grazing. Our study adds to existing knowledge of zebra migration patterns in northern Botswana, where four distinct migrating zebra populations have been identified. Each population is likely to be exposed to different environmental threats and pressures, which must be considered in conservation and management plans.

Key words: Adaptive foraging, floodplains, forage dynamics, key resources, marsh, migration

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Introduction

Large herbivore migrations between discrete seasonal habitats are a global phenomenon (Berger, 2004; Harris *et al.*, 2009). Scientific research to date suggests that these movements are driven by seasonal fluctuations in forage quantity and quality and surface water availability (McNaughton, 1985; Fryxell & Sinclair, 1988; Williamson *et al.*, 1988; Murray, 1995; Boone *et al.*, 2006). However, many migrations have either been severely disrupted or lost entirely as a result of anthropogenic disturbances (Harris *et al.*, 2009). For example, in Africa, habitat fragmentation has severely disrupted zebra *Equus quagga* and blue wildebeest *Connochaetes taurinus* migrations in the Athi-Kapiti plains - Nairobi National Park ecosystem, Kenya (Ogutu *et al.*, 2013), the Kruger National Park, South Africa (Whyte & Joubert, 1998), Etosha National Park, Namibia (Berry, 1997), the Loita Plains-Mara ecosystem, Kenya (Serneels & Lambin, 2001; Serneels, Said & Lambin, 2001), and the Tarangire National Park - Simanjiro Plains ecosystem, Tanzania (Morrison, Link, Newmark, Foley & Bolger, 2016).

Southern Africa has lost almost all of its previously diverse herbivore migrations, including some of Africa's greatest in terms of size, such as the vast springbok *Antidorcas marsupialis*, black wildebeest *Connochaetes gnou* and blesbok *Damaliscus pygargus* migrations (Harris *et al.*, 2009), as well as migrations of red hartebeest *Alcelaphus buselaphus*, zebra and blue wildebeest (Fynn & Bonyongo, 2011). However, Botswana is probably the last remaining country in southern Africa where some migrations still occur in relatively unfragmented landscapes (Fynn & Bonyongo, 2011). The northern conservation area of Botswana links to conservation areas in Namibia and Zimbabwe, providing a vast, relatively unfragmented area of wetlands, woodlands, and saline grasslands (Fynn & Bonyongo, 2011; Naidoo, Du Preez, Stuart-Hill, Beytell & Taylor, 2014; Chase *et al.*, 2016). Four distinct zebra migrations have been

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described in northern Botswana (Fig. 1): (i) from the Boteti River in the dry season to Makgadikgadi Pans saline grasslands in the wet season (BR-MP migration; Brooks, 2005; Bradley, 2012), (ii) from the Okavango Delta flood plains and grasslands in the dry season to Makgadikgadi Pans saline grasslands in the wet season (OD-MP migration; Bartlam-Brooks, Bonyongo & Harris, 2011), (iii) from the Chobe River floodplains in the dry season to the Nxai Pan saline grasslands in the wet season (CR-NP migration; Naidoo *et al.*, 2014) and (iv) between the Linyanti Swamps, upper Savuti Channel and adjacent woodlands in the dry season to the Mababe Depression in the wet season (LS-MD migration) (Joos-Vandewalle, 2000; Sianga, 2014). The OD-MP (Bartlam-Brooks *et al.*, 2011) and CR-NP (Naidoo *et al.*, 2014) migrations were re-established in the last 10 years through the use of GPS-enabled collars.



Figure 1. Zebra migration routes in northern Botswana; (1) – Brooks, 2005; Bradley, 2012, (2) - Bartlam-Brooks *et al.*, 2011, (3) - Naidoo *et al.*, 2014, and (4) - Joos-Vandewalle, 2000; Fynn *et al.*, 2014 and Sianga, 2014.

The LS-MD migration occurs in a region of northern Botswana encompassing the eastern Okavango Delta floodplains, the Linyanti Swamps, the Mababe Depression mineral-rich saline grasslands, and the woodlands between these grasslands and two wetland systems, and is referred to as the Savuti-Mababe-Linyanti ecosystem, SMLE (Fig. 2; Sianga & Fynn, 2017; Sianga, Fynn & Bonyongo, 2017; Sianga, van Telgen, Vrooman, Fynn & van Langevelde, 2017). Across Africa, wetlands form critical dry season habitats for herbivores, providing reliable water and adequate-quality forage (Fynn, Murray-Hudson, Dhliwayo & Scholte, 2015). Although Cape buffalo *Syncerus caffer caffer* migrate to woodlands during the wet season in northern Botswana (Bennitt, Bonyongo & Harris, 2014; Sianga *et al.*, 2017), all recorded migratory zebra in this region move to mineral-rich saline grasslands (Bartlam-Brooks *et al.*, 2011; Naidoo *et al.*, 2014), which likely meet their elevated resource requirements for growth and reproduction, as has also been documented elsewhere in Africa (Murray, 1995; Hopcraft, Olff & Sinclair, 2010; Fynn & Bonyongo, 2011).

One of the key features of the SMLE is that its landscapes still contain most of their historical wet and dry season ranges and these have remained relatively unmodified by artificial water provision. As a result herbivores move away from woodland and grassland systems during the dry season, i.e. the SMLE is still relatively pristine and functional, in contrast to most protected areas in Africa (Fynn & Bonyongo, 2011). Thus, studies of seasonal herbivore movements and habitat selection within the SMLE are likely to yield key insights into migrations and adaptive foraging strategies along unfragmented ecological gradients, in contrast with studies conducted in more anthropogenically modified ecosystems. Although zebra migration in the SMLE has been studied (Joos-Vandewalle, 2000; Sianga, 2014), the spatial determinants of migrations remain poorly understood. Here we study the seasonal habitat selection and

movement patterns of zebras during their seasonal migrations in the SMLE. We fitted GPS collars to six female zebra in different herds in the LS-MD population to: (i) identify their seasonal home ranges, (ii) quantify seasonal habitat selection by zebra, and (iii) compare seasonal forage quality and abundance in habitats selected by zebra.

Materials and methods

Study area

The SMLE, northern Botswana (Fig. 2), is characterized by a semi-arid climate with mean annual rainfall ranging between 500 and 600 mm, in the Okavango and Chobe Enclave regions, respectively, most of which falls between November and April (Botswana Meteorological Services). Seasons were defined as wet (December - March), early dry (April - July) and late dry (August - November; see Fynn *et al.*, 2014 for greater detail on the seasonal dynamics of rainfall and temperature). We only used fixes collected during two months per season to avoid effects of seasonal transition, as observed in movement patterns of zebra (Sianga, 2014). We used January and February for the wet season because these are the two wettest months of the year, where forage resources are of optimal maturity/height and quality. For the early dry season, we used June and July because these are the two coldest dry months of the year, and for the late dry season, we used September and October because these are the two hottest dry months of the year. Hereafter, all mention of seasons will refer to these two-month periods.



Figure 2. Study area showing vegetation types in the Savuti-Mababe-Linyanti ecosystem, northern Botswana (vegetation map sourced from Sianga & Fynn, 2017).

Vegetation in the SMLE includes wetland habitats fringed by riverine habitats in the Okavango Delta and Linyanti Swamps; dryland woodland habitats away from permanent water; and vast open grasslands in the Mababe Depression, far from permanent water (Fig. 2). Some of the grasslands adjacent to the Okavango Delta and Linyanti Swamps were historically flooded, but have not been flooded for several decades, so we refer to them as dry floodplains. Dryland woodlands are dominated by a mosaic of mopane and sandveld woodlands, which occur on alluvial soils and Kalahari sands, respectively (Fig. 2, Wolski & Murray-Hudson, 2006; Sianga & Fynn, 2017). Baikiaea forests (Miombo) also occur in deep Kalahari sands in the northern edge of the Mababe Depression near Ghoha hills and extend north east into Zimbabwe (Sianga &

Fynn, 2017). In the eastern section of the SMLE, the heavy clay soils of the Mababe Depression (Teter, 2007) are characterized by open grassland and sparse savanna (Sianga & Fynn, 2017). Sianga and Fynn (2017) provide a detailed description of the habitats in the SMLE.

Collaring

Six zebra mares from six different herds were fitted and tracked with GPS-enabled collars (4 satellite and 2 data logger collars; Africa Wildlife Tracking, Pretoria, South Africa) in November 2011, at the onset of the wet season, for a full year. Mares were collared rather than stallions to minimize risks of collar damage during intrasexual fighting (Brooks & Harris, 2008). Zebra were sedated with 7 mg M99 (Etorphine hydrochloride), 80 mg Azaperone and 2500 iu Hyalase, and sedation was reversed with 21 mg Naltrexone after collar fitting. Mares were observed until they rejoined their herds. Collars were programmed to take six fixes per day (Table 1).

 Table 1: Number of GPS fixes per zebra over the wet, early dry, and late dry seasons. Z1-7 denotes collared zebra.

Season	Number of GPS fixes per zebra						
	Z1	Z2	Z3	Z4	Z5	Z6	
Wet	345	364	364	363	364	349	
Early dry	359	374	364	364	360	150	
Late dry	361	369	364	362	361	0	

Ethics statement

All darting operations were conducted by a veterinarian registered with the government of Botswana. Darting operations were conducted from a vehicle under research permit EWT 8/36/4 XVII (31) and supplementary permit EWT 8/36/4 XVII (41) issued by the Ministry of Environment, Wildlife, and Tourism and the Department of Wildlife and National Parks (Gaborone, Botswana). During darting operations, we poured water over the animals while fitting the collars to prevent heat stress. After collaring, we monitored the collared zebra regularly to ensure that collars were not having any detrimental effects. Most collars recorded GPS fixes for a full year, but one malfunctioned on 3rd July 2012. The defective collar was not recovered immediately as it was difficult to dart the zebra in dense woodlands and floodplains in its dry season range. We removed five collars after a year, but the defective collar was not located despite several searches by helicopter. The zebra has not been seen by any tourism operators in the areas since, so it was probably predated by lion *Panthera leo*.

Vegetation sampling

GPS coordinates from collars identified positions used by zebra during the wet and dry seasons. We also located sites where zebra were observed foraging when they were in their wet season range (Mababe Depression). Their wet season range was characterized by short and open grasslands hence it was easier to observe the zebra foraging than when they were in their dry season range, which was characterized by woodland habitats with low visibility. GPS locations from collared zebra that were accessible on foot within 5 km of the road were selected and sampled. Due to funding limitation, vegetation was sampled during the 2011/2012 wet and 2012 late dry seasons only. In the wet season, 25 acacia grasslands and 15 sandveld sites were sampled. Eighty-nine (89) sites were sampled during the dry season (20 wetlands, 26 mopane, 27 sandveld and 16 acacia grasslands). We sampled all accessible sites, resulting in seasonally variable sample sizes. Foraging sites were sampled as follows: five 0.25 m² quadrats were laid down at the GPS position obtained from the collar (or where zebra were observed to be grazing). The first quadrat was laid down at the zero meter position on the hand held GPS (Garmin GPS Map 62s) and the other four quadrats 5m (measured by a measuring tape) each side of the first (central) quadrat. For comparison purposes, habitats not used by collared zebra (20 wetlands and 25 mopane woodlands) during the wet season were sampled as well following the above procedure.

Grass greenness in used and unused habitats was estimated visually as the percentage of green tissue of grasses and sedges rooted within the quadrat. Maximum grass height, an important factor in determining risk of predation and forage quality, was measured by a ruler in every habitat type sampled. All grass in 0.25 m² quadrats placed on grass height sampling sites was clipped to ground surface level and air-dried for 72 hours. The air-dried grasses were ovendried at 60 °C for 48 hours and weighed for biomass at the Okavango Research Institute laboratory (Maun, Botswana). These samples were mixed to form a composite sample, which was milled for Ca, Na and P analysis. Due to funding limitations, nutrient analyses were done only for the wet season samples collected. Sodium was determined using the Sherwood Flame Photometer 410, while Calcium was measured colourimetrically (Cottenie, Verloo, Kiekens, Velghe & Camerlynck, 1982).

Statistical analyses

Seasonal home ranges

We used location data from each collared zebra to calculate seasonal 95 % Minimum Convex Polygons (MCPs) and seasonal 95 % kernel utilisation distributions (UDs) using the adehabitatHR package (Calenge, 2007) in R version 3.3.0 (RCore-Team, 2013). The reference bandwidth was used as a smoothing parameter to estimate the UDs (Calenge, 2007). Proportions of habitat types within MCPs varied seasonally (Table A1).

Habitat selection

The latest habitat map developed by Sianga & Fynn (2017) was used as a template for these analyses. For a detailed description of the habitats, see Sianga & Fynn (2017). Ground-truthing showed that the habitat map was approximately 70 % accurate, so some habitats may have been misclassified (Sianga, 2018). Individual seasonal Manly habitat selection ratios (Manly, McDonald, Thomas, McDonald & Erickson, 2002) were computed using the adehabitatHS package in R version 3.3.0 (RCore-Team, 2013). For the sixth zebra there were insufficient points during the early and late dry seasons to calculate UDs. Second order habitat selection (Johnson, 1980) was defined as habitat use in the seasonal MCPs compared to habitat availability in the seasonal range used by the entire population as a design II analysis (Thomas & Taylor, 1990). Third order habitat selection (Johnson, 1980) was defined as comparing UD-weighted use (Millspaugh et al., 2006) to availability in seasonal MCPs as a design III analysis (Thomas & Taylor, 1990). According to Neu, Byers and Peek (1974), values are considered significant when their 95 % confidence intervals did not include 1 (> 1 = selection, < 1 = avoidance). The seasonal selection ratios were independently subjected to Shapiro-Wilk Test (test of normality) and Levene Statistic (test of homogeneity of variance) in R version 3.3.0 (RCore-Team, 2013). Failure to satisfy assumptions of normality or homogeneity of variance by the datasets resulted in

the data being transformed using natural log transformation in R version 3.3.0 (R Core Team, 2013). The transformed habitat selection ratios were compared between seasons for each order of selection using Multivariate Analyses of Variance (MANOVA) in R version 3.3.0 (RCore-Team, 2013).

Grass characteristics

Data from greenness, height, biomass and mineral nutrient were independently subjected to the Shapiro-Wilk Tests (test of normality) and Levene Statistic (test of homogeneity of variance) in R version 3.3.0 (RCore-Team, 2013). Since the data sets failed assumptions of normality or homogeneity of variance, they were analyzed using Kruskal-Wallis tests. The 'kruskalmc' function in 'pgirmess' package in R version 3.3.0 (R Core Team, 2013) was used to analyze data sets.

Results

Seasonal home ranges

The wet and dry season home ranges of the herds were geographically distinct (Fig. 3), with dramatic differences in the proportion of various habitat types in their seasonal MCPs (Table 1-A1). For example, tall open grassland made up 44 % and 0 %, while riverine woodland made up 16 % and 57 % of the wet and dry season MCP, respectively (Table 1- A1). The collared herds moved to the southern half of the paleolake Mababe during the wet season and back to the Linyanti Swamp region during the dry seasons (Fig. 3).



Figure 3. Wet and dry season utilization distribution polygons for six zebra herds in the Savuti-Mababe-Linyanti ecosystem, northern Botswana in 2011 (see Fig. 2 for detail on the habitats, map sourced from Sianga & Fynn, 2017).

Habitat selection

Overall second order habitat selection was significant during the wet ($X^{2}39 = \infty$, p < 0.01), early dry ($X^{2}28 = 11.86$, p < 0.01), and late dry seasons ($X^{2}31 = \infty$, p < 0.01), but third order habitat selection was not significant during the wet ($X^{2}38 = 13.11$, p = 0.99), early dry ($X^{2}28 = 17.66$, p =

0.93), or late dry seasons (X^{2} 31 = 8.44, p = 0.99). The observed differences in degrees of freedom resulted from the absence of some habitat types in individual MCPs. During the wet season, zebra avoided Baikiaea forests at the second order level (Table 2). During the early dry season, zebra avoided sandveld and tall open grasslands (Table 2) at the second order level, and showed some preference for riverine habitat, although confidence intervals indicated that selection for the latter habitat was not significant. Second order selection showed that, during the late dry season, zebra avoided Acacia grasslands, dry floodplains and tall open grasslands (Table 2).

 Table 2: Seasonal second and third order habitat selection ratios and confidence intervals. Significant results are in bold.

Habitat type	Order	Habitat selection ratios (95% confidence intervals)			
		Wet season	Early dry season	Late dry season	
Acacia grassland	Second	1.17 (0.89- 1.44)	1.45 (0.27-2.63)	0.53 (0.12-0.93)	
	Third	1.23 (0.99-1.47)	1.01 (0.82-1.19)	0.92 (0.43-1.42)	
Baikiaea forest	Second	0.36 (0.26-0.46)	0.37 (-0.80-1.56)	1.67 (-1.74-2.09)	
	Third	0.36 (0.26-0.46)	0.23 (0.23-0.23)	0.66 (0.51-0.80)	
Dry floodplain	Second	1.30 (-0.10-2.70)	1.09 (-0.52-2.72)	0.43 (0.10-0.75)	
	Third	0.90 (0.71-1.10)	0.74 (0.57-0.91)	0.91 (0.48-1.33)	
Mopane	Second	0.86 (0.71-1.02)	1.02 (0.57-1.47)	1.47 (0.87-2.07)	
	Third	0.82 (0.71-0.92)	1.05 (0.74-1.37)	1.04 (0.90-1.18)	
Riverine	Second	1.06 (0.83-1.29)	1.73 (0.91-2.55)	1.17 (0.73-1.61)	
	Third	1.00 (0.87-1.12)	1.11 (0.86-1.35)	0.98 (0.86-1.10)	
Sandveld	Second	1.18 (0.47-1.89)	0.70 (0.44-0.97)	0.82 (0.26-1.37)	
	Third	0.87 (0.35-1.39)	0.83 (0.67-0.98)	1.01 (0.66-1.36)	
Tall open grassland	Second	3.25 (0.95-6.20)	0.01 (-0.03-0.06)	0.002 (-0.002-0.007)	
	Third	1.03 (0.91-1.15)	0.86 (0.86-0.86)	0.66 (-0.51-1.84)	
Wetland	Second	0.88 (0.60-1.15)	0.97 (0.54-1.40)	0.86 (0.56-1.17)	
	Third	0.82 (0.58-1.05)	0.54 (0.22-0.87)	0.69 (0.51-0.88)	

Overall, MANOVA indicated that there were no significant differences between seasons in terms of second or third order habitat selection indices (Table 3).

Table 3: Results from MANOVA comparing seasonal second and third order habitat selection ratios.

Seasons		Second order	Third order
Wet vs Early dry season	Overall	Pillai _{1,8} = 0.999, P = 0.063	Pillai _{1,8} = 0.632, P = 0.936
Wet vs Late dry season	Overall	Pillai _{1,8} = 0.918, P = 0.576	$Pillai_{1,8} = 0.970, P = 0.362$
Early dry vs Late dry season	Overall	Pillai _{1,8} = 0.918, P = 0.576	Pillai _{1,8} = 0.632, P = 0.936

Grass characteristics

Sandveld habitat had lower greenness than other habitats during the wet season, but was not different from wetland habitats (Fig. 4, Table 2-A1). Greenness was not different between most habitats, but was higher in Acacia grasslands than in wetland during the wet season (Fig. 4, Table 2-A1). During the wet season, grass height in Acacia grasslands and mopane woodland was lower than in wetland and sandveld woodland. Biomass in Acacia grasslands was lower than in wetland, but not different from sandveld and mopane during the wet season (Fig. 4, Table 2-A1).



Figure 4. Wet and dry season grass characteristics in the Savuti-Mababe-Linyanti ecosystem, northern Botswana. Error bars represent confidence intervals. Different letters indicate significant differences.

During the late dry season, greenness in wetland habitat was higher than in mopane, sandveld and Acacia grasslands (Fig. 4, Table 3-A2). Wetland habitat was different in height and biomass from mopane woodland and Acacia grasslands respectively, but not different from sandveld habitat during the late dry season (Fig. 4, Table 3-A2).

Na and Ca concentration in forage was significantly higher in the Acacia grasslands in the southern Mababe Depression than in wetland and mopane woodlands during the wet season respectively (Fig. 5, Table 2-A1). The Acacia grasslands had significantly higher P than sandveld woodland but not other habitats during the wet season (Fig. 5, Table 2-A1).



Figure 5. Nutrient concentrations of grasses in the Savuti-Mababe-Linyanti ecosystem, northern Botswana. Error bars represent confidence intervals. Different letters indicate significant differences.

Discussion

Our 4-hourly GPS collar data combined with the recent habitat map of the SMLE (Sianga & Fynn, 2017) enabled us to make the first quantitative analysis of zebra seasonal habitat selection in the SMLE. Zebra in the SMLE migrate south from their dry season range along the Linyanti Swamps and Savuti Channel to the open saline grasslands of the Mababe Depression, where clay and nutrients have been deposited into an ancient lake bed sump, thereby resulting in much greater soil fertility than the surrounding matrix of Kalahari sands (Teter, 2007; Sianga & Fynn, 2017). Home ranges varied seasonally in their habitat composition (Table 1 - A1), but zebra used all habitats within their seasonal home ranges in proportion to their availability.

The core wet season range, in the southern part of the Mababe Depression, is characterized by acacia grasslands on silty clay soils dominated by high quality annual grasses on the edge of the sump of the Mababe Depression, with taller grasses on vertisols occurring further into the sump (Sianga & Fynn, 2017; Photo 1). These two adjacent habitats (Acacia grasslands and tall open grasslands) have the highest soil sodium content of all habitats in the SMLE (Sianga & Fynn, 2017).



Photo 1. Wet season range photo from a helicopter showing the edge of the Mababe Depression and several zebra concentrations in the acacia grasslands (photo credit Izak Smit).

In addition, the tall open grasslands have the highest soil calcium content, while the acacia grasslands in the southern part of the Mababe Depression have among the highest soil phosphorus content (Sianga & Fynn, 2017). This high soil fertility translates into higher protein and mineral (Ca, Mg, Na, K and P) content in grasses than other habitats in the SMLE (Fynn *et al.*, 2014). Finally, the Acacia grasslands around the southern edge of the sump of the Mababe Depression are dominated by short, soft leaved grasses such as *Urochloa trichopus* and *Chloris*

virgata. These grasses are highly digestible owing to their low amount of indigestible stem, which combined with their high mineral concentrations in leaf tissue, likely allows higher levels of energy and nutrient intake (Wilmshurst *et al.*, 2000). The taller *Cenchris ciliarus* of the tall open grasslands may allow greater intake of calcium and sodium. Observations of zebra foraging behaviour in these tall grasslands shows that zebra graze off the top leafy parts of the taller *C. ciliarus* plants, avoiding the lower parts with a high proportion of stems (pers. obs.).

In combination, the Acacia and tall open grasslands that constitute the vegetation of the southern Mababe Depression provide the highest quality forage in the SMLE. Thus, foraging adaptively between the short Acacia grasslands and tall open grasslands in the sump of the Mababe Depression during the wet season would likely enable optimal nutrient intake at this critical time of growth and reproduction, when demands for mineral, protein and energy are greatly elevated (Taylor, 1985; Murray, 1995; Hopcraft et al., 2010), explaining why zebra migrate to the southern Mababe Depression for the wet season. Indeed, selection for protein and mineral-rich grasslands is common strategy for herbivores during the wet season (Kreulen, 1975; Murray, 1995; Fynn & Bonyongo, 2011). In Botswana, several examples exist of preferential selection for saline grasslands of lacustrine origin, as at Mababe. For example, zebra migrate from the Chobe River floodplains to the Nxai Pan saline grasslands for the wet season (Naidoo et al., 2014). Similarly, zebra migrate from the Okavango Delta to the Makgadikgadi saline grasslands for the wet season (Bartlam-Brooks et al., 2011), as do the Boteti river zebra (Brooks, 2005; Bradley, 2012). In the Central Kalahari Game Reserve wildebeest and several other herbivores favour the saline pan grasslands as long as water is available (Selebatso *et al.*, 2017).

Thus selection for the elevated mineral and protein content of saline grasslands of lacustrine origin (paleolake systems) in the wet season range appears to be the mechanism driving wet season home range selection in all four zebra migrations documented in northern Botswana, as was the case for Etosha wildebeest and zebra (Gasaway, Gasaway & Berry, 1996; Fynn & Bonyongo, 2011). In a region dominated by infertile Kalahari sands, these endorheic paleolake systems have clay and nutrient concentrated by river deposits and evaporative processes well above the levels found in the matrix of Kalahari sands (Sianga & Fynn, 2017; Selebatso *et al.*, 2017). Similarly, zebra, wildebeest, and Thomson's gazelles in the Serengeti ecosystem, Tanzania, migrate to the saline grasslands of the Serengeti plains during the wet season, where nutrients have been concentrated by volcanic ash deposits combined with lowrainfall conditions (Sinclair, 1979; Murray, 1995).

Zebra migration to their dry season range along the Linyanti Swamps, Savuti Channel and adjacent woodlands may have been linked to the long-term water availability and access to sufficient adequate-quality forage in wetland habitats and adjacent woodlands when water had dried up inland and forage quality was lowest in most other habitats (Vesey-FitzGerald, 1960; Prins & Beekman, 1989; Fynn *et al.*, 2014; Photo 2).



Photo 2. Dry season range photo on the Savuti Channel floodplains (photo credit Richard Fynn).

Wetlands are critical dry season habitats for wild and domestic herbivores across Africa because they provide green forage in bulk when forage in other habitats is dry and often depleted (Fynn *et al.*, 2015). However, in the dry season range of zebra in the SMLE, zebra appeared to use a mix of woodlands and wetland habitats in proportion to their availability. Most of the suitable wetland habitat in the dry season range of these zebra is found along the upper Savuti Channel as linear riverine grasslands (see distinction between riverine grasslands and floodplains in Fynn *et al.*, 2015), in contrast to the broad extensive floodplains of the Okavango Delta, because the Linyanti Swamps is characterized by steep sloping sides off the Linyanti fault line,

leading to dominance by deep-flooded wetlands. Thus suitable wetland habitat, while present, was limited in spatial extent in the dry season range of this zebra population. This is probably why the UDs of each collared zebra were centered along the upper Savuti Channel, where they had greatest access to heterogeneity of habitat types, such as water, suitable wetland grazing, riparian woodland and mopane woodland, which they used in proportion to their availability.

The lack of significant second order selection for particular habitats may have been caused by some of the limitations of the study. Ground-truthing showed that the habitat map was approximately 70 % accurate, so some habitats may have been misclassified. More frequent GPS fixes from the collars may also have permitted higher resolution analyses of habitat selection, which could have given more definite results. A larger sample size of collared zebra relative to eight habitats could have given more definitive results, but due to funding limitations we were only able to collar a small number of animals for this study (Sianga, 2018). The birthing period of this zebra population was not determined in this study, and hence the birthing season remains unknown. However, despite these limitations, the combination of remotely sensed data and the ground field sampling is important, as the latter is sadly missing these days from many movement ecology studies (Ríos-Saldaña, Delibes-Mateos & Ferreira, 2018).

Our study provides seasonal movements and habitat selection patterns by plains zebra, and hence adds to existing data from zebra migrations across northern Botswana. Each migration encompasses a dry season range with permanent water and a saline grassland-based wet season range of lacustrine origin. Factors that concentrate nutrients in landscapes at large scales, such as ancient lake systems in the Kalahari Basin or volcanic deposits and landscape catenas elsewhere, appear to be key factors in determining the wet season ranges of migratory herbivores in Africa. Thus our study highlights key factors determining the functionality of seasonal home ranges, providing an understanding of the mechanisms driving migration in African herbivore populations. In addition, our results emphasize the importance of keeping migratory corridors open to maintain habitat connectivity between functional seasonal home ranges of various herbivores.

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Data accessibility

Data (grass characteristics and GPS data) used in this paper will be freely available on the Okavango Delta Information System (ODIS) at the Okavango Research Institute (ORI), Maun Botswana.

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Appendix

 Table 1-A1: The proportion of each habitat on the seasonal Minimum Convex Polygons of the six collared

 zebra herds in the Savuti-Mababe-Linyanti Ecosystem, northern Botswana. SE denotes standard error of the

 mean.

Wet	Early dry	Late dry
Mean±SE	Mean±SE	Mean±SE
0.173±0.030	0.514 ± 0.340	$0.359 {\pm} 0.080$
10.895 ± 1.442	29.538±5.364	19.655±2.625
0.008 ± 0.008	0.082 ± 0.050	$0.219{\pm}0.058$
14.465 ± 4.283	$21.190{\pm}1.468$	19.212±2.887
$16.434{\pm}1.181$	36.795±8.170	57.043±2.812
13.178±1.432	10.816±3.497	3.177±0.399
44.655±5.215	0.367±0.367	0.000 ± 0.000
0.191±0.096	0.698±0.507	0.336±0.126
	Wet Mean±SE 0.173±0.030 10.895±1.442 0.008±0.008 14.465±4.283 16.434±1.181 13.178±1.432 44.655±5.215 0.191±0.096	Wet Early dry Mean±SE Mean±SE 0.173±0.030 0.514±0.340 10.895±1.442 29.538±5.364 0.008±0.008 0.082±0.050 14.465±4.283 21.190±1.468 16.434±1.181 36.795±8.170 13.178±1.432 10.816±3.497 44.655±5.215 0.367±0.367 0.191±0.096 0.698±0.507

 Table 2-A1: Kruskal Wallis Multiple Comparison Test (*. Significant difference at the 0.05 level) on grass

 characteristics during the wet season in the Savuti-Mababe-Linyanti Ecosystem, northern Botswana.

Habitat characteristics	Habitat	Habitat	Test statistic	P value
Grass greenness (%)	Sandveld	Wetland	10.872	0.793
	Sandveld	Mopane	27.635	0.001*
	Sandveld	Acacia grasslands	34.235	0.001*
	Wetland	Mopane	-16.764	0.142
	Wetland	Acacia grasslands	23.364	0.004*
	Mopane	Acacia grasslands	6.600	1.000

Grass height (cm)	Sandveld	Wetland	12.273	0.621
	Sandveld	Mopane	-17.167	0.077
	Sandveld	Acacia grasslands	-22.812	0.001*
	Wetland	Mopane	29.439	0.001*
	Wetland	Acacia grasslands	-35.085	0.001*
	Mopane	Acacia grasslands	-5.646	1.000
Grass biomass (g/m ²)	Sandveld	Wetland	19.219	0.065
	Sandveld	Mopane	-22.435	0.007*
	Sandveld	Acacia grasslands	-12.194	0.290
	Wetland	Mopane	41.655	0.001*
	Wetland	Acacia grasslands	-31.413	0.001*
	Mopane	Acacia grasslands	10.242	0.662
Sodium (g/kg)	Sandveld	Wetland	8.267	1.000
	Sandveld	Mopane	27.124	0.008*
	Sandveld	Acacia		
		grasslands	51.154	0.001*
	Wetland	Mopane	-18.857	0.238
	Wetland	Acacia grasslands	42.887	0.001*
	Mopane	Acacia	24 030	0 025*
		Stubblunub	21.050	0.023
Calcium (g/kg)	Sandveld	Wetland	-43.012	0.001*
	Sandveld	Mopane	-21.788	0.060

	Sandveld	Acacia grasslands	-17.709	0.190
	Wetland	Mopane	-21.224	0.124
	Wetland	Acacia grasslands	25.304	0.029*
	Mopane	Acacia grasslands	4.079	1.000
Phosphorus (g/kg)	Sandveld	Wetland	19.673	0.177
	Sandveld	Mopane	29.846	0.002*
	Sandveld	Acacia grasslands	31.231	0.001*
	Wetland	Mopane	-10.172	1.000
	Wetland	Acacia grasslands	11.558	1.000
	Mopane	Acacia grasslands	1.384	1.000

Table 3-A1: Kruskal Wallis Multiple Comparison Test (*. Significant difference at the 0.05 level) on grasscharacteristics during the late dry season in the Savuti-Mababe-Linyanti Ecosystem, northern Botswana.

Habitat characteristics	Habitat	Habitat	Test statistic	P value
Grass greenness (%)	Sandveld	Wetland	17.682	0.006*
	Sandveld	Mopane	-8.040	0.887
	Sandveld	Acacia grasslands	-9.818	1.000
	Wetland	Mopane	25.722	0.001*
	Wetland	Acacia grasslands	-27.500	0.001*
	Mopane	Acacia grasslands	-1.778	1.000

Grass height (cm)	Sandveld	Wetland	10.212	0.739
	Sandveld	Mopane	-8.732	0.955
	Sandveld	Acacia grasslands	-13.455	0.528
	Wetland	Mopane	18.944	0.002*
	Wetland	Acacia grasslands	-23.667	0.005*
	Mopane	Acacia grasslands	-4.722	1.000
Grass biomass (g/m ²)	Sandveld	Wetland	13.455	0.187
	Sandveld	Mopane	-7.934	1.000
	Sandveld	Acacia grasslands	-23.045	0.009*
	Wetland	Mopane	21.389	0.001*
	Wetland	Acacia grasslands	-36.500	0.001*
	Mopane	Acacia grasslands	-15.111	0.194

Chapter 7

Synthesis

African savannas are important in supporting the diversity and abundance of domestic and wild herbivores (Smithers 1983, Coppock et al. 1986, Scholte et al. 2007, Homewood 2008, Fynn and Bonyongo 2011), and their long-range migrations (Homewood 2008, Harris et al. 2009, Fynn et al. 2015), and hence considered important for global conservation. However, there are two major challenges for conservation in African savannas: (1) protected areas in Africa were designed around expediency, not according to ecological requirements for conservation, and as result adaptive foraging options for herbivores is compromised, ultimately resulting in declining wildlife populations. (2) Artificial water points establishment in landscapes is another problem facing conservation in Africa. The establishment of artificial water points may result in loss of habitat heterogeneity, with negative impacts on biodiversity. However, the Savuti-Mababe-Linyanti ecosystem (SMLE) in northern Botswana gives an opportunity to examine these two challenges/problems for conservation in an ecosystem that still encompasses large ecological gradients and has large waterless regions. This study generated important findings on;

- Key ecological gradients and vegetation types.
- Forage quantity and quality, structure and the seasonal distribution of forage resources on these ecological gradients.
- The effect of herbivory on plant composition, structure and diversity, as mediated by distance to water.
- Habitat selection by zebra and buffalo within this functional heterogeneity of resources on these ecological gradients.

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In chapter 1, an account on factors influencing vegetation heterogeneity and its influence on spatial distribution of large herbivores such as the buffalo, zebra and African elephant was detailed. Chapter 2 identified 15 plant communities in the SMLE which are characterised by varying gradients of soil texture / fertility and wetness. In chapter 3, i determined forage quantity and quality, structure and the seasonal distribution of forage resources on these ecological gradients. Chapter 4 determined the effect of herbivory on plant composition, structure and diversity. In chapters 5 and 6, i determined habitat selection by zebra and buffalo to functional heterogeneity of resources on these ecological gradients.

Sianga and Fynn (2017) identified 15 plant communities in the SMLE which are characterized by varying gradients of soil texture, fertility and soil moisture regime, which appear to be key factors driving functional heterogeneity in the ecosystem (Chapter 2). Of the identified communities, seven occurred on sandy soils, four on alluvial loam soils, and four on lacustrine clay soils of the MD. Seven communities were identified on sandy soils and these appeared to be differentiated by subtle variations in clay content, which was determined by their distance from core regions of ancient sediment deposition such as in Paleolake Mababe or from flood deposition in areas adjacent the Okavango Delta and Linyanti Swamps (Sianga and Fynn 2017). Sandveld communities, such as the Ipomea chloroneura – Oxygonum alatum and the Eragrostis pallens - Ochna pulchra communities, occur in Kalahari sandy soils among an alluvial soil matrix dominated by mopane woodland (Sianga and Fynn 2017). This mosaic of sandveld and mopane is a critical feature of the functional heterogeneity of the region because it provides key habitat for herbivore species preferring medium and tall grasses, such as buffalo, roan, sable, and elephant (Taolo 2003, Bennitt et al. 2014, Fynn et al. 2014, Sianga 2014, Bennitt et al. 2015), probably because of the abundance of digestible, leafy forage of high-quality grass species dominant in sandveld woodland (e.g. Digitaria eriantha, Brachiaria nigropedata,

Panicum maximum and *Schmidtia papophoroides*), as well as *Digitaria milanjiana* and *P. maximum* in mopane woodland (Sianga et al. 2017b, Chapter 4).

These high-quality grasses are most abundant distant from the permanent water bodies of the Okavango Delta and Linyanti Swamps (>15 km - 20 km) whereas high-quality short grasses such as Urochloa trichopus were most abundant within 5 km of these permanent water bodies (Sianga et al. 2017b, Chapter 4). Despite the presence of the large elephant population in Africa in northern Botswana (ca 130, 000; Chase et al. 2017), their impact on preferred woody plants in sandveld and mopane woodland was strongly constrained by these distance to water gradients. One of the most impacted trees by elephant during the dry season, Terminalia sericea, which is dominant in sandveld woodland, has been reduced to shrubland within 5 km of permanent water bodies of the Okavango Delta and Linyanti Swamps, but beyond 15 km from these water bodies, this species remains as intact tall woodland (Sianga et al. 2017b, Chapter 4). This demonstrates that these long-distances away from permanent surface water in the SMLE make these woodland landscapes resilient to the impacts of a massive elephant population, with spatial refuges for high-quality tall grasses and tall woodland existing beyond 15 km from permanent water bodies. This probably explains why buffalo tend to prefer the woodlands distant from permanent surface water during the wet season (Bennitt et al. 2014, Sianga 2014, Sianga et al. 2017a, Sianga et al. 2017b, chapter 5), as do roan and sable antelope (Hensman et al. 2013, Haveman 2014). Also important are more extensive areas of sandveld east of the MD classified as Commiphora angolensis - Combretum collinum sandveld (Sianga and Fynn 2017, Chapter 2), another key wet season habitat for tall grass grazers such as buffalo, eland and roan antelope (pers. obs. February 2015), probably because of the abundance of taller tufted D. eriantha and occurs distant from any permanent water sources. In contrast, short grass grazers such as wildebeest and impala were

more abundant within 5 km of permanent water (Fynn et al. 2014), where high-quality short grasses were most abundant (Sianga et al. 2017b). These associations of short and tall grass grazers with short and tall grassland, respectively, have also been observed in the Masai-Mara and adjacent pastoral areas in Kenya (Bhola et al. 2012).

Grass and forb richness decreases with distance from water in sandveld woodland but shows the opposite response in mopane woodland (Sianga et al. 2017b, Chapter 4). The contrasting responses of forb and grass richness to herbivory and distance from permanent water in mopane and sandveld woodlands are probably related to interactions of herbivory and habitat productivity, whereby species richness is decreased and increased by herbivory in less and more productive habitats, respectively (Proulx and Mazumder 1998, Osem et al. 2002, Bakker et al. 2006, Burkepile et al. 2017). In more productive habitats, herbivory reduces competition from dominant herbaceous species, while in unproductive habitats dominants are not productive enough to exclude other species, but instead herbivory increases stress on many species (Burkepile et al. 2017). Sandveld woodland generally has a taller and denser grass layer (83.4% \pm 29.3% grass cover) than mopane woodland (56.9% \pm 12.9 % grass cover) which has a lot of bare ground. Thus it appears that insufficient fire or herbivory in sandveld woodland results in large dominant herbaceous species excluding small grasses and forbs (Koerner et al. 2014). Thus overall richness does not appear to have declined under foraging and trampling impacts of a large herbivore biomass, but rather responds to herbivory positively or negatively depending upon habitat productivity and the potential for competitive exclusion (Owensby et al. 1970, Proulx and Mazumder 1998, Bakker et al. 2006, Burkepile et al. 2017).

Clearly, distant away from permanent water bodies play a critical role in maintaining ecological function and biodiversity in the SMLE because they create heterogeneity in woodland structure, grass composition and grass and forb diversity, which creates niche heterogeneity and improves biodiversity. However, significant numbers of artificial water points in the habitats distant from permanent surface water, would result in elephant and other large herbivores affecting the structure of preferred woody species, as well as composition and structure of grasses right across the landscape. A decline in the abundance of high-quality tall grasses with year-round grazing in the woodlands distant from permanent surface water would be expected to negatively impact tall-grass grazers such as buffalo, sable and roan antelope (Fynn et al. 2016). This might have negative knock-on effects on other biota such as various birds, bats, insects, and others that rely on mature woodland or taller grasses as optimal habitat (Cumming et al. 1997). Creation of heterogeneity in woodland structure (zones of short, immature and tall, mature woodland) and in grass composition and structure may be expected to maximise niches for various biota, some of which may prefer different structural and compositional states of woodland and grassland, as observed for birds with woodland structural heterogeneity (Bradbury et al. 2005) and for birds and insects with grassland structural heterogeneity (Chambers and Samways 1998, Fuhlendorf et al. 2006, Krook et al. 2007).

Consequently, these communities > 15 km from water are key wet season habitats for taller grass grazers including buffalo (Fynn et al. 2014, Sianga 2014, Sianga and Fynn 2017), sable and roan antelopes (Hensman et al. 2013, Haveman 2014) and elephants, probably because of the abundance of taller-tufted perennial grasses growing there during that time (Sianga et al. 2017b). In the SMLE, collared buffalo herds moved from wetland habitats of the Linyanti Swamps, Okavango Delta and Selinda Spillway during the wet season into mopane and sandveld communities distant in parts of the landscape in the Linyanti Swamps and Okavango Delta and the Chobe Enclave region, respectively (Sianga and Fynn 2017, Sianga et al. 2017a, Sianga and

Fynn in review, Chapter 3 and 5). It is the mosaic of sandveld and mopane that serves as a key wet season habitat – neither sandveld nor mopane alone is sufficient as a wet season habitat. Generally, sandveld has no water, but provides the best grasses, while mopane has poor grazing but has water and minerals. In combination, these two habitats provide a single ideal habitat during the wet season (Sianga and Fynn 2017, Chapter 2). This sandveld and mopane woodland mosaic allows buffalo and other large herbivores to forage adaptively, selecting their preferred leafy grasses such as *D. eriantha*, *B. nigropedata* and *S. papophoroides*, and some *Eragrostis spp* in the sandveld, and then easily accessing water in the many pans in the adjacent mopane (Sianga and Fynn 2017, Chapter 2).

An intriguing feature of mopane woodland is distinct patchy structural heterogeneity characterised by patches of stunted trees (< 1.5m high) directly adjacent to taller patches (> 5m high). Very tall cathedral mopane may be found on deeper soils adjacent to permanent water bodies of the Okavango Delta, Linyanti Swamps, Savuti Channel and Selinda Spillway (>10m high). Mopane trees are kept in a short state in the stunted mopane patches because of its occurrence on heavier soils derived from basic materials, whereas cathedral mopane is most common on sandier soils (Pellacani 2017). Furthermore, Pellacani (2017) found that stunted mopane occurred on alkaline soils than cathedral mopane, and that cation exchange capacity of Na, K and Ca was higher in soils in stunted mopane than in cathedral mopane. However, other studies suggested that mopane woodlands occur in stunted forms due to elephant browsing (Smallie and O'Connor 2000) or frequent fires (Mlambo and Mapaure 2006). In addition, the structural differences of mopane woodland further contribute to heterogeneity in the region. Stunted mopane has several short grasses such as *Eragrostis nindensis*, *D. milanjiana* and *Heteropogon contortus* which provide good grazing for various herbivores (Sianga and Fynn

2017). Stunted mopane patches provide grasses higher in Na and Ca content than cathedral mopane (Mlambo 2007, Pellacani 2017). Thus grasses growing in this stunted mopane are likely to provide high minerals in forage, and are hence important to herbivores such as buffalo, roan and sable which utilize this habitat during the wet season. These woodland systems are therefore important as key habitats providing high-quality forage farther from permanent surface water during the wet season and low predation risk annually.

Woody plant species preferred by elephants during the dry season included taller mature tree populations farther away from permanent surface water (> 10km) while those closer to permanent surface water (< 5km) were characterized and dominated by pollarded trees (Sianga et al. 2017b). To conclude then, patterns of short and tall grasses and woodland structure with distance from water suggests that the spatial refuges in the relatively unmodified landscapes of this study area during the dry season, provides a buffering effect against negative effects on vegetation composition, structure and diversity across the landscape by a large elephant population and populations of buffalo and other large herbivores. Sianga and Fynn (in review, chapter 3) found that grasses and sedges in wetland habitats had higher protein levels than dryland woodlands during the dry season, demonstrating the importance of wetland habitats as dry season ranges for various herbivores (Bell 1970, Sinclair 1979, Macandza et al. 2012, Bennitt et al. 2014, Fynn et al. 2014). This study (Sianga and Fynn in review, Chapter 3) demonstrated that within the wetland habitats, sedgelands had intermediate protein content but higher biomass, whereas the wet sandveld had higher protein content but very low biomass. This demonstrates the importance of wetland habitats in providing heterogeneity in forage quality and quantity over the dry season, and thus probably the reason why large herbivores in this region switch to these habitats during the dry season. As the depth and duration of flooding increases in

wetland habitats, floodplains become increasingly dominated by taller more productive sedges and swamp grasses (Murray-Hudson et al. 2014, Fynn et al. 2015). Thus while the deeper parts of floodplains (i.e sedgelands) provide more reliable green forage during the late dry season, their tall fibrous grasses and sedges are of lower digestibility and quality owing to greater cellulose and lignin content (Wilmshurst et al. 2000). In addition, Mosimane (2015) found that wetland grasses and sedges had higher silica content in tissues, which lowers their digestibility and palatability. Thus foraging adaptively between a higher-biomass, adequate-quality resource (sedgeland) and a high-quality but low-quantity resource (wet sandveld) ensures a balanced protein and fibre intake during the late dry season, as was demonstrated for buffalo foraging between taller sedgelands and short but higher quality Cynodon dactylon lawns around Lake Manyara, Tanzania (Prins and Beekman 1989). Heterogeneity in flooding depth and duration in wetlands provides key heterogeneity in forage quantity and quality to enable herbivores to balance protein vs fibre intake (Fynn et al. 2015).

The wetland community composition differs by gradients of flood depth and duration; with *C. dactylon* often associated with the parts of the gradient with the lowest depth and duration of flooding, while *Panicum repens* and *Setaria sphacelata* often characterises areas with intermediate depth and duration of flooding, whereas tall sedges and grasses such as *Oryza longistaminata* and *Vossia cuspidata* characterise areas of the gradient with the largest depth and duration of flooding (Murray-Hudson et al. 2011, Murray-Hudson et al. 2014, Fynn et al. 2015). This variation in composition and phenology on flooding gradients is important in providing the variation in green forage supply for herbivores from the early to late dry season, owing to variation in availability of soil moisture for growth, allowing for adaptive foraging over the dry season. Generally, edges of floodplain grasslands and shallow – intermediate depth floodplains

are favoured by herbivores over the early dry season, while deep floodplains and swamps are used over the late dry season and during droughts (Fynn et al. 2015).

Vegetation in the MD provides mineral rich forage in the ecosystem, and hence serves as key wet season ranges for various herbivores such zebra, wildebeest and impala. Collared zebra migrated from their dry season ranges along the Linyanti Swamps and Savuti Channel region into the nutrient rich grasslands of the MD, where Chloris virgata – Boerhavia coccinea and Cenchrus ciliaris - Senegalia mellifera occurring on the lacustrine clays were favoured (Sianga and Fynn 2017, Sianga et al. in review, Chapter 6). Selection for nutrient rich communities of the MD was an important strategy associated with enhancing nutrient intake by pregnant females and during lactation (Kreulen 1975, Murray 1995, Joos-Vandewalle 2000, Fynn and Bonyongo 2011, Fynn 2012). Thus these communities occurring on lacustrine clay soils regarded as fertile soils are critical key wet season habitats for the migratory zebra population, impala and wildebeest in the SMLE (Joos-Vandewalle 2000, Fynn et al. 2014, Sianga 2014, Sianga and Fynn 2017, Sianga et al. in review). Sianga and Fynn (2017) and Fynn et al (2014).) demonstrated that P concentrations in soils and grasses respectively in the SMLE were higher in the Acacia grasslands (*Chloris virgata – Boerhavia coccinea*) along the southern edge of the MD near Mababe, and the zebra moved there and favoured this habitat for the wet season (Sianga et al. in review, Chapter 6), most likely to maximize P intake, a critical mineral for pregnant and lactating females (Murray 1995). Additionally, while in their favoured wet season range, zebra foraged adaptively between the short Acacia grasslands on the edge of the sump of the MD and the taller grasslands (Cenchrus ciliaris – Senegalia mellifera) further into the sump (Sianga et al. in review, Chapter 6). This may be a strategy to maximize intake of P, which was highest in the soils of Acacia grasslands than in the soils of tall open grasslands (19.8 Vs. 11.2 mg kg⁻¹,

respectively) and Ca, which was higher in the soils of the tall open grasslands than in the soils of Acacia grasslands (6018 Vs. 2975 mg kg⁻¹, respectively, Sianga and Fynn 2017). In addition to the soils and grasses of the Acacia grassland of the MD having the highest P levels, they are dominated by short, soft leaved grasses such as *U. trichopus*, compared with the taller stemmy *C. ciliarus* of the tall open grasslands, which likely results in greater forage digestibility compared with the tall open grasslands and other habitats in the ecosystem. In addition to selection for nutrient rich habitats, some large herbivores incorporate predation risk in their decision-making processes (Rettie and Messier 2000). The open short Acacia grasslands of the MD provide better visibility, which reduces predation risk and is thus suitable as a birthing ground for this zebra population. Thus, optimizing intake of all important essential elements requires adapting spatially to this variation in functional heterogeneity in the ecosystem, while minimising predation risk.

Drying up of ephemeral pans in the dryland woodlands in the Chobe Enclave, and between the Linyanti Swamps and Okavango Delta, and MD over the dry season, forced buffalo and zebra to shift away from favoured wet season habitats towards wetland and riverine habitats along the Linyanti Swamps, Selinda Spillway and Savuti Channel (buffalo), and Linyanti Swamps and Savuti Channel (zebra) respectively (Sianga et al. 2017a, Sianga et al. in review, Sianga and Fynn in review, Chapter 3, 5 and 6). It is this forced movement away from favoured wet season ranges towards permanent water that likely contributes to reduced grazing pressure in favoured wet season ranges and, therefore, higher abundances of favoured grasses such as *D*. *eriantha* farther from permanent water.

Limitations of the study

This study did not;

- Demonstrate whether the mapped vegetation units have changed in the past decade.
- Map the geographical distribution of functional resources such as bridging and buffer resources.
- Investigate the effects of fire on elephant and herbivore dung.
- Investigate whether habitat selection by buffalo and zebra in the SMLE are influenced by other factors such as predation pressure other than forage quality and water availability.
- The study probably misclassified other habitats in the classification as the analysis suggested that map accuracy was about 70 %.

Future work

This study produced a detailed baseline vegetation map of the SMLE (northern Botswana) which is important for wildlife studies being conducted in the region. However, future reaserch may focus on;

- Determining landcover changes in the SMLE in the past decade.
- Map the distribution of functional resources (i.e bridging and buffer resources) in the SMLE.
- Fire effects on elephant and herbivore dung as a role on the effects of herbivory on plant diversity, composition and structure with distance from permanent water.
- Investigate the effect of predation pressure on habitat selection by buffalo and zebra in the SMLE.

Conclusion and management implications

This study demonstrated that effective conservation of African wildlife requires extensive protected areas that include key ecological gradients such as gradients of soil texture and gradients of wetness from moisture limited saline grasslands through to deep floodplains, as well as long distance gradients away from permanent water bodies. Gradients of soil texture and wetness allowed development of critical heterogeneity in vegetation composition and phenology, which enabled herbivores to adapt to seasonal variability in forage and water availability. Herbivory on the large distance gradients away from permanent water (> 20 km) in the SMLE has created key diversity, compositional and structural heterogeneity in grass, forb and woody species that is likely to result in greater niche diversity and adaptive foraging options that will enhance biodiversity and herbivore population stability and productivity. This study shows that spatial refuges for both grass and woody species operated beyond 15 km from permanent water of the Okavango Delta and Linyanti Swamps. Water provision in the form of artificial water holes in the dryland woodlands of the SMLE will allow elephants, buffalo and other herbivores to spend a long time farther from permanent water during the dry season, leading to over-grazing of taller tufted and high-quality grasses and destruction of tall woodland, ultimately homogenising vegetation composition and structure across large landscapes, with negative consequences for biodiversity. Therefore artificial water provision in woodlands distant from permanent surface water in this ecosystem should be limited as it will have dramatic effects on both large herbivores and vegetation.

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