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

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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 m x 20 m (800 m²) plots in which the coverage of all plant species was estimated. Non-metric multidimensional scaling (NMS) demonstrated that plant communities were determined by gradients in soil texture or fertility and wetness. NMS 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 mixed *Senegalia/Vachellia* (*Acacia*) savanna, with the mineral-rich soils supporting grasses high in minerals such as phosphorus, calcium, sodium and potassium, 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 provide critical grazing for taller grass grazers such as buffalo, roan and sable antelope, whereas wetland communities provide reliable green forage during the dry season for a variety of herbivores, including elephant. This study has demonstrated how large-scale environmental gradients determine functional habitat heterogeneity for wildlife.

Conservation implications: Our study demonstrated that the functionality of protected areas is determined by large-scale environmental gradients. Thus conservation science must aim to ensure that protected areas cover the full range of key environmental gradients in a region (soil texture and wetness in our study). Our habitat map provides a data base for wildlife habitat use studies in the region.

Introduction

There is growing recognition of the importance of spatial heterogeneity in determining biodiversity (MacFayden et al. 2016) and adaptive foraging options for herbivores (Hobbs et al. 2008; Hopcraft, Olff & Sinclair 2010; Owen-Smith 2004) and predators (Hopcraft, Sinclair & Packer 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 (Fynn, Chase & Roder 2014; Hopcraft et al. 2010). Functional differences among different plant communities in meeting the seasonally varying needs of animals have been referred to as functional habitat heterogeneity and play a key role in determining the viability of herbivore populations (Hopcraft et al. 2010; Owen-Smith 2004). Environmental factors such as soil fertility, forage quality and water availability, which covary strongly with vegetation, may also influence human settlement, crop field and livestock distribution patterns.

Development of detailed vegetation maps is, therefore, essential for (1) understanding the distribution of biodiversity across a region, (2) research on wildlife species' home range and habitat use, (3) conservation planning and (4) understanding socio-ecological interactions.

Vegetation maps are especially useful for determining seasonal habitat use of collared wildlife species where thousands of global positioning systems (GPS) locations may be obtained from a collared animal, which cannot 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 to these wetland systems. The Savuti-Mababe-Linyanti ecosystem (SMLE) with its extensive wetlands and woodlands and the open grasslands of the Mababe Depression (MD) 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 (Fynn et al. 2014; Naidoo et al. 2014; Sianga 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 article 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 (1) classify the vegetation of the SMLE of northern Botswana, (2) develop a detailed vegetation map that provides a reliable habitat template of the SMLE for wildlife habitat use studies and for future studies and (3) discuss how the heterogeneity in vegetation and soils of the SMLE contributes to functional habitat heterogeneity for wildlife.

Materials and methods

Study area

This study was done in the 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 characterised by a semi-arid climate with an annual rainfall of around 500 mm on the western side (Okavango Delta) and increasing eastwards to around 600 mm in the Chobe Enclave region (Botswana Meteorological Services). The climate is characterised by a wet season (December–April), cool, early dry season (May–August) and a hot, late dry season (September–November), where the daily maximum temperatures are regularly between 35 °C and 40 °C during 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 to 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 MD (Figure 1), characterised 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 the Kalahari sands. Vegetation on the clay soils of the MD is characterised by open *Senegalia/Vachellia* (*Acacia*) spp. savanna grasslands and higher forage quality (Fynn et al. 2014).

Vegetation sampling

Vegetation composition was sampled using 40 m × 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 that plants had attained inflorescences for easier identification. Certain remote habitats of 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 to 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). A total of 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, with nomenclature for all species following The Plant List (http://www.theplantlist.org). Five soil samples collected from each plot were mixed to form a composite sample, which was brought to the Okavango Research Institute laboratory for texture and nutrient analysis.

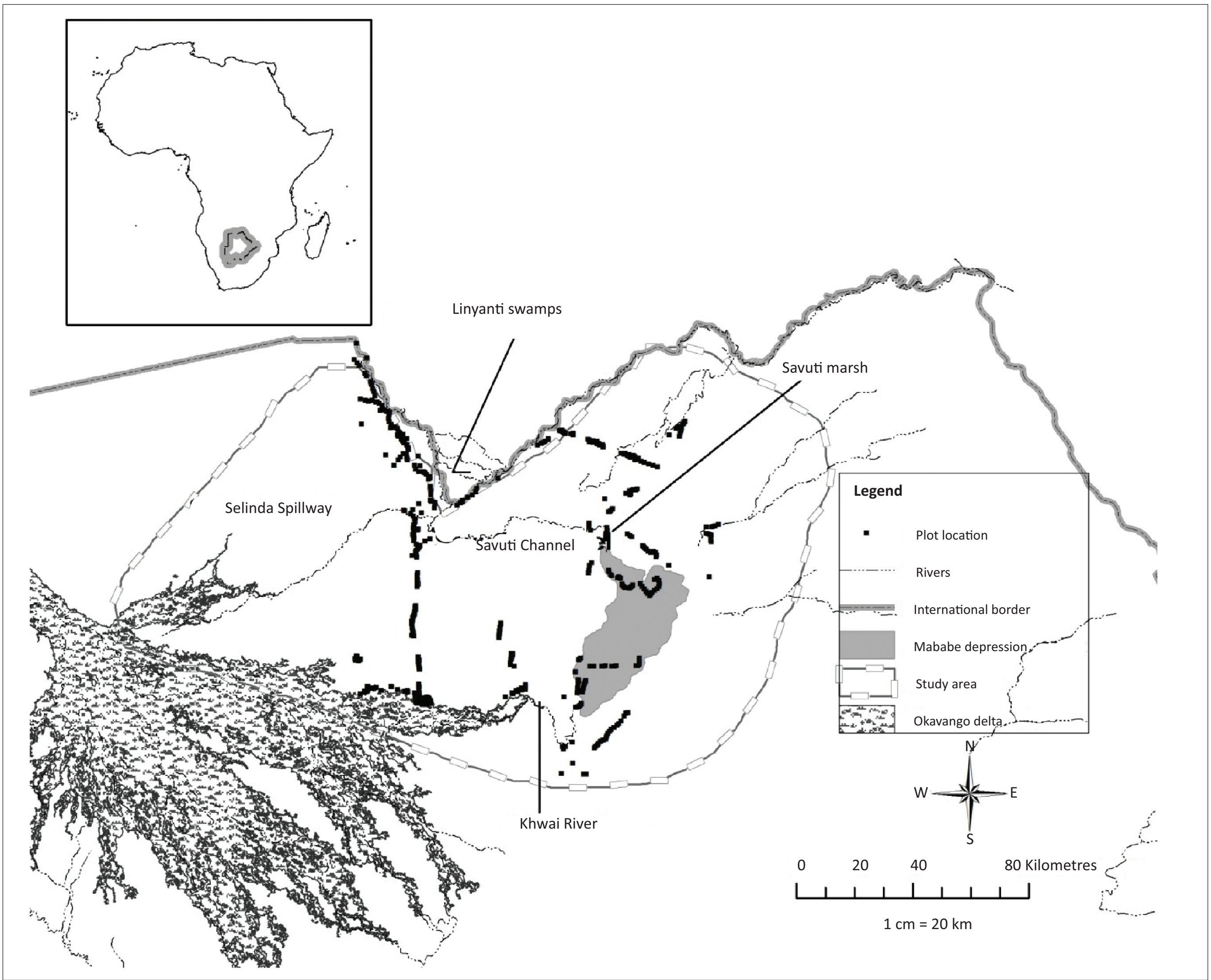


FIGURE 1: Study area depicting the Savuti-Mababe-Linyanti ecosystem and locations of sampling positions.

Vegetation classification

The data for all 801 vegetation plots (% cover abundance of species) were standardised using relativisations by maximum in Principal Component Ordination 6 (PCORD) (McCune, Grace & Urban 2002). These data were subjected to hierarchical cluster analysis (β linkage, β = -0.25, Sorensen distance) in PCORD 6 (McCune et al. 2002), comprising 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 ecologically meaningful communities, and indicator values (IVs) were examined for statistical significance using Monte Carlo technique in PCORD 6 (McCune et al. 2002). Differences between communities were examined using multiresponse 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 the 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 1-A1) 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 (e.g. wetland vs. mopane or riparian forests vs. dry floodplains) and could be easily distinguished through remote sensing and thus were mapped separately. With regard to the communities on heavy lacustrine clay soils, two distinct, functionally different communities occur, (1) the short grasslands with *acacia* spp. on silty soils and (2) the tall, open grasslands on vertisols, thus, functionally for herbivores, we chose to map them as two classes.

Classification

A coincident minimum of ISA *p*-value and maximum number of significant indicator species were found in seven and nine communities, respectively. Another coincident minimum of ISA *p*-value and maximum number of significant indicator species were found in 15 communities and were considered a meaningful ecological level of communities for a detailed vegetation classification. Thus, hierarchical cluster analysis done on all 801 vegetation plots recognised 15 main vegetation communities within which many sub-communities occurred (Figure 1-A1). MRPP tests of 15 communities suggested significant differences between communities ($p < 0.000$, Table 1-A1) with chance-corrected within group agreement, $A = 0.265$. Pairwise comparisons between communities suggested significant differences ($p < 0.000$, Table 1-A1).

The first axis of the NMS1 analysis appears to be a gradient of soil texture and fertility, with communities on the most sandy soils having the most negative values, communities on loam soils having intermediate values and communities on extremely high clay soils having the most positive values on NMS1, respectively (Figure 3; Table 1). The second NMS axis (NMS2) appears to be a weak gradient of wetness, with communities having the most positive values on NMS2 being those 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).

TABLE 1: Soil texture and nutrient characteristics in the Savuti-Mababe-Linyanti ecosystem, northern Botswana.

Community	*N*	Phosphorus (Mean ± SE)	Potassium (Mean ± SE)	Sodium (Mean ± SE)	Calcium (Mean ± SE)	Magnesium (Mean ± SE)	Sand (Mean ± SE)	Silt (Mean ± SE)	Clay (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 – Senegalia 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 ± 2211.5	729.3 ± 260.8	61.3 ± 12.5	19.6 ± 5.9	19.1 ± 6.6

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 1). In the vegetation or 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 1), we refer to it in the map as Baikiaea forest, not as sandveld (Figure 2).

Baikiaea plurijuga – Baphia massaiensis

This community is associated with high sand and low clay content of the soil (Table 1). 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 Tsum Tsum 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 2). 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.

Apart from the 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 among the highest sand and lowest silt and clay contents, as well as the lowest phosphorus, potassium, sodium and magnesium contents (Table 1), and is recognised 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 2).

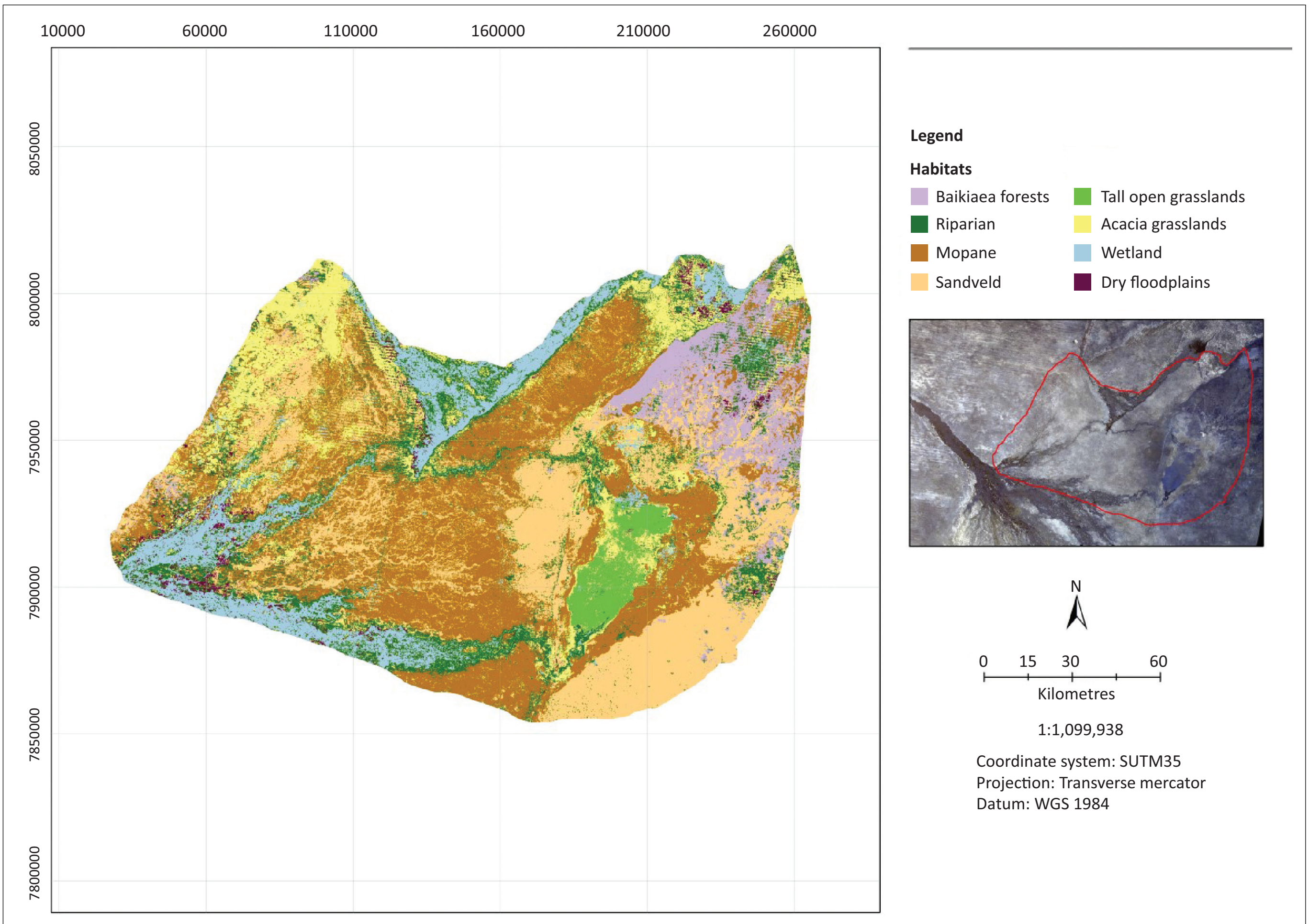


FIGURE 2: Map of Savuti-Mababe-Linyanti ecosystem Vegetation (northern Botswana).

TABLE 2: Indicator species characteristics for 15 class divisions of plant communities in the Savuti-Mababe-Linyanti ecosystem (northern Botswana).

Indicator species	Indicator values	*P*
Baikiaea plurijuga – Baphia massaiensis		
Baikiaea plurijuga	98.7	0.0002
Baphia massaiensis	70.2	0.0002
Croton gratissimus	65.9	0.0002
Hibiscus lobatum	48.8	0.0002
Panicum maximum	39.7	0.0002
Thunbergia reticulata	38.6	0.0006
Combretum apiculatum	34.2	0.0002
Vigna stenophylla	22.5	0.0018
Dipcadi marlothii	22.2	0.0016
Citrullus lanatus	20.8	0.0010
Cyperus margaritaceus	14.9	0.0114
Merremia pinnata	11.5	0.0292
Ledebouria revoluta	10.3	0.0330
Ipomoea chloroneura – Oxygonum alatum		
Ipomoea chloroneura	66.5	0.0002
Oxygonum alatum	66.0	0.0002
Hibiscus mastersianus	55.8	0.0002
Charmocresta stricta	55.24	0.0002
Erlangea misera	54.4	0.0002
Pavania senegalensis	45.4	0.0002
Charmocresta absus	32.4	0.0002
Ceratotheca sesmoides	25.2	0.0012
Basananthe pedata	21.4	0.0012
Philenoptera nelsii	20.4	0.0038
Eragrostis pallens – Ochna pulchra		
Eragrostis pallens	50.0	0.0002
Ochna pulchra	41.2	0.0002
Burkea africana	31.2	0.0002
Aristida stipitata	32.0	0.0002
Phyllanthus burchellii	32.8	0.0008
Phyllanthus mendesii	29.6	0.0012
Digitaria eriantha	18.1	0.0028
Dicoma schinzii	18.1	0.0056
Euphorbia crotonoides	11.1	0.0504
Commiphora angolensis – Combretum collinum		
Commiphora angolensis	94.6	0.0002
Combretum collinum	80.8	0.0002
Senegalia ataxacantha	76.1	0.0002
Combretum molle	73.7	0.0002
Evolvulus alsinoides	73.4	0.0002
Neorautanenia amboensis	73.3	0.0002
Xenostegia tridentata	72.1	0.0002
Waltheria indica	68.7	0.0002
Ochna serrulata	65.4	0.0002
Bauhinia petersiana	52.0	0.0002
Duosperma crenatum	48.8	0.0002
Acanthosicyos naudinianus	45.4	0.0002
Commiphora africana	42.6	0.0004
Boscia albitrunca – Dactyloctenium giganteum		
Boscia albitrunca	44.0	0.0002
Dactyloctenium giganteum	35.6	0.0004
Indigofera flavicans	33.0	0.0016
Sida chrysantha	27.4	0.0010
Mundulea sericea	21.3	0.0036
Ocimum gratissimum	20.0	0.0122
Digitaria ternata	15.5	0.0058
Cleome hirta	12.5	0.0442
Brachiaria nigropedata – Combretum hereroense		
Brachiaria nigropedata	85.6	0.0002
Combretum hereroense	68.0	0.0002

Table 2 continues →

TABLE 2 (Continues...): Indicator species characteristics for 15 class divisions of plant communities in the Savuti-Mababe-Linyanti ecosystem (northern Botswana).

Indicator species	Indicator values	*P*
Brachiaria nigropedata – Combretum hereroense		
Lantana angolensis	65.0	0.0002
Andropogon gayanus	63.2	0.0002
Dalbergia melanoxylon	55.8	0.0002
Schmidtia pappophoroides	46.5	0.0002
Polydora poskeana	33.9	0.0008
Vachelliaerioloba	32.7	0.0014
Anthephora pubescens	31.2	0.0006
Aristida stipoides	24.8	0.0014
Tribulus terrestris – Senna obtusifolia		
Tribulus terrestris	70.5	0.0002
Senna obtusifolia	36.7	0.0002
Sida cordifolia	33.8	0.0002
Commelina benghalensis	23.0	0.0028
Dichrostachys cinerea	22.5	0.0158
Zehneria marlothii	17.1	0.0122
Gloriosa superba	15.9	0.0186
Colophospermum mopane – Jasminum stenolobum		
Colophospermum mopane	76.0	0.0002
Jasminum stenolobum	54.6	0.0002
Tragus berteronianus	50.2	0.0004
Zornia glochidiata	46.4	0.0002
Kyllinga buchananii	43.5	0.0002
Commelina forskaolii	41.7	0.0006
Aristida adscensionis	36.9	0.0002
Brachiaria deflexa	36.0	0.0004
Ipomoea plebiea	30.3	0.0018
Ipomoea coptica	27.8	0.0034
Cyperus esculentus	24.0	0.0076
Pycreus macrostachyos	21.6	0.0062
Clerodendrum ternatum	18.3	0.0152
Ampeloscissus africana	12.8	0.0158
Barleria mackenii	12.3	0.0260
Setaria sphacelata – Gomphocarpus fruticosus		
Setaria sphacelata	99.0	0.0002
Gomphocarpus fruticosus	96.2	0.0002
Cyperus longus	89.2	0.0002
Crotalaria platysepala	83.0	0.0002
Momordica balsamina	80.5	0.0002
Sesamum triphyllum	67.8	0.0002
Bulbostylis hispidula	66.1	0.0002
Cymbopogon caesius	56.0	0.0002
Limeum viscosum	49.0	0.0010
Melinis repens	30.4	0.0018
Acrotome inflata	28.6	0.0018
Urochloa trichopus	24.4	0.0004
Justicea divaricata – Eragrostis superba		
Justicea divaricata	21.1	0.0050
Eragrostis superba	15.8	0.0186
Eragrostis trichophora	14.7	0.0128
Geigeria schinzii	13.9	0.0116
Orthanthera jasminiflora	13.0	0.0408
Justicia betonica	12.7	0.0240
Imperata cylindrica	11.7	0.0274
Polygonum decipiens	11.7	0.0158
Croton megalobotrys – Setaria verticillata		
Croton megalobotrys	92.6	0.0002
Setaria verticillata	76.6	0.0002
Diospyros mespiliformis	64.5	0.0002
Philenoptera violacea	57.2	0.0002
Senegalia nigrescens	62.1	0.0002

Table 2 continues on the next page →

TABLE 2 (Continues...): Indicator species characteristics for 15 class divisions of plant communities in the Savuti-Mababe-Linyanti ecosystem (northern Botswana).

Indicator species	Indicator values	*P*
***Croton megalobotrys – Setaria verticillata*†**		
Asystasia gangetica	54.8	0.0002
Astripomoea lachnosperma	49.2	0.0002
Blainvillea acmella	44.4	0.0002
Berchemia discolor	43.7	0.0002
Acalypha indica	42.5	0.0002
Combretum mossambicense	39.4	0.0004
Cocculus hirsutus	37.7	0.0004
Hibiscus ovalifolius	37.5	0.0004
Blepharis Maderaspatensis	35.9	0.0004
Chloris virgata – Boerhavia coccinea		
Chloris virgata	74.8	0.0002
Boerhavia coccinea	52.3	0.0002
Vachellia tortilis	33.7	0.0006
Hermannia kirkii	31.8	0.0008
Vachellia hebeclada	29.4	0.0010
Cucumis anguria	28.2	0.0004
Dicoma tomentosa	26.7	0.0046
Aerva leucura	26.4	0.0010
Cenchrus ciliaris – Senegalia mellifera		
Cenchrus ciliaris	76.5	0.0002
Senegalia mellifera	67.9	0.0002
Indigofera scaberrima	20.8	0.0020
Euphorbia polycephala	20.1	0.0022
Bothriochloa insculpta – Rhynchosia minima		
Bothriochloa insculpta	57.6	0.0002
Rhynchosia minima	39.4	0.0004
Cyathula orthacantha	34.0	0.0004
Leonotis nepetifolia	32.2	0.0004
Dinebra retroflexa	30.6	0.0002
Setaria incrassata – Dichanthium annulatum		
Setaria incrassata	99.9	0.0002
Dichanthium annulatum	92.3	0.0002
Enicostema axillare	70.3	0.0002
Panicum coloratum	63.2	0.0002
Cynodon dactylon	53.8	0.0002
Digitaria milanjiana	34.5	0.0006
Aristida scrabrivalvis	28.5	0.0006
Indigofera schimperi	28.4	0.0004
Aristida hordeacea	20.1	0.0028
Bracharia eruciformis	15.4	0.0066
Brachiaria retiforms	14.9	0.0054

†, Data continues from previous page.

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 content and lowest phosphorus, potassium, sodium and magnesium contents (Table 1). Like the previous community, it is recognised by the dominance of *T. sericea* in the woody layer; however, *Eragrostis pallens*, *Ochna pulchra*, *Burkea africana*, *Aristida stipitata*, *Phyllanthus burchellii*, *D. eriantha*, *Dicoma schinzii*, *Euphorbia critonoides* and *Phyllanthus mendesii* are some of the characteristic species which separate it from the previous community (Table 2).

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 soils of the lowest clay contents and highest sand contents, as well as the lowest phosphorus, potassium, sodium and magnesium contents (Table 1), and and is characterised by woody species not seen in typical sandveld communities west of the MD, such as *Commiphora angolensis*, *Combretum collinum* and *Senegalia* (*Acacia) ataxacantha*. This community's position in the NMS (Figure 3), however, suggests that its plant composition is more similar to the communities with soils of intermediate clay content, and therefore, we suspect 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 woodlands, 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 *C. angolensis*, *C. collinum*, *S. ataxacantha*, *Combretum molle*, *Evolvulus alsinoides*, *Neorautanenia amboensis*, *Xenostegia tridentata*, *Waltheria indica*, *Ochna serrulata*, *Bauhinia petersiana*, *Duosperma crenatum*, *Acanthosicyos naudinianus* and *Commiphora africana* (Table 2). 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 among the highest cover of the high-quality grass *D. eriantha*.

Boscia albitrunca – Dactyloctenium giganteum

This community, although still a sandveld community on sandy soils, was associated with higher clay and calcium and phosphorus contents than other sandveld types (similar to *Brachiaria nigropedata – Combretum hereroense* community in clay content) (Table 1). It is mainly found around the peripheries of Paleolake Mababe (MD) (Figure 2), where there was some moderate deposition of clay and silt by the paleolake waters. Indicator species are *Boscia albitrunca*, *Dactyloctenium giganteum*, *Indigofera flavicans*, *Sida chrysantha*, *Mundulea sericea*, *Ocimum gratissimum*, *Digitaria ternata* and *Cleome hirta* (Table 2). There is an abundance of the high-quality grazing grass *D. giganteum* which, together with the important browse provided by *B. 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, similar to 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 1). It serves as a key wet season habitat for buffalo because of an abundance of one of their most favoured grasses, *B. nigropedata*. Indicator species include *B. nigropedata*, *C. hereroense*, *Lantana angolensis*, *Andropogon* *gayanus*, *Dalbergia melanoxylon*, *Schmidtia pappophoroides* and *Polydora poskeana* (Table 2).

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 the Savuti Channel. Although the sands of this community are deep, they have higher clay content (Table 1), which again is likely associated with ancient sediment deposition from previous water bodies or extreme floods. This community is recognised by the dominance of the woody layer by tall *P. nelsii* (Kalahari appleleaf) and with very little *T. sericea* occurrence (as opposed to other sandveld communities where *T. sericea* is common), which is likely because of the higher clay content in these sandy soils. Indicator species included *T. terrestris*, *S. obtusifolia*, *Sida cordifolia*, *Dichrostachys cinerea* and *Zehneria marlothii* (Table 2).

Vegetation on alluvial loam soils

These communities occur at intermediate levels of silt and clay (as compared with 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 recognised by the dominance of the woody layer by *C. 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 1). 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 *C. mopane*, *J. stenolobum*, *Tragus berteronianus*, *Zornia glochidiata*, *Kyllinga buchananii*, *Brachiaria deflexa* and *Aristida adscensionis* (Table 2).

Setaria sphacelata – Gomphocarpus fruticosus

This community was associated with high silt–clay and intermediate sand contents of the soil (Table 1), 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; hence, 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 2). 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 by intermediate sand, phosphorus, potassium and calcium contents of the soil (Table 1). 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 2).

Croton megalobotrys – Setaria verticillata

This is a riparian woodland community (Figure 2), associated with major water bodies in the region (Table 1). Species including *Croton megalobotrys*, *Setaria verticillata*, *Diospyros mespiliformis*, *Philenoptera violacea*, *Senegalia* (*Acacia) nigrescens* and *Asystasia gangetica* characterised this community (Table 2). Riparian woodlands can occur as open or closed woodlands. Open riparian woodlands are structurally characterised by open canopy woodlands dominated by *P. violacea*, *S. nigrescens* and *C. imberbe*, whereas closed riparian woodlands are characterised by tall, closed canopy woodlands dominated by *C. megalobotrys*, *D. mespiliformis*, *P. violacea*, *S. nigrescens* and *C. imberbe*. In the map, these two riparian woodland communities were mapped as riparian woodlands (Figure 2).

Vegetation on heavy clay lacustrine deposits of the sump of the Mababe Depression

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 to the Linyanti Swamps and Kwando River) and was associated with high silt, phosphorus and calcium (Table 1). It is included under Acacia grasslands in the vegetation map (Figure 2), named as such because these communities are characterised by short grasslands with acacia species in the woody layer (of varying tree density). This 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 Paleolake Mababe or the Kwando/Linyanti Swamps (Figure 2). This community was characterised by *Chloris virgata*, *Boerhavia coccinea*, *Vachellia* (*Acacia) tortilis*, *Hermannia kirkii*, *Vachellia (Acacia) hebeclada*, *Cucumis anguria*, *Dicoma tomentosa* and *Aerva leucura* (Table 2). The community is dominated by the highly palatable annual grasses, *C. 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 1).

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, (1) the *Cenchrus ciliaris – Senegalia* (*Acacia) mellifera* community and (2) the *Bothriochloa insculpta – Rhynchosia minima* community.

Cenchrus ciliaris – Senegalia mellifera

This open savanna grassland community occurs on deep black clay soils (vertisols) deeper into the MD and was associated with soils 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 1). Indicator species are *C. ciliaris*, *S. mellifera*, *Indigofera scaberrima* and *Euphorbia polycephala* (Table 2). The very high soil fertility of the *Cenchrus ciliaris – Senegalia mellifera* community (Table 1) 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 1), but it makes up much less area on the MD. *Bothriochloa insculpta*, *Rhynchosia minima*, *Cyathula orthacantha*, *Leonotis nepetifolia* and *Dinebra retroflexa* characterised this community (Table 2). Dominance by the unpalatable *B. 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 characterised by seasonal flooding from rainfall. Soils in this community are not as high clay as others on the MD (Table 1); however, 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 characterised this community (Table 2). The community appears to be utilised by many roan antelope over the dry season.

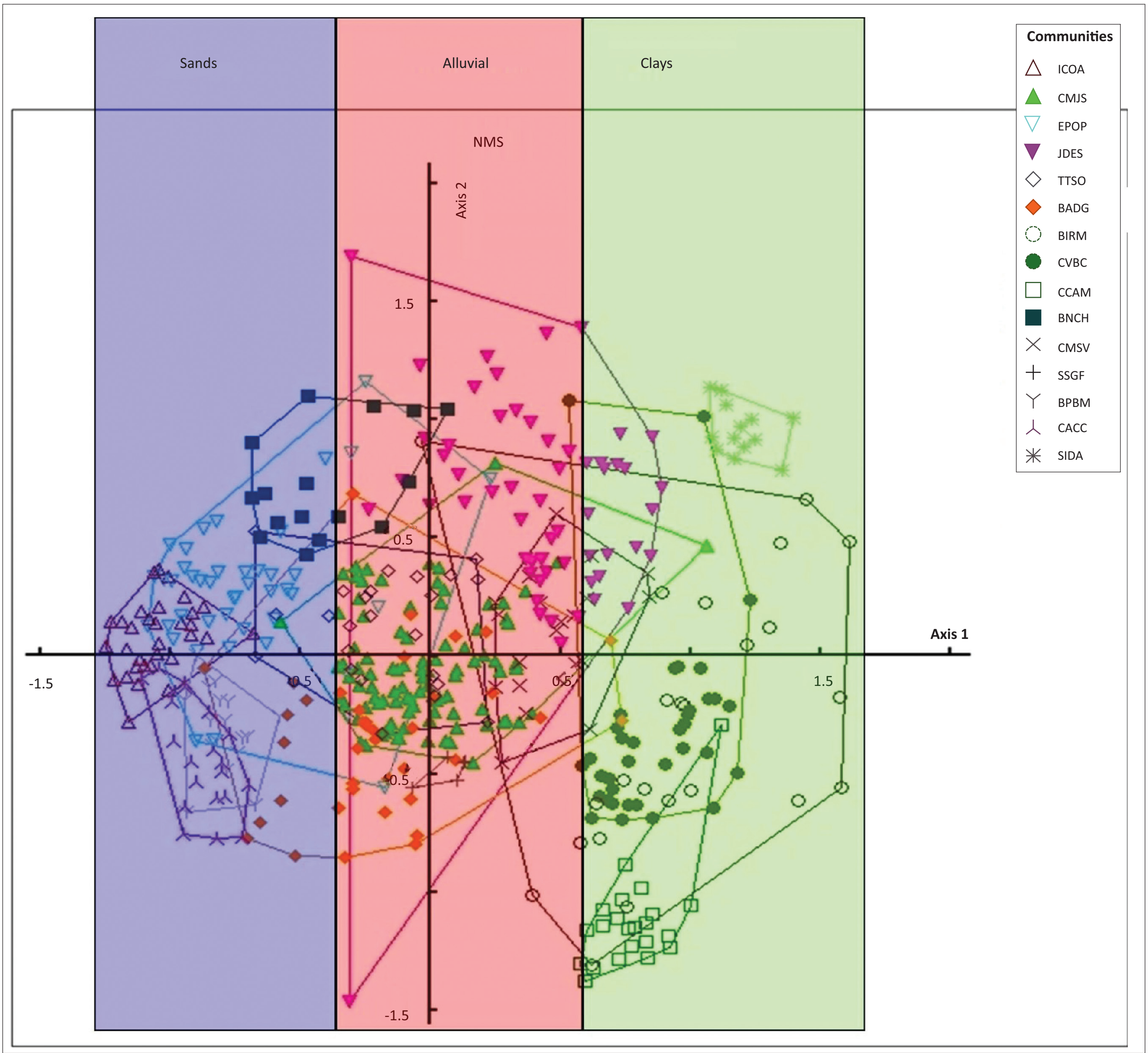
Discussion

Vegetation classification and mapping of the Savuti-Mababe-Linyanti ecosystem

The vegetation of the SMLE was clustered into 15 major vegetation communities characterised 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 1). 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 paleoriver channels among alluvial deposits that supports the mopane–sandveld woodland mosaic between the Okavango Delta and the Linyanti Swamps was formed by ancient wetlands similar to the current delta, with the river channels subsequently becoming infilled by Kalahari sands of aeolian origin (McCarthy, Gumbricht & Mccarthy 2005). Similarly, the deep sands supporting the Baikiaea forests are of aeolian origin (McCarthy et al. 2005). The vast 3000 km^2 MD originates from Paleolake Mababe (Teter 2007), which has a central sump of about 70 km × 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 soils of the highest clay content supporting the *Bothriochloa insculpta – Rhynchosia minima* and *Cenchrus ciliaris – Senegalia 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 the 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 contents 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 *C. angolensis*, *C. collinum*, *B. plurijuga*, *B. massaiensis*, *P. nelsii*, *O. pulchra, B. africana* and *T. 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 1), as observed elsewhere (Tedder 2012; Tedder et al. 2013;



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.*

FIGURE 3: Non-metric multidimensional scaling ordination of plant communities on 801 plots.

Van Voorthuizen 1976; Wolski & Murray-Hudson 2006). 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 paleoriver channels infilled with Kalahari sands (Figure 2). The mopane–sandveld mosiac (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 (Bennitt, Bonyongo & Harris 2014, 2015; Fynn et al. 2014; Sianga 2014; Taolo 2003), because of the abundance of digestible, leafy forage of high-quality grass species dominant in sandveld woodland (e.g. *D. eriantha*, *Panicum maximum* and *Schmidtia papophoroides*), as well as *D. milanjiana* and *Panicum maximum* in mopane woodland (Sianga et al. 2017b). Importantly, these high-quality grasses are most abundant far from permanent water (>15 km – 20 km) (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, Fynn & Bonyongo 2017a; Sianga et al. 2017b), as do roan and sable antelope (Havemann 2014; Hensman et al. 2014). In addition, the numerous ephemeral waterholes of the 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 3–4 days to drink and then return back to the safety of the woodlands far from water (Havemann 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*, *P. violacea*, *Combretum mossambicense*, *D. mespiliformis* and *S. nigrescens*, which are adapted to obtaining soil moisture through lateral ground-water discharge from higher water tables (Ellery, Ellery & Mccarthy 1993; Hamandawana 2011; Ringrose et al. 2007). The *Setaria sphacelata – Gomphocarpus fruticosus* community, a floodplain grassland type found along watercourses, had grass (*S. sphacelata*) and sedge (*C. longus*) or forbs (*G. 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 (*C. platysepala*, *M. balsamina*, *S. triphyllum* and *B. hispidula*). Variation in wetland community composition is driven by gradients of flood depth and duration, with *C. dactylon* often characterising the parts of the gradient with the lowest depth and duration of flooding, *Panicum repens* and *S. sphacelata* often characterising areas with intermediate depth and duration of flooding and tall sedges and grasses such as *Oryza longistaminata* and *Vossia cuspidata* characterising areas of the gradient with the largest depth and duration of flooding (Fynn et al. 2015; Murray-Hudson et al. 2011, 2014). 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; 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 recognised 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, Bonyongo & Harris 2013; Bennitt et al. 2014; Fynn 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 (Fynn et al. 2015; Hopcraft et al. 2010).

Communities on the high clay soils of the MD, especially the *Chloris virgata – Boerhavia coccinea* and *Cenchrus ciliaris – Senegalia mellifera* communities, are critical wet season habitats for the large zebra migration in the region, as well as for wildebeest, tsessebe and impala (Fynn et al. 2014; Joos-Vandewalle 2000; 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) (Fynn et al. 2014; Joos-Vandewalle 2000; 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 (Hopcraft et al. 2010; Owen-Smith 2004). 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 1), while the vertisols of the *Cenchrus ciliaris – Senegalia mellifera* communities deeper into the MD have the highest concentrations of potassium and calcium. This may explain why zebra are observed to switch their foraging bouts between *Chloris virgata – Boerhavia coccinea* community and the *Cenchrus ciliaris – Senegalia mellifera* community over the day (Sianga 2014), which may be a mechanism to maximise 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 *S. 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 *C. ciliaris* is informative as this species is often found in areas with elevated levels of P in soils (Blackmore, Mentis & Scholes 1990), which demonstrates why the MD is an important wet season range for herbivores. The *Bothriochloa insculpta – Rhynchosia minima* community is dominated by *B. 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 (*B. insculpta* and *C. 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 *S. incrassata*, *D. annulatum*, *P. coloratum*, *C. dactylon* and *D. 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 *S. incrassata* and *D. 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 large heterogeneity of plant communities driven by gradients in soil texture or fertility and wetness plays a key role in providing critical functional resource and habitat heterogeneity that allows (1) herbivores to adapt to seasonal variation in resources and (2) allows 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, whereas the vast woodland mosaic of mopane and sandveld on alluvial soils and Kalahari sands provides 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 (Bennitt et al. 2014; Naidoo 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. *B. albitrunca*), which provide an important reserve resource for browsers at this 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 ecosystem, 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, our results demonstrate that a key point of general significance for conservation science is that protected areas need to cover 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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Competing interests

The authors declare that they have no financial or personal relationships that may have inappropriately influenced them in writing this article.

Authors' contributions

All authors directly participated in the planning, execution and analysis of this study.

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Appendix 1

TABLE 1-A1: Multiresponse permutation procedure pairwise comparisons between identified classes for plant communities in the Savuti-Mababe-Linyanti ecosystem (northern Botswana).

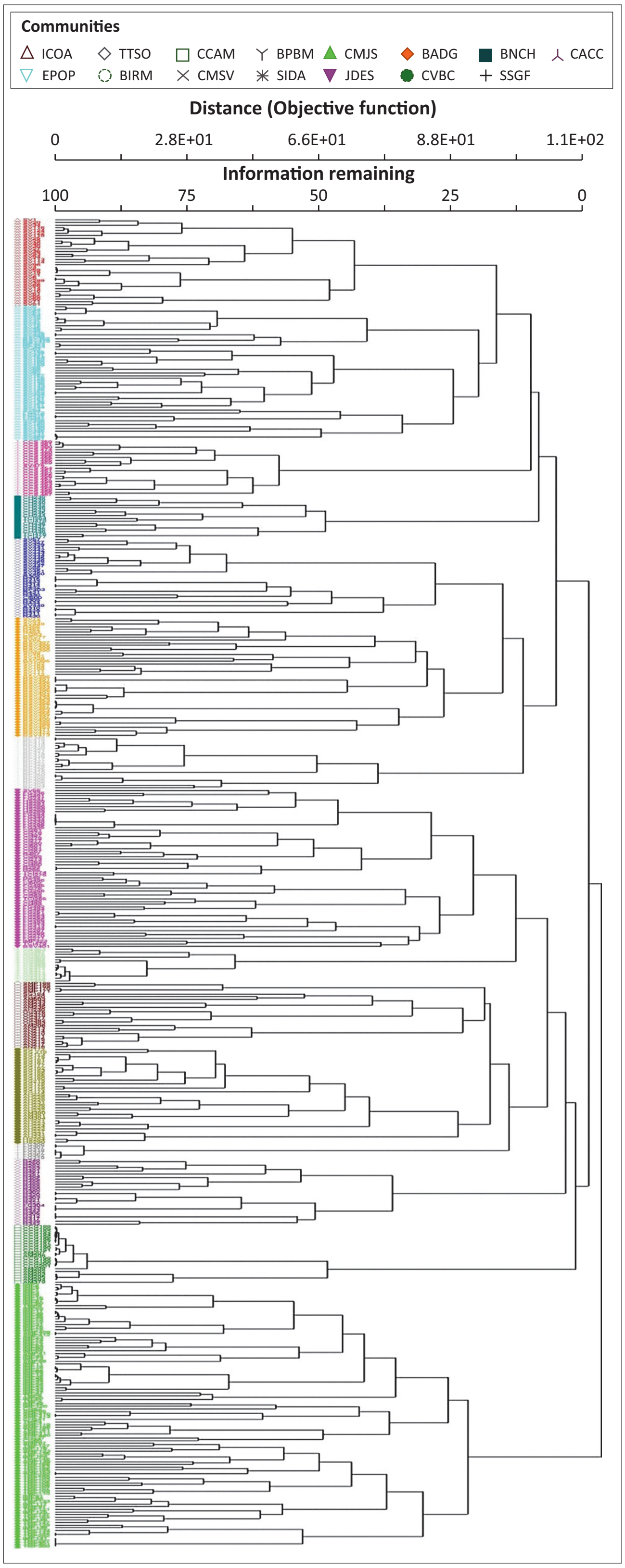
Classes	*T*	A	*p*
Ipomoea chloroneura – Oxygonum alatum vs. *Colophospermum mopane – Jasminum stenolobum*	-70.288	0.146	0.00000000
Ipomoea chloroneura – Oxygonum alatum vs. *Eragrostis pallens – Ochna pulchra*	-25.515	0.073	0.00000000
Ipomoea chloroneura – Oxygonum alatum vs. *Justicea divaricata – Eragrostis superba*	-52.784	0.155	0.00000000
Ipomoea chloroneura – Oxygonum alatum vs. *Tribulus terrestris – Senna obtusifolia*	-34.107	0.188	0.00000000
Ipomoea chloroneura – Oxygonum alatum vs. *Boscia albitrunca – Dactyloctenium giganteum*	-35.861	0.128	0.00000000
Ipomoea chloroneura – Oxygonum alatum vs. *Bothriochloa insculpta – Rhynchosia minima*	-32.637	0.176	0.00000000
Ipomoea chloroneura – Oxygonum alatum vs. *Chloris virgata – Boerhavia coccinea*	-42.954	0.243	0.00000000
Ipomoea chloroneura – Oxygonum alatum vs. *Cenchrus ciliaris – Senegalia mellifera*	-35.628	0.350	0.00000000
Ipomoea chloroneura – Oxygonum alatum vs. *Brachiaria nigropedata – Combretum hereroense*	-27.609	0.186	0.00000000
Ipomoea chloroneura – Oxygonum alatum vs. *Croton megalobotrys – Setaria verticillata*	-36.111	0.240	0.00000000
Ipomoea chloroneura – Oxygonum alatum vs. *Setaria sphacelata – Gomphocarpus fruticosus*	-22.085	0.227	0.00000000
Ipomoea chloroneura – Oxygonum alatum vs. *Baikiaea plurijuga – Baphia massaiensis*	-30.746	0.216	0.00000000
Ipomoea chloroneura – Oxygonum alatum vs. *Commiphora angolensis – Combretum collinum*	-29.920	0.192	0.00000000
Ipomoea chloroneura – Oxygonum alatum vs. *Setaria incrassata – Dichanthium annulatum*	-28.894	0.282	0.00000000
Colophospermum mopane – Jasminum stenolobum vs. *Eragrostis pallens – Ochna pulchra*	-68.981	0.110	0.00000000
Colophospermum mopane – Jasminum stenolobum vs. *Justicea divaricata – Eragrostis superba*	-72.744	0.103	0.00000000
Colophospermum mopane – Jasminum stenolobum vs. *Tribulus terrestris – Senna obtusifolia*	-60.097	0.117	0.00000000
Colophospermum mopane – Jasminum stenolobum vs. *Boscia albitrunca – Dactyloctenium giganteum*	-60.269	0.096	0.00000000
Colophospermum mopane – Jasminum stenolobum vs. *Bothriochloa insculpta – Rhynchosia minima*	-44.257	0.078	0.00000000
Colophospermum mopane – Jasminum stenolobum vs. *Chloris virgata – Boerhavia coccinea*	-69.154	0.136	0.00000000
Colophospermum mopane – Jasminum stenolobum vs. *Cenchrus ciliaris – Senegalia mellifera*	-67.546	0.171	0.00000000
Colophospermum mopane – Jasminum stenolobum vs. *Brachiaria nigropedata – Combretum hereroense*	-40.435	0.081	0.00000000
Colophospermum mopane – Jasminum stenolobum vs. *Croton megalobotrys – Setaria verticillata*	-57.794	0.115	0.00000000
Colophospermum mopane – Jasminum stenolobum vs. *Setaria sphacelata – Gomphocarpus fruticosus*	-29.134	0.068	0.00000000
Colophospermum mopane – Jasminum stenolobum vs. *Baikiaea plurijuga – Baphia massaiensis*	-55.264	0.119	0.00000000
Colophospermum mopane – Jasminum stenolobum vs. *Commiphora angolensis – Combretum collinum*	-55.555	0.115	0.00000000
Colophospermum mopane – Jasminum stenolobum vs. *Setaria incrassata – Dichanthium annulatum*	-46.653	0.106	0.00000000
Eragrostis pallens – Ochna pulchra vs. *Justicea divaricata – Eragrostis superba*	-49.379	0.098	0.00000000
Eragrostis pallens – Ochna pulchra vs. *Tribulus terrestris –Senna obtusifolia*	-29.657	0.096	0.00000000
Eragrostis pallens – Ochna pulchra vs. *Boscia albitrunca – Dactyloctenium giganteum*	-31.090	0.071	0.00000000
Eragrostis pallens – Ochna pulchra vs. *Bothriochloa insculpta – Rhynchosia minima*	-30.758	0.096	0.00000000
Eragrostis pallens – Ochna pulchra vs. *Chloris virgata – Boerhavia coccinea*	-47.404	0.161	0.00000000
Eragrostis pallens – Ochna pulchra vs. *Cenchrus ciliaris – Senegalia mellifera*	-43.302	0.226	0.00000000
Eragrostis pallens – Ochna pulchra vs. *Brachiaria nigropedata – Combretum hereroense*	-24.656	0.090	0.00000000
Eragrostis pallens – Ochna pulchra vs. *Croton megalobotrys – Setaria verticillata*	-39.310	0.145	0.00000000
Eragrostis pallens – Ochna pulchra vs. *Setaria sphacelata – Gomphocarpus fruticosus*	-20.552	0.105	0.00000000
Eragrostis pallens – Ochna pulchra vs. *Baikiaea plurijuga – Baphia massaiensis*	-32.165	0.127	0.00000000
Eragrostis pallens – Ochna pulchra vs. *Commiphora angolensis –Combretum collinum*	-30.257	0.108	0.00000000
Eragrostis pallens – Ochna pulchra vs. *Setaria incrassata – Dichanthium annulatum*	-32.926	0.161	0.00000000
Justicea divaricata – Eragrostis superba vs. *Tribulus terrestris – Senna obtusifolia*	-36.206	0.091	0.00000000
Justicea divaricata – Eragrostis superba vs. *Boscia albitrunca – Dactyloctenium giganteum*	-38.259	0.074	0.00000000
Justicea divaricata – Eragrostis superba vs. *Bothriochloa insculpta – Rhynchosia minima*	-26.907	0.061	0.00000000
Justicea divaricata – Eragrostis superba vs. *Chloris virgata – Boerhavia coccinea*	-45.638	0.115	0.00000000
Justicea divaricata – Eragrostis superba vs. *Cenchrus ciliaris – Senegalia mellifera*	-47.411	0.186	0.00000000
Justicea divaricata – Eragrostis superba vs. *Brachiaria nigropedata – Combretum hereroense*	-26.545	0.077	0.00000000
Justicea divaricata – Eragrostis superba vs. *Croton megalobotrys – Setaria verticillata*	-34.705	0.090	0.00000000
Justicea divaricata – Eragrostis superba vs. *Setaria sphacelata – Gomphocarpus fruticosus*	-22.260	0.080	0.00000000
Justicea divaricata – Eragrostis superba vs. *Baikiaeaplurijuga – Baphia massaiensis*	-41.162	0.133	0.00000000
Justicea divaricata – Eragrostis superba vs. *Commiphora angolensis – Combretum collinum*	-42.738	0.134	0.00000000
Justicea divaricata – Eragrostis superba vs. *Setaria incrassata – Dichanthium annulatum*	-29.816	0.093	0.00000000
Tribulus terrestris – Senna obtusifolia vs. *Boscia albitrunca – Dactyloctenium giganteum*	-22.155	0.073	0.00000000
Tribulus terrestris – Senna obtusifolia vs. *Bothriochloa insculpta – Rhynchosia minima*	-25.073	0.129	0.00000000
Tribulus terrestris – Senna obtusifolia vs. *Chloris virgata – Boerhavia coccinea*	-36.188	0.182	0.00000000
Tribulus terrestris – Senna obtusifolia vs. *Cenchrus ciliaris – Senegalia mellifera*	-31.904	0.309	0.00000000
Tribulus terrestris – Senna obtusifolia vs. *Brachiaria nigropedata – Combretum hereroense*	-23.736	0.173	0.00000000
Tribulus terrestris – Senna obtusifolia vs. *Croton megalobotrys – Setaria verticillata*	-25.049	0.137	0.00000000
Tribulus terrestris – Senna obtusifolia vs. *Setaria sphacelata – Gomphocarpus fruticosus*	-16.579	0.185	0.00000000
Tribulus terrestris – Senna obtusifolia vs. *Baikiaea plurijuga – Baphia massaiensis*	-23.740	0.159	0.00000000

TABLE 1-A1 continues on the next page →

TABLE 1-A1 (Continues...): Multiresponse permutation procedure pairwise comparisons between identified classes for plant communities in the Savuti-Mababe-Linyanti ecosystem (northern Botswana).

Classes	*T*	A	*p*
Tribulus terrestris – Senna obtusifolia vs. *Commiphora angolensis – Combretum collinum*	-28.344	0.204	0.00000000
Tribulus terrestris – Senna obtusifolia vs. *Setaria incrassata – Dichanthium annulatum*	-24.258	0.240	0.00000000
Boscia albitrunca – Dactyloctenium giganteum vs. *Bothriochloa insculpta – Rhynchosia minima*	-24.395	0.079	0.00000000
Boscia albitrunca – Dactyloctenium giganteum vs. *Chloris virgata – Boerhavia coccinea*	-39.658	0.130	0.00000000
Boscia albitrunca – Dactyloctenium giganteum vs. *Cenchrus ciliaris – Senegalia mellifera*	-38.826	0.216	0.00000000
Boscia albitrunca – Dactyloctenium giganteum vs. *Brachiaria nigropedata – Combretum hereroense*	-25.765	0.108	0.00000000
Boscia albitrunca – Dactyloctenium giganteum vs. *Croton megalobotrys – Setaria verticillata*	-30.694	0.115	0.00000000
Boscia albitrunca – Dactyloctenium giganteum vs. *Setaria sphacelata – Gomphocarpus fruticosus*	-17.100	0.099	0.00000000
Boscia albitrunca – Dactyloctenium giganteum vs. *Baikiaea plurijuga – Baphia massaiensis*	-30.725	0.135	0.00000000
Boscia albitrunca – Dactyloctenium giganteum vs. *Commiphora angolensis – Combretum collinum*	-28.082	0.115	0.00000000
Boscia albitrunca – Dactyloctenium giganteum vs. *Setaria incrassata – Dichanthium annulatum*	-29.545	0.160	0.00000000
Bothriochloa insculpta – Rhynchosia minima vs. *Chloris virgata – Boerhavia coccinea*	-23.551	0.100	0.00000000
Bothriochloa insculpta – Rhynchosia minima vs. *Cenchrus ciliaris – Senegalia mellifera*	-24.442	0.200	0.00000000
Bothriochloa insculpta – Rhynchosia minima vs. *Brachiaria nigropedata – Combretum hereroense*	-19.987	0.140	0.00000000
Bothriochloa insculpta – Rhynchosia minima vs. *Croton megalobotrys – Setaria verticillata*	-24.052	0.133	0.00000000
Bothriochloa insculpta – Rhynchosia minima vs. *Setaria sphacelata – Gomphocarpus fruticosus*	-13.788	0.158	0.00000000
Bothriochloa insculpta – Rhynchosia minima vs. *Baikiaea plurijuga – Baphia massaiensis*	-23.962	0.179	0.00000000
Bothriochloa insculpta – Rhynchosia minima vs. *Commiphora angolensis – Combretum collinum*	-25.536	0.178	0.00000000
Bothriochloa insculpta – Rhynchosia minima vs. *Setaria incrassata – Dichanthium annulatum*	-19.200	0.178	0.00000000
Chloris virgata – Boerhavia coccinea vs. *Cenchrus ciliaris – Senegalia mellifera*	-35.426	0.287	0.00000000
Chloris virgata – Boerhavia coccinea vs. *Brachiaria nigropedata – Combretum hereroense*	-29.563	0.191	0.00000000
Chloris virgata – Boerhavia coccinea vs. *Croton megalobotrys – Setaria verticillata*	-34.587	0.187	0.00000000
Chloris virgata – Boerhavia coccinea vs. *Setaria sphacelata – Gomphocarpus fruticosus*	-20.598	0.171	0.00000000
Chloris virgata – Boerhavia coccinea vs. *Baikiaea plurijuga – Baphia massaiensis*	-33.380	0.234	0.00000000
Chloris virgata – Boerhavia coccinea vs. *Commiphora angolensis – Combretum collinum*	-34.826	0.235	0.00000000
Chloris virgata – Boerhavia coccinea vs. *Setaria incrassata – Dichanthium annulatum*	-28.163	0.228	0.00000000
Cenchrus ciliaris – Senegalia mellifera vs. *Brachiaria nigropedata – Combretum hereroense*	-24.087	0.347	0.00000000
Cenchrus ciliaris – Senegalia mellifera vs. *Croton megalobotrys – Setaria verticillata*	-29.356	0.320	0.00000000
Cenchrus ciliaris – Senegalia mellifera vs. *Setaria sphacelata – Gomphocarpus fruticosus*	-16.892	0.425	0.00000002
Cenchrus ciliaris – Senegalia mellifera vs. *Baikiaea plurijuga – Baphia massaiensis*	-26.684	0.386	0.00000000
Cenchrus ciliaris – Senegalia mellifera vs. *Commiphora angolensis – Combretum collinum*	-27.856	0.382	0.00000000
Cenchrus ciliaris – Senegalia mellifera vs. *Setaria incrassata – Dichanthium annulatum*	-22.269	0.433	0.00000000
Brachiaria nigropedata – Combretum hereroense vs. *Croton megalobotrys – Setaria verticillata*	-23.983	0.202	0.00000000
Brachiaria nigropedata – Combretum hereroense vs. *Setaria sphacelata – Gomphocarpus fruticosus*	-13.628	0.298	0.00000043
Brachiaria nigropedata – Combretum hereroense vs. *Baikiaea plurijuga – Baphia massaiensis*	-21.706	0.246	0.00000000
Brachiaria nigropedata – Combretum hereroense vs.*Commiphora angolensis – Combretum collinum*	-22.341	0.214	0.00000000
Brachiaria nigropedata – Combretum hereroense vs. *Setaria incrassata – Dichanthium annulatum*	-18.366	0.304	0.00000004
Croton megalobotrys – Setaria verticillata vs. *Setaria sphacelata – Gomphocarpus fruticosus*	-17.090	0.230	0.00000000
Croton megalobotrys – Setaria verticillata vs. *Baikiaea plurijuga – Baphia massaiensis*	-26.743	0.238	0.00000000
Croton megalobotrys – Setaria verticillata vs. *Commiphora angolensis – Combretum collinum*	-28.762	0.252	0.00000000
Croton megalobotrys – Setaria verticillata vs. *Setaria incrassata – Dichanthium annulatum*	-22.958	0.266	0.00000000
Setaria sphacelata – Gomphocarpus fruticosus vs. *Baikiaea plurijuga – Baphia massaiensis*	-15.172	0.313	0.00000003
Setaria sphacelata – Gomphocarpus fruticosus vs. *Commiphora angolensis – Combretum collinum*	-16.610	0.300	0.00000001
Setaria sphacelata – Gomphocarpus fruticosus vs. *Setaria incrassata – Dichanthium annulatum*	-11.836	0.457	0.00000431
Baikiaea plurijuga – Baphia massaiensis vs. *Commiphora angolensis – Combretum collinum*	-24.821	0.258	0.00000000
Baikiaea plurijuga – Baphia massaiensis vs. *Setaria incrassata – Dichanthium annulatum*	-20.584	0.339	0.00000000
Commiphora angolensis – Combretum collinum vs. *Setaria incrassata – Dichanthium annulatum*	-21.901	0.334	0.00000000

t, test statistic; *A*, chance-corrected within group agreement; *p*, probability of a smaller or equal δ (not corrected for multiple comparisons).



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.*

FIGURE 1-A1: Cluster analysis showing the 15 plant communities identified in the Savuti-Mababe-Linyanti ecosystem, northern Botswana.