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

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Introduction

Environmental heterogeneity across savanna landscapes may play key roles in determining plant (MacFayden *et al.* 2016), large mammal and bird diversity (Harrington *et al.* 1999; Fuhlendorf *et al.* 2006; Krook *et al.* 2007). This heterogeneity also determines the strength of density-dependent feedbacks on large herbivore population growth and their viability (Hobbs *et al*. 2008; Hopcraft *et al*. 2010).

The Savuti-Mababe-Linyanti ecosystem, northern Botswana is a relatively pristine region of the northern conservation area containing extensive savanna woodlands sandwiched between the permanent water sources of the Okavango Delta and Linyanti Swamps, where large areas of woodland may occur > 20 km from permanent water sources, beyond the maximum movement distance of the more mobile bull elephants during the dry season.

Objective

1. To determine the effect of herbivory on plant composition, structure and diversity with distance from permanent water.

Study site

The study was conducted in Savuti-Mababe-Linyanti ecosystem, northern Botswana (Fig 1)

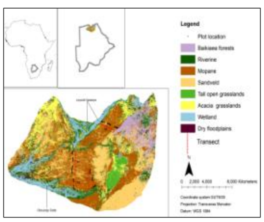

Fig 1: Savuti-Mababe-Linyanti ecosystem

Materials & methods

Vegetation composition, structure and richness in two different vegetation types (mopane and sandveld woodland) at three distance zones (0-5, 10-15 and > 20 km) from the permanent water of the Okavango Delta and Linyanti Swamps were surveyed (Fig 1). We modeled vegetation response of the most abundant species to herbivory in relation to distance from permanent water, and included fire frequency as a covariate.

Results

Trees favoured by elephants during the dry season occurred typically as immature, pollarded populations within 5 km of permanent water sources while mature tall populations of these species were found far from water (> 10-15 km, Fig 2 & 4). Similarly, short high-quality grazing grasses were higher in abundance within 5 km of permanent water whereas taller high-quality perennial grasses peaked in abundance beyond 20 km from permanent water (Fig 3). Trends in herbaceous richness with distance from water were contingent upon vegetation type, while tree richness did not change with distance from water(Table 1).

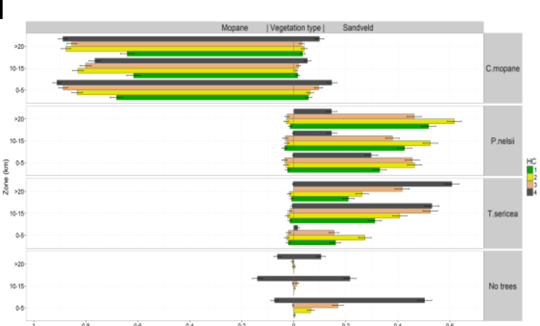

Fig 2: Relationship between height structure of the three most dominant tree species of the study area and distance zone from permanent water. HC = Height class (1: 0-1 m, 2: 1-2 m, 3: 2-4 m and 4: > 4 m), *C. mopane* = *Colophospermum mopane*, *P. Nelsii* = *Philenoptera nelsii* and *T. sericea* = *Terminalia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

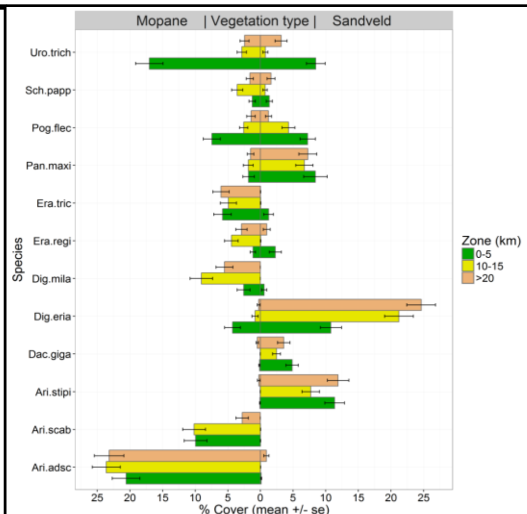

Fig 3: Relationship between cover of the major grasses of the study area and distance zone from permanent water. Uro.trich = *Urochloa trichopus*, Sch.papp = *Schmidtia pappophoroides*, Pog.flec = *Pogonarthria fleckii*, Pan. Maxi = *Panicum maximum*, Era.tric = *Eragrostis trichophora*, Era.regi = *Eragrostis rigidior*, Dig.mila = *Digitaria milanjiana*, Dig.eria = *Digitaria eriantha*, Dac.giga = *Dactyloctenium giganteum*, Ari.stipi = *Aristida stipitata*, Ari.scab = *Aristida scrabrivalvis*, Ari.adsc = *Aristida adscensionis.*

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

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

MCMC								
Grasses	Mopane				Sandveld			
Variable	Post. Mean	Lower CI	Upper CI	pMCMC	Post. Mean	Lower CI	Upper CI	pMCMC
Intercept	2.22409	2.04225	2.40356	<3e-04	1.87523	1.64360	2.10593	<3e-04
Zone 2	-0.06946	-0.3438	0.22440	0.62500	-0.15135	-0.52249	0.22733	0.44200
Zone 3	-0.03411	-0.3271	0.24297	0.80200	-0.49862	-0.89228	-0.10933	**0.01200**
Fire	0.02679	-0.0998	0.14635	0.65700	0.06136	-0.08926	0.21421	0.41050
Zone 2:Fire	0.09890	-0.0854	0.27494	0.28100	0.00180	-0.21427	0.22520	0.99750
Zone 3:Fire	0.04279	-0.1401	0.19470	0.61300	0.19445	-0.01006	0.40049	0.06450
Intercept	2.20136	2.05532	2.33642	<3e-04	1.54702	1.34921	1.77001	<3e-04
E.Dung	-0.00048	-0.0089	0.00667	0.91900	0.00929	0.00112	0.01830	**0.03300**
Fire	0.08018	-0.0086	0.15753	0.07000	0.15630	0.04498	0.26772	**0.00550**
E.Dung:Fire	-0.00120	-0.0071	0.00480	0.68800	-0.00217	-0.00676	0.00283	0.35400
Intercept	2.20615	2.07878	2.32941	<3e-04	1.65394	1.47749	1.84133	<3e-04
H.Dung	-0.00945	-0.0721	0.04554	0.754	0.02493	-0.03005	0.0743	0.358
Fire	0.072843	-0.0003	0.14629	**0.053**	0.13796	0.04831	0.22172	**0.0015**
H.Dung:Fire	-0.00131	-0.0342	0.03064	0.954	-0.01142	-0.06086	0.03934	0.657
Forbs								
Intercept	3.55230	3.44039	3.65256	<3e-04	3.69706	3.59712	3.79533	<3e-04
Zone 2	0.02557	-0.1442	0.18676	0.76500	-0.08621	-0.24687	0.07482	0.27550
Zone 3	0.24796	0.08323	0.39824	**0.00400**	-0.22532	-0.37550	-0.04891	0.00550
Fire	-0.06195	-0.1351	0.01624	0.10900	0.00654	-0.05933	0.07359	0.83750
Zone 2:Fire	0.06764	-0.0420	0.17971	0.24400	0.03394	-0.06100	0.13115	0.48300
Zone 3:Fire	0.06308	-0.0320	0.16845	0.20700	0.06791	-0.01770	0.16448	0.13450
Intercept	3.63079	3.53999	3.72541	<3e-04	3.53599	3.44915	3.62710	<3e-04
E.Dung	-0.00195	-0.0071	0.00317	0.46100	0.00526	0.00110	0.00888	**0.00800**
Fire	0.04478	-0.0110	0.10084	0.10700	0.06102	0.01256	0.11055	**0.01450**
E.Dung:Fire	-0.00549	-0.0097	-0.0009	**0.00900**	-0.00191	-0.00406	0.00022	0.08500
Intercept	3.605146	3.51427	3.69615	<3e-04	3.572131	3.49808	3.64817	<3e-04
H.Dung	0.006931	-0.0309	0.04547	0.737	0.028307	0.00676	0.0497	**0.0095**
Fire	0.013994	-0.0404	0.06601	0.61	0.048589	0.00783	0.08369	**0.015**
H.Dung:Fire	0.000175	-0.0227	0.02179	0.978	-0.01446	-0.0368	0.00628	0.1785
Trees								
Intercept	1.86873	1.65504	2.08320	<3e-04	1.87771	1.63194	2.10895	<3e-04
Zone 2	-0.00147	-0.3702	0.35343	0.99500	-0.41440	-0.82848	0.00662	0.05500
Zone 3	-0.04993	-0.4031	0.28506	0.78900	-0.28358	-0.65677	0.12384	0.16200
Fire	-0.10026	-0.2644	0.05877	0.21800	-0.10368	-0.27068	0.06374	0.23100
Zone 2:Fire	0.01066	-0.2407	0.25998	0.94100	0.13277	-0.11361	0.39494	0.30400
Zone 3:Fire	0.09558	-0.1243	0.30662	0.38100	0.14158	-0.07948	0.37012	0.22200
Intercept	1.84200	1.66000	2.01800	<3e-04	1.61508	1.40903	1.84147	<3e-04
E.Dung	0.00008	-0.0090	0.01007	0.97200	0.00519	-0.00342	0.01450	0.26200
Fire	-0.02390	-0.1356	0.08372	0.67300	-0.05893	-0.18405	0.07043	0.37100
E.Dung:Fire	-0.00378	-0.0124	0.00403	0.36500	0.00176	-0.00366	0.00625	0.48200
Intercept	1.837142	1.66894	1.98848	<3e-04	1.64481	1.44272	1.83091	<3e-04
H.Dung	0.008271	-0.0633	0.07838	0.798	0.041822	-0.01006	0.09265	0.115
Fire	-0.03664	-0.1368	0.05631	0.445	0.002977	-0.09611	0.09916	0.964
H.Dung:Fire	-0.0148	-0.0609	0.02859	0.511	-0.0486	-0.10664	0.00763	0.091

Discussion

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

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