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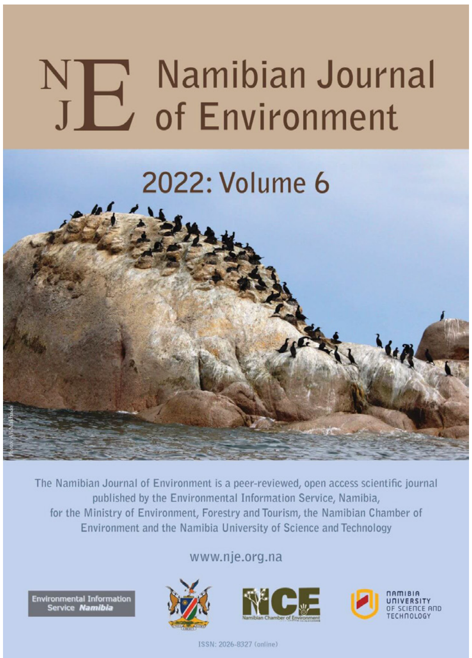

SECTION A: RESEARCH ARTICLES

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Spatio-temporal functional diversity of large herbivores in Mudumu National Park, northeastern Namibia

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ABSTRACT

Functional diversity is a component of biodiversity that includes the range of roles that organisms perform in communities and can explain and predict the impact of organisms on ecosystems. Mudumu National Park is an important ecosystem that acts as a wildlife corridor for migratory fauna moving between Botswana, Namibia, Angola and Zambia. Thus, a thorough understanding of the functional diversity of large herbivores would assist with the management of the park. The present study examined large herbivore species contribution to total large herbivore biomass; dominant species' functional similarities; and whether or not functional diversity is affected by increasing distance from the Kwando River. A total of twenty-two roads were selected that provided good coverage of the park and were surveyed using the line transect distance sampling method. All large herbivores seen on either side of the transects were identified to species level and recorded. The hierarchical cluster analysis in SPSS was used to classify the herbivores into functional groups. Only a small number of species were found to be dominant in both numbers and biomass. Furthermore, dominant species were found to be functionally distinct, and functional dominance changed with respect to season and distance from the river.

Keywords: dominant species; functional diversity; functional similarity; functional traits; large herbivores; Mudumu National Park; Namibia

INTRODUCTION

Large herbivores are a crucial component of biodiversity in the world's ecosystems. They provide important ecological services such as the regulation of vegetation dynamics, seed dispersal and pollination, as well as nutrient cycling among others (Duffus & Dearden 1990, Jefferies *et al.* 1994, Wilson & Reeder 2005, Lapeyre & Laurans 2017). Large herbivores are at the centre of wildlife tourism, making up three of Africa's famed Big Five – tourists' most sought-after animals on the continent (Owen-Smith 1982). Their products, skins and horns, have cultural importance in rural African societies where they are used as utensils and decorations, particularly on ceremonial occasions.

Large herbivores are among the most widespread animals on the continent where they actively affect the structure and processes of the African savanna (Owen-Smith 1982). According to Owen-Smith (1982) the African continent is home to about 44 large herbivore species. The term large herbivore here refers exclusively to ungulates (artiodactyls and perissodactyls), as well as elephants from the order Proboscidea. Other large herbivores like the ostrich (*Struthio camelus*) and primates were not considered.

Due to the undeveloped nature of the field of functional ecology, there still is no consensus on the one true definition of functional diversity. However, a widely accepted definition is "the value and the range of those species and organismal traits that influence ecosystem functioning" (Tilman 2001). Unlike classical measures of biodiversity such as species richness which assume that all species and individuals are equal despite size differences, functional diversity is a trait-based measure of diversity (Petchey *et al.* 2004, Petchey & Gaston 2006, Mouchet *et al.* 2010, Laureto *et al.* 2015, Zhu *et al.* 2017, Ahmed *et al.* 2019). A functional trait is any measurable feature of an individual that potentially impacts fitness of the organism and can be physical, biochemical, behavioural, and temporal or phenological. Traits can determine how organisms utilise resources and how they react to environmental pressure, and consequently determine the varying contributions of species to ecosystem function and processes (Mokany *et al.* 2008, Lavorel *et al.* 2011). In its true essence, functional diversity represents trait diversity but is usually taken to represent the diversity of niches or functions in an ecosystem (Petchey *et al.* 2004, Petchey & Gaston 2006, McGill *et al.* 2006, Villéger *et al.* 2008). Moreover, functional diversity has been successfully used to understand how classical measures of species richness and diversity relate to ecosystem function

(Petchey *et al.* 2004, Cadotte *et al.* 2009, Flynn *et al.* 2011) and how organisms respond to environmental disturbance (Norberg *et al.* 2001, Suding *et al.* 2008). Although there is a plethora of research on functional diversity of ecosystems around the world, there is a paucity of information on trait ecology in all parts of Namibia. A number of studies have been carried out on species diversity and abundance (e.g. Griffin 1998, Robertson *et al.* 1998, Naidoo *et al.* 2011), however studies on the functional diversity of wildlife have not yet been carried out.

Namibia has a vast diversity of mammals, including large herbivores (Griffin 1998), and the present study area sits at the heart of one of the world's most important biodiversity hotspots: the Kavango-Zambezi Transfrontier Conservation Area (KAZA TFCA). Mudumu National Park (hereafter the park) is surrounded by a mosaic of communal areas that are partitioned into different land uses, such as residential, agricultural land, community forestry and community wildlife managed areas under the Community-Based Natural Resources Management (CBNRM) model. The park serves as a source of wildlife resources to the surrounding community conservation areas. Furthermore, the park also forms part of the Kwando corridor, a wildlife dispersal area that links northern Botswana through Namibia to western Zambia and Eastern Angola. However, it is also a source of human-wildlife conflict to adjacent communities. Thus, understanding the dynamics of biodiversity in the park can aid in the management of the park, as well as that of conservancies and forestry areas at a landscape level.

We tested the hypotheses that:

1) The abundance and biomass of the large herbivore community in Mudumu National Park are dominated by a few species,
2) Dominant species are functionally distinct because they occupy different ecological niches (hence perform different functions), and
3) A decline in dominant large herbivore species, for example away from the Kwando River in the dry season, resulted in an increase in abundance of functionally similar minor species.

METHODS

Study Area

Mudumu National Park is found in the south-central part of Namibia's Zambezi Region (Figure 1). The park was established in 1990 and covers an area of 737 square kilometres. Its borders, apart from its western border on the Kwando River, are entirely

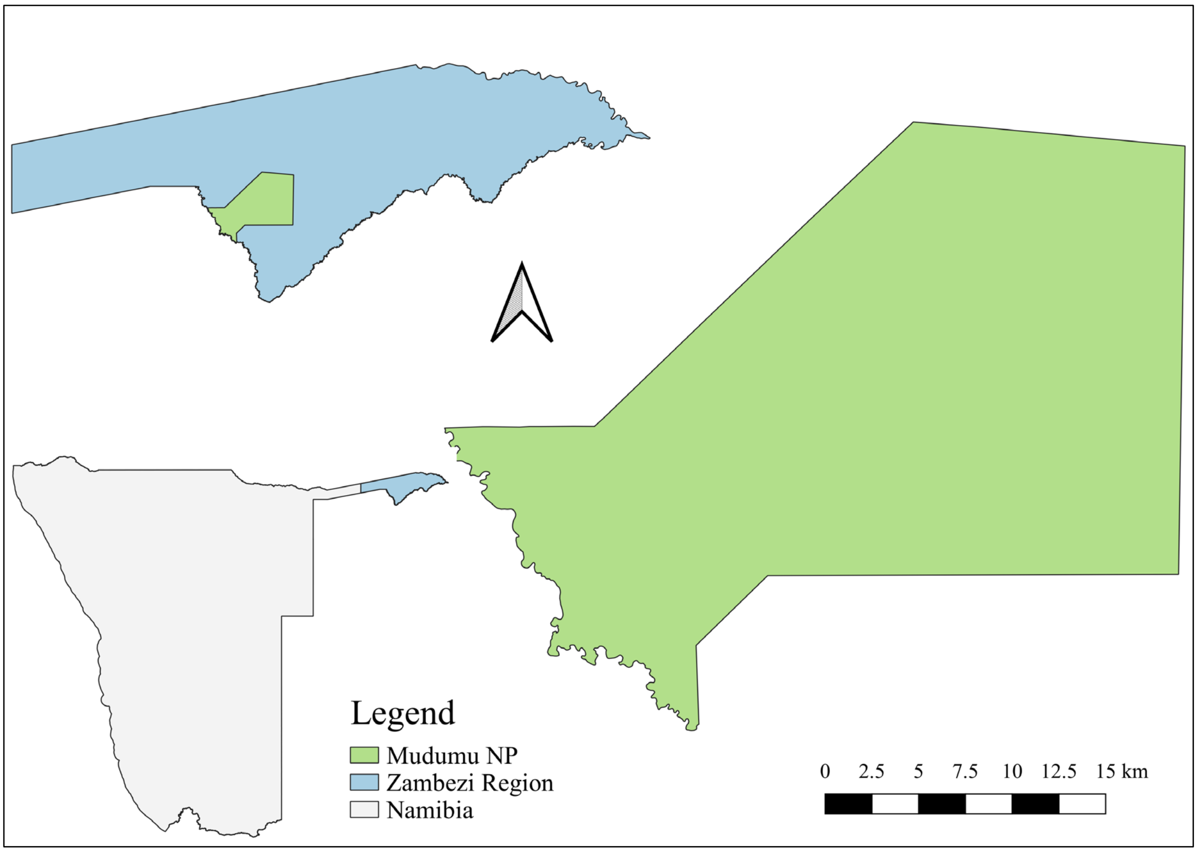

Figure 1: *Mudumu National Park and its location in the Zambezi Region of Namibia.*

surrounded by various communal area conservancies and community forests. It is located in the centre of the KAZA TFCA and provides a corridor for wildlife movement from Botswana through Namibia and into Angola and Zambia of many important large herbivores such as elephant, buffalo, roan and sable antelope. The area is easily accessible by road and is about 1 173 km from the capital city of Windhoek, and 461 km and 116 km from the two regional towns of Rundu and Katima Mulilo respectively.

Sampling design

The line transect method was used to effectively survey the species diversity and abundance of large herbivores. All routes were pre-established as part of an annual long-term game count system used by park staff to monitor wildlife. Transect routes were of varying lengths and only about half of each transect was surveyed. The entire study area was stratified into two sections, (i) near to the river - up to about 9 km, and (ii) away from the river – from about 13 km on a line created by the C49 road passing through the park and connecting the villages of Kongola and Sangwali.

Field Survey

The study was conducted in the dry season (June 2019) and in the wet season (December 2019), and each transect route was only visited once per season. A total of 22 transect routes of varying lengths were surveyed. The routes provided good coverage of the park. Six routes are situated near the river (west of the C49 road) and 16 are found away from the river (east of the C49 road).

Large herbivores were counted from a vehicle at a constant speed of ~15 km/h during the morning and late afternoon when they are most active, and within a transect width of ~100 meters on either side of the track. A hand-held GPS was used to record the coordinates of each sighting.

Species were assigned to functional groups using traits that are known to influence ecosystem functions and processes such as: body mass, feeding guild, feeding habitat, activity time, social behaviour, metabolic rate, fecundity, digestive physiology, home range size, water requirements, gestation period, foraging behaviour, gape width, lifespan, and breeding among others. Information on these attributes was acquired from southern African wildlife literature (e.g. Skinner & Chimimba 2005, Bothma & du Toit 2016). Following Walker *et al.* (1999) and McCarthy *et al.* (1998) the attributes were standardised on a scale of 1 to 5 for comparisons.

Data Analysis

On each transect route, species abundances were ranked and their relative proportion to total abundance was determined. The number of animals of each species was used to calculate each species' biomass and their respective contribution to total large herbivore biomass. For a well sampled community, the proportion of individuals found in a species (P_i) is estimated as:

$$P_i = \frac{n_i}{N}$$

where n_i is the number/biomass of individuals in species i and N is the total number/biomass of individuals in the community. P_i ranges from 0 to 1.

Species with a collective relative abundance ≥ 80% on each transect were considered to be dominant. Ecological distances for all species on each transect were determined and summed up for each distance category. Ecological distance here refers to the chasm between two species in attribute space, and is used as a measure of functional diversity and functional redundancy (Walker *et al*. 1999).

A Fisher's exact test for homogeneity (Fisher 1935) was performed to test frequencies by spatio-temporal categories between dominant species and all species in the park. Correspondingly, another test was performed to test functional similarities by spatio-temporal categories of dominant species between population numbers and biomass.

The hierarchical classification in SPSS was performed in order to classify species into functional groups. Subsequently, a k-classification was performed on the clusters obtained from the hierarchical classification, as well as the Euclidean Distance (ED) to estimate ecological differences among species. The simplified version of ED has the formula:

$$ED_{jk} = \sum (A_{ij} - A_{ik})^2$$

where ED_{jk} is the ecological distance between species j and k, and A_{ij} and A_{ik} are values of species j and k for trait i.

Following (Walker et al., 1999), the expression:

$$\frac{dry\ season\ abundance\ near\ the\ river}{wet\ season\ abundance\ far\ from\ the\ river}$$

was used to examine differences in abundances for each functional group between season and distance from the Kwando River, in order to predict the spatio-temporal increase or decrease in functional abundance. Values < -1 or > 1 denote a significant increase or decrease in abundance, respectively.

RESULTS

Proportional Contribution

Overall, 17 large herbivore species were recorded in the park (see Table 1 for the list and scientific names). In general, it was found that large mammal herbivores were dominated by only a few species (Figure 2). In terms of numbers, the dominant species were buffalo, impala, zebra, elephant, blue wildebeest and roan antelope with a collective population contribution of 0.84. The other 11 species shared the remaining 0.16 with duiker and bushbuck having the lowest numbers. In terms of biomass, the dominant species were elephant, buffalo, zebra and blue wildebeest with a collective biomass contribution of 0.86. The other 13 species shared the remaining 0.14 with duiker and bushbuck having the lowest biomass contribution.

In the dry season, 16 species were recorded, with 16 found near the river (Figure 3) and four found away from the river (Figure 4). In terms of numbers near the river (Figure 3a), the dominant species were impala, elephant, kudu, buffalo, zebra and blue wildebeest with a collective population contribution

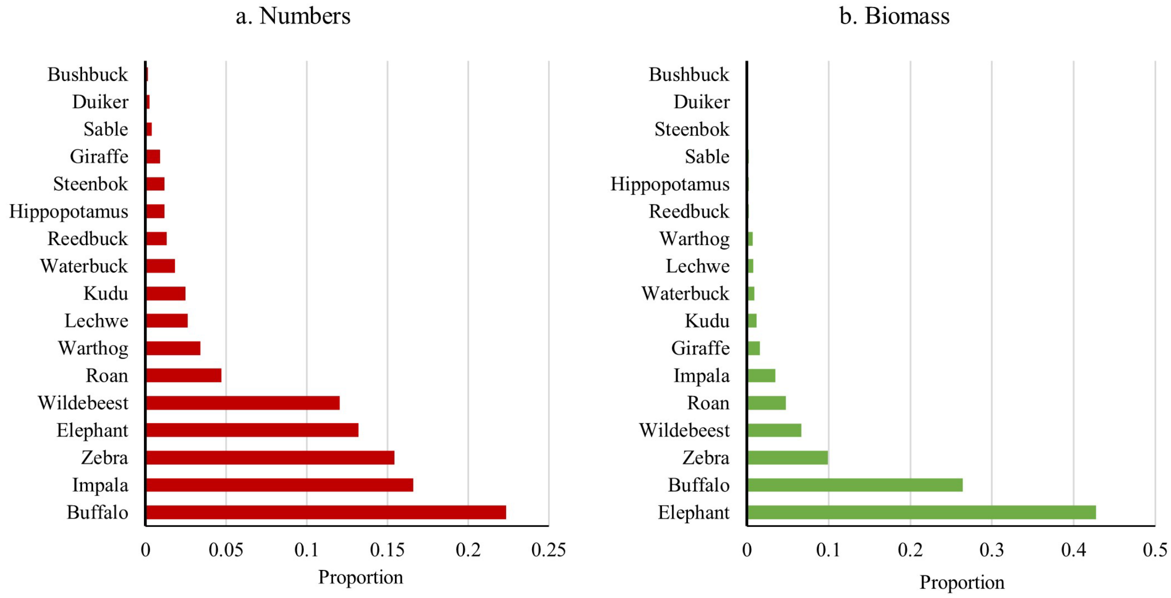

Figure 2: *Proportion of each large mammal herbivore species to total a) numbers and b) biomass of large mammal herbivores in Mudumu National Park.*

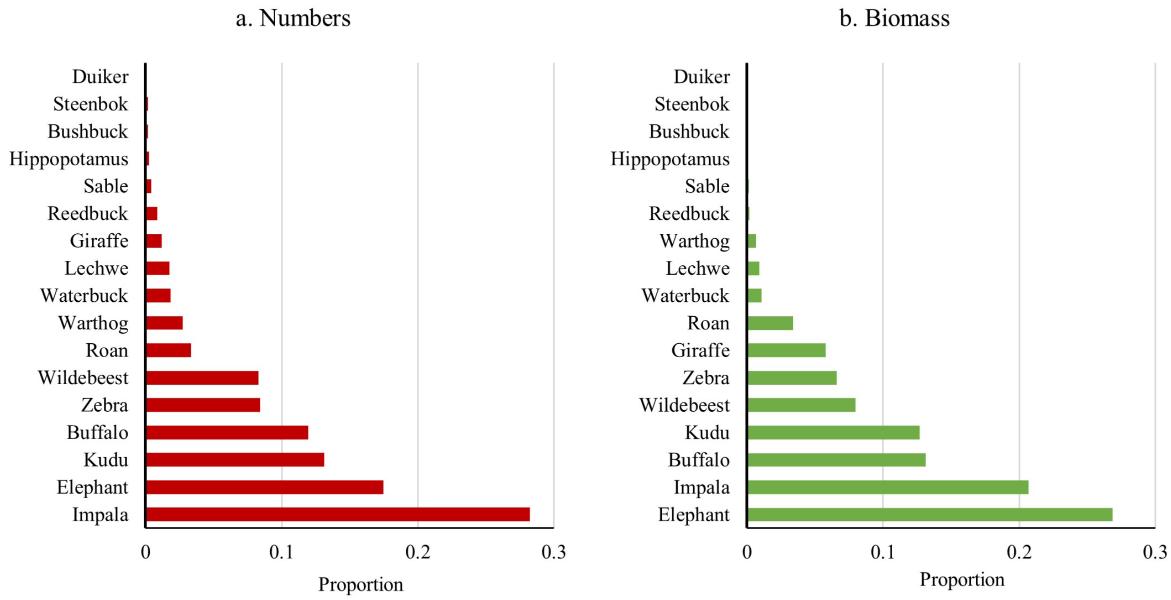

Figure 3: *Proportion of each large mammal herbivore species to total a) numbers and b) biomass of large mammal herbivores in Mudumu National Park in the dry season, near to the river.*

of 0.86. In terms of biomass near the river (Figure 3b), the dominant species were elephant, impala, buffalo, kudu and blue wildebeest with a collective biomass contribution of 0.82. Away from the river, the most dominant species in both numbers and biomass were steenbok and zebra with a collective contribution of 0.84 in terms of numbers and 0.94 in terms of biomass.

In the wet season, 13 species were recorded, with only one species, impala, found near the river (Figure 5) and 13 species away from the river (Figure 6). Away from the river, the dominant species in terms of numbers were kudu, buffalo, roan antelope, steenbok, zebra and blue wildebeest with a collective population contribution of 0.84 (Figure 6a). In terms of biomass, the most dominant species were kudu, buffalo, roan antelope, giraffe and blue wildebeest with a collective biomass contribution of 0.82 (Figure 6b).

There was no significant difference between the whole park and the spatio-temporal scales within the park for both the abundance (number) and biomass (Fisher Exact Test, $p > 0.05$ for all tests). However, the composition of dominant species at different

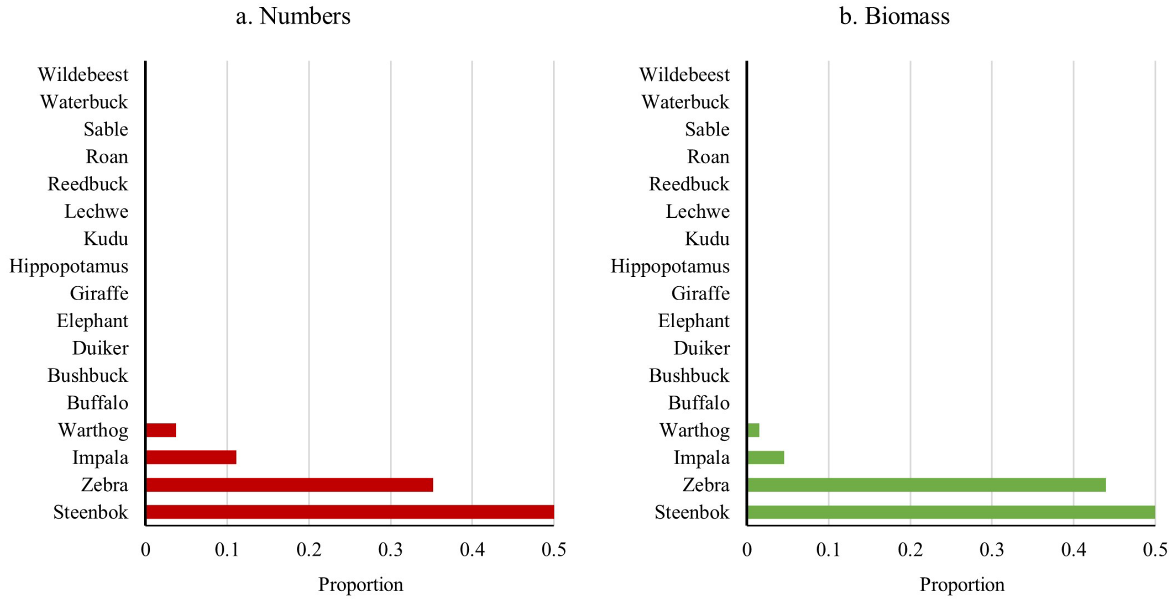

Figure 4: *Proportion of each large mammal herbivore species to total a) numbers and b) biomass of large mammal herbivores in Mudumu National Park in the dry season, away from the river.*

Figure 5: *Proportion of each large mammal herbivore species to total a) numbers and b) biomass of large mammal herbivores in Mudumu National Park in the wet season, near to the river.*

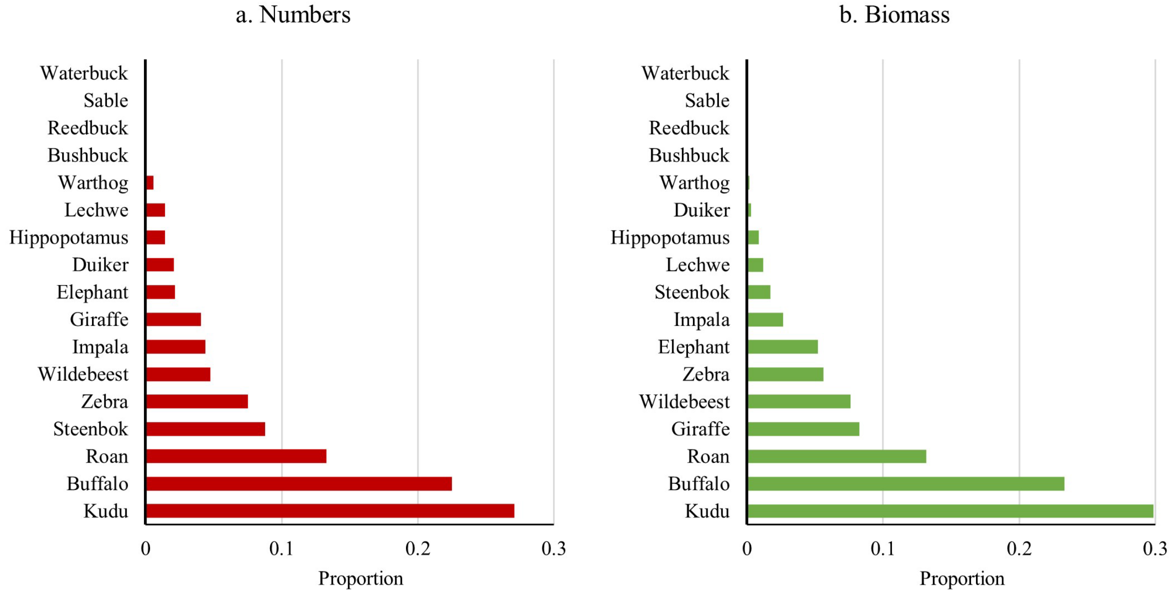

Figure 6: *Proportion of each large mammal herbivore species to total a) numbers and b) biomass of large mammal herbivores in Mudumu National Park in the wet season, away from the river.*

spatio-temporal categories differs from the overall dominant species of the park. For dry season and near to the river, species composition of dominant species was similar to those of the entire park for both abundance and biomass (Morisita similarity index (Cm) = 0.85 for abundance and 0.80 for biomass). For dry season and away from the river, species composition of dominant species was different to those of the entire park for both abundance and biomass (Cm = 0.30 for abundance and 0.13 for biomass). For wet season and away from the river, species composition of dominant species was approximately 50% of those of the entire park for both abundance and biomass (Cm = 0.62 for abundance and 0.47 for biomass).

Functional Dissimilarity

To determine the functional dissimilarity of the dominant species in the park, pairwise comparisons were performed. Out of the 15 pairwise comparisons produced by matching the six dominant species in population numbers, it was found that 27% (4) of the pairs were similar, 33% (5) were intermediate, and 40% (6) were dissimilar (Figure 7). In terms of biomass contribution, the four dominant species compared generated six pairwise comparisons out of which 33%, (2) were similar; none were intermediate; and 67%, (4) were dissimilar (Figure 7).

In the dry season near the river, in terms of numbers, the six dominant species generated 15 pairwise comparisons, out of which 27% were similar, 33% were intermediate and 40% were dissimilar (Figure 8). In terms of biomass, the five dominant species generated 10 pairwise comparisons, out of which 30% were similar, 40% were intermediate and 30% were dissimilar. Far from the river, the dominant species in both numbers and biomass contribution were steenbok and zebra only. The two dominant species allowed only one pairwise comparison, resulting in only a single intermediate relationship.

In the wet season near the river, only one species was recorded, allowing no pairwise comparisons for numbers and biomass. Away from the river, the six dominant species in terms of numbers provided 15 pairwise comparisons, of which 40% were similar, 33% were intermediate and 27% were dissimilar (Figure 8). In terms of biomass, the five dominant species provided 10 pairwise comparisons, of which all were similar.

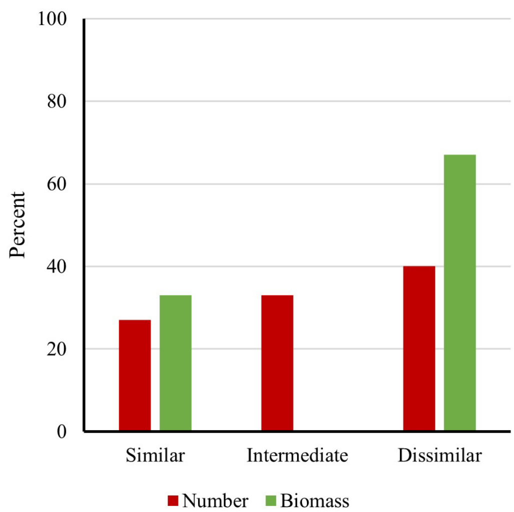

Figure 7: *Functional dissimilarity among dominant large herbivore species in Mudumu National Park.*

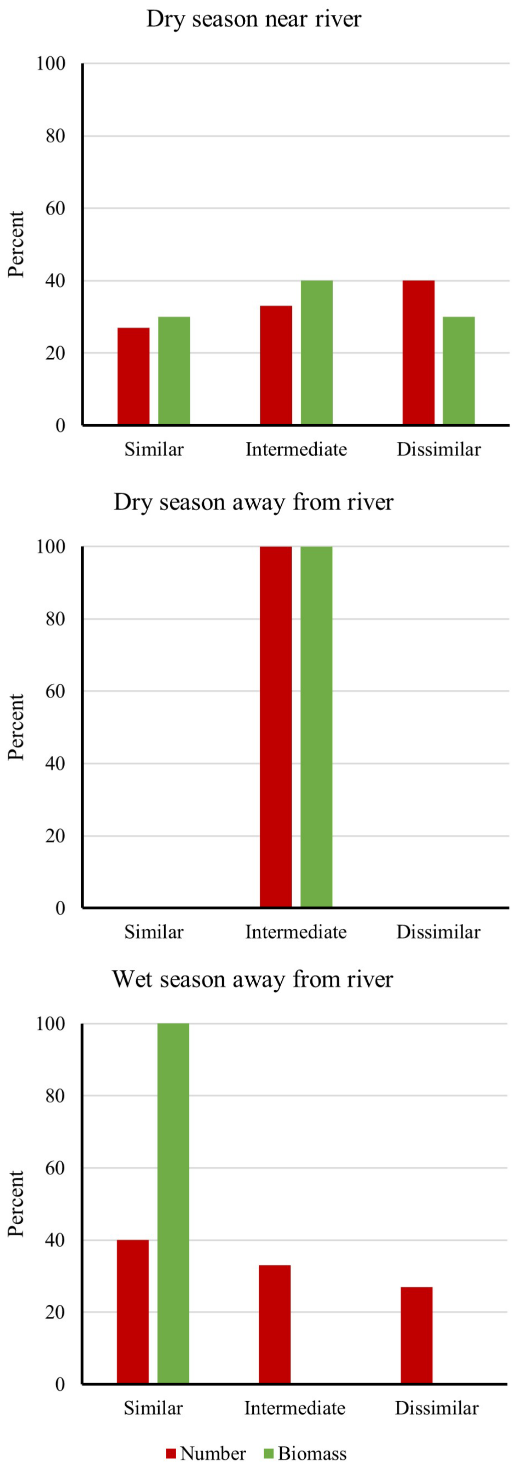

Figure 8: *Functional dissimilarity of dominant large herbivore species in different spatio-temporal categories.*

A hierarchical cluster analysis was also used to classify the herbivores into functional groups and substantiate the functional dissimilarity results yielded by the pairwise comparison method. All 17 species were divided into three functional groups according to their trait similarities and differences (Table 1). Dominant species are evenly represented in all three functional groups, suggesting good functional diversity.

Table 1: *Functional group membership of large herbivores in Mudumu National Park. Dominant species (numbers # and biomass *) are evenly distributed among the three functional groups. Distance refers to the gap between an observation or the collective attributes of a particular species and the centroid of that group. The average distance from a species to the group centroid is a measure of the functional variability of the species within each group. A group that has a larger average distance is more diverse.*

Group	Species	Distance
1	Elephant # * *Loxodonta africana*	0.94
	Burchell's Zebra # * *Equus burchellii*	1.37
	Hippopotamus *Hippopotamus amphibius*	1.60
2	Common warthog *Phacochoerus africanus*	1.75
	Red lechwe *Kobus leche*	0.96
	Southern reedbuck *Redunca arundinum*	1.75
	Common impala # *Aepyceros melampus*	0.45
	Grey duiker *Sylvicapra grimmia*	0.45
	Steenbok *Raphicerus campestris*	0.45
	Bushbuck *Tragelaphus sylvaticus*	0.96
3	Giraffe *Giraffa camelopardalis*	1.25
	Greater kudu *Tragelaphus strepsiceros*	1.00
	Roan antelope # *Hippotragus equinus*	0.54
	Sable antelope *Hippotragus niger*	0.54
	Waterbuck *Kobus ellipsiprymnus*	0.54
	Blue wildebeest # * *Connochaetes taurinus*	0.54
	African savanna buffalo # * *Syncerus caffer*	1.51

Spatial Functional Variation

In terms of numbers, five large mammal herbivore species belonging to all three functional groups (elephant and zebra – group 1, impala – group 2, and buffalo and wildebeest – group 3) were dominant near the river (Table 2). Away from the river, three species (elephant, impala and zebra) declined in numbers. Of the declining species, only elephant lost its dominance. It was replaced by a functionally similar species, the hippopotamus, which was not dominant near the river. Kudu (group 3) also became

Table 2: *Change in the contribution of numbers and biomass of large herbivore species in Mudumu National Park from the river inland.*

	Numbers		Biomass	
Group	***Decreased***	***Increased***	***Decreased***	***Increased***
1	Elephant Zebra	Hippopotamus	Elephant	Hippopotamus Zebra
2	Bushbuck Impala Reedbuck Warthog	Duiker Lechwe Steenbok	Bushbuck Reedbuck	Duiker Impala Lechwe Steenbok Warthog
3	Roan Sable Waterbuck	Buffalo Giraffe Kudu Wildebeest	Roan Sable Waterbuck	Buffalo Giraffe Kudu Wildebeest

dominant away from the river. This changed the contribution of functional groups from 40%, 20% and 40% to 33%, 17% and 50% for group 1, 2 and 3 respectively, away from the river.

In terms of biomass, three large mammal herbivore species belonging to two functional groups (elephant and zebra – group 1, and buffalo – group 3) were dominant near the river (Table 2). Away from the river, only the elephant declined in dominance. Despite the decline, the elephant remained dominant away from the river, along with zebra and buffalo. Two more species, kudu and wildebeest in group 3 joined these. This changed the contribution of functional groups from 67%, 0% and 33% to 40%, 0% and 60% for group 1, 2 and 3, respectively, away from the river.

DISCUSSION

Proportional Contribution

This study shows that only a few species make up most of the large herbivore numbers and biomass in the park. Other studies (Walker *et al.* 1999, Rutina & Moe 2014) also found that ecosystems comprise a few dominant species that are functionally more effective and a multitude of minor species. This dominant-minor species relationship occurs when, despite performing similar functions, a single species or a relatively small group of species exert more pressure on their environment in comparison to all other species in the area. These minor species have relatively trivial functional influence but may help keep the system stable in case of an extinction event (Walker 1992, 1995, Duffy *et al.* 2001, Philpott *et al.* 2012, Kang *et al.* 2015, Biggs *et al.* 2020).

The study also revealed that high population numbers do not always guarantee high biomass contribution, as is the case with impala and roan antelope that were dominant in numbers but not in biomass. Another noteworthy case is the elephant which had lower population numbers in relation to some other species but still contributed the most in terms of biomass. This suggests that besides species richness, biomass contribution and ecological function are highly affected by ecological traits, such as the size or behaviour of an animal. Body size is one of the most fundamental traits of an organism (White *et al.* 2007). It is related to lifespan, home range size and other aspects of life history and ecology, and is one of the primary determinants of metabolism and therefore, resource use (Brown *et al.* 2004). The overwhelming influence of this trait is apparent in the role that the elephant plays in the savanna ecosystem.

Furthermore, zebra, which was dominant in numbers during the dry season near the river lost its dominance in terms of biomass contribution; and steenbok and zebra that were dominant in numbers during the wet season away from the river were not dominant in biomass contribution. Giraffe, which was not dominant in numbers, was one of the dominant species in terms of biomass. This further demonstrates the restricted association between how much a particular species affects its environment and how many individuals of that species are present.

Functional Dissimilarity

The study revealed that dominant species are dissimilar in terms of both population numbers and biomass contribution in the entire national park. This is in line with (Walker *et al.* 1999) who also found that the dominant species among their sampled vegetation were diverse. The findings also confirm the resilience hypothesis, first defined by (Holling 1973), as the amount of disturbance that an ecosystem can withstand without changing self-organised processes and structures. Resilience here means the persistence of function, or the capacity for function to be restored after a major change, rather than just the rate of return following a minor disturbance (Ludwig *et al.* 1997, Walker *et al.* 1999). The functional dissimilarity of the dominant species shows that the area has diverse large herbivore driver traits affecting ecological processes and that, should a disturbance of some kind destabilise the ecosystem, there would be enough large herbivore trait variation to restore the system back to equilibrium.

When seasonal and spatial variation were considered, the pattern was different from that of the whole park. In the dry season, there was average functional dissimilarity between dominant species, peaking near the river, most likely due to the movement of large herbivores to the river when water becomes scarce elsewhere. However, during the wet season there was less large herbivore functional dissimilarity, especially near the river, most likely due to the animals dispersing back into the park in response to water availability in waterholes and lush pastures.

The hierarchical cluster analysis revealed that the area had three large herbivore functional groups. The first group comprised ecosystem engineers such as elephant (Mosepele *et al.* 2009, Sidle & Ziegler 2010) and hippopotamus (McCarthy *et al.* 1998, Deocampo 2002, McCauley *et al.* 2015). The third group comprised megaherbivores such as giraffe and buffalo, while the middle group contained small herbivores such as duiker and impala.

Spatial Functional Variation

Large herbivore functional diversity changed with an increase in distance from the Kwando River. This change resulted from a change in dominant species. Dominant species that were absent or lost their dominance either near or away from the river were replaced by functionally similar minor species. These results are consistent with other studies that show that environmental and spatial variation has an effect on the species richness of organisms (Fierer & Jackson 2006, Chen *et al.* 2017). Stevens *et al.* (2003) also observed an abrupt increase in functional diversity of bats towards the equator when travelling from the tropics and concluded that increase in species richness alone could not account for that change.

CONCLUSIONS AND RECOMMENDATIONS

The effective management of protected areas is greatly improved by precise knowledge of the functional diversity of species contained within. This study confirmed that only a small number of large herbivore species contribute the most in terms of numbers and biomass within the park, and that species with large population numbers did not always have the most functional influence due to constraints in communal body mass and related ecological traits. Moreover, the park was found to have three diverse functional clades and that season and distance from the river greatly influenced the distribution of functions across space and time. Lastly, there is need to further investigate and understand the functional ecology of the park to help facilitate management efforts.

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