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Woody Vegetation Utilisation in Tembe Elephant Park, Kwazulu-Natal, South Africa

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Abstract

A survey of woody plant species utilisation by large (excluding elephants), medium and small browsers,man and "natural damage", was conducted in nine vegetation units of Tembe Elephant Park, KwaZulu-Natal, South Africa. Woody species use and canopy removal were evaluated within two age ranges, (a) recent, ≤ 12 months prior to study and (b) old, > 12 months prior to the study. The results show that recent canopy removal by medium and small browsers was intensive and generally represented one third of height classes available to the agents which were consistently used withinall vegetation types. The overall utilisation pattern indicated that medium and small browsers may be removing the regeneration classof the woody plants layer. Natural damage was found to be considerable and it was hypothesized that it may be linked and possibly amplified by prior elephant utilisation. In conclusion, it is possible to suggest that the regular use of the sapling level by small and medium browsers could promote woodland to grassland retrogression, as was found in east Africa under high densities of animals.

Keywords: browsers, Maputaland, sand forest, tree utilisation, woodland

1. Introduction

Numerous ecological problems have been documented regarding over-concentration of animals; in small or large, fenced or even open systems (Walpole et al., 2004; Western, 2007; Eckhardt et al., 2000; Mosugelo et al., 2002). Among them is the transformation of a woodland landscape into shrubby grassland, or the suppression of woody vegetation growth (Western & Maitumo, 2004). Growing animal populations confined in reserves in Africa has come to the forefront of conservation issues because public, scientific, and conservation opinions are divided on how to manage this problem (Lombard et al., 2001; van Aarde & Jackson, 2007).

When the vegetation type supporting growing animal populations is endangered, poorly known or sensitive to utilisation, understanding the impact of animal populations is essential (Lombard et al., 2001; O'Connor et al., 2007). In Tembe Elephant Park (Tembe), a South African reserve, Sand Forest is considered one of the most valuable vegetation types of the Maputaland – Pondoland – Albany hotspot of biodiversity (Smith et al., 2006). In Tembe, conservation authorities indicated that Sand Forest conservation prevails over animal conservation targets (Matthews, 2006). However, subsequent to the park's fencing in 1989 and successful conservation measures, without limiting larger carnivores, animal populations have grown and appeared unlimited by density dependence (Guldemond & van Aarde, 2007). This is a concern as Sand Forest has been shown to react to large herbivore utilisation (Gaugris & van Rooyen, 2008), and requires that utilisation levels be established to understand the pressure and potential impact.

As Sand Forest origin remains in debate and because arguments exists that it may develop from a woodland succession sequence (Gaugris & van Rooyen, 2008), the present study investigated woody vegetation utilisation by small to large mammalian browsing herbivores in woodlands and Sand Forest of Tembe (excluding elephants) , to quantify utilisation. Human use although anecdotal is also reported. Finally the occurrence of what can be considered as "natural damage" is considered. These aspects are examined by evaluating general woody species utilisation and canopy removal within two different periods (≤ 12 months prior to the study and > 12 months prior to the study) and considering the implications of results observed.

2. Methodology

2.1 Objectives of the Study

The present study was undertaken to measure the utilisation of woody species in a fenced off conservation area. The study was considered urgent as growing numbers of browsing mammalian herbivores were considered to have a significant impact on the regeneration of woody plant species. The present study is therefore a description of the measured utilisation levels of woody plants by small to large herbivores (excluding elephants).

2.2 Study Area

The study area lies in Maputaland, KwaZulu-Natal, South Africa. Tembe's 30,000 ha (proclaimed in 1983) were completely fenced in 1989. Tembe is characterised by sandy plains interspersed with ancient littoral dunes and a north flowing swamp (Muzi Swamp) along the park's eastern boundary. Tembeis covered by a mixture of habitats types such as grasslands, woodlands and Sand Forest patches (Matthews et al., 2001). Summers are hot, wet, and humid, while winters are cool to warm and dry. The mean annual rainfall is 700 mm (Gaugris, 2008).

Tembe's larger mammalian herbivore populations are composed of the following species (re-established species are marked with an asterisk) with the numbers in brackets representing 2000 census – 2005census (Matthews, 2006):

- African elephant *Loxodonta africana* (130 - 179 (195 (Note 1))
- White rhinoceros* *Ceratotheriumsimum* (35 - 43)
- Black rhinoceros* *Dicerosbicornis* (22 - 20)
- Giraffe* *Giraffacamelopardalis* (100 - 131)
- Hippopotamus *Hippopotamusamphibius* (14 - 20)
- Plain's zebra* *Equusquagga* (200 - 176)
- Eland* *Tragelaphusoryx* (40 - 0)
- Buffalo *Syncerus caffer* (60 -100)
- Kudu* *Tragelaphusstrepsiceros* (290 - 532)
- Blue wildebeest* *Connochaetestaurinus* (130 - 434)
- Waterbuck* *Kobus ellipsiprymnus* (360 - 419)
- Impala* *Aepycerosmelampus* (600 - 694)
- Nyala *Tragelaphusangasii* (300 - 1800)
- Bushbuck *Tragelaphus scriptus* (unknown - 40)
- Reedbuck *Reduncaarundinum* (880 - 268)
- Grey duiker *Sylvicapragrimmia* (unknown - 200)
- Red duiker *Cephalophus natalensis* (unknown - 400)
- Suni *Neotragusmoschatus* (estimated > 500)
- Warthog *Phacochoerus africanus* (260 - 300)
- Bush pig *Potamochoerus porcus* (unknown)

3. Methods

3.1 Fieldwork

A total of 135 rectangular plotsof density-dependent size (15 m by 2 m to a maximum of 45 m by 19 m) placed throughout Tembe by stratified random sampling were surveyed between May and October 2004. Plots were located at least 50 m away from management tracks and 100 m away from tourist tracks.

Plots were divided into two halves lengthwise. All woody individuals (defined as plants with an erect to scrambling growth form and ligneous trunk) were identified to the species in the first half, but only individuals' ≥ 0.4 m tall were recorded on the return leg. Live and dead stems were counted and diameters (D) measured at 30 cm or above the basal swelling. Plant height (H) and height to base of the canopy (HBC – defined as the height where the larger lowest branches were found) were measured, followed by the largest canopy diameter (D1) and the canopy diameter perpendicular (D2) to D1. Standing dead trees were measured, while fallen dead trees were reconstructed using best fit relationships based on live trees.

Utilisation was evaluated for each plant and each utilisation episode was scored separately. The following parameters were recorded for each plant (Figure 1):

- Plant state;
- Utilisation type;
- Presumed agent for the observed utilisation event;
- Utilisation event age;
- Estimated percentage of material removed (canopy/bark/roots …) by utilisation event;
- Growth response to the damage/utilisation.

State of the woody plant as encountered	
1	Normal growth
2	Normal with branch regrowth from breakage
3	Pollarded (main stem snapped off, height reduced) – tree living, resprouting
4	Pollarded (main stem snapped off, height reduced) – tree living, coppicing
5	Pollarded (main stem snapped off, height reduced) – tree living, no growth response
6	Pushed over, stem intact, still partially rooted - living
7	Pushed over, stem partially broken - living
8	Mostly normal growth with some hedge growth
9	Hedge growth from continuous, regular browsing
10	Coppice growth from larger (older) dead stem
11	Coppice growth from accumulated browsing of young plant
12	Coppice growth from repeated fire
13	Coppice growth from repeated moisture stress
20	Senescent
30	Tree dead - main stem partially broken
31	Tree dead - main stem completely broken (pollarded)
32	Tree dead - main stem pushed over (partially uprooted)
33	Tree dead - main stem debarked
34	Tree dead - main stem intact, accumulated branch removal
35	Tree dead - debarking and branches / stems removed
50	Tree dead - intact - cause of death unknown
51	Tree dead - intact - killed by moisture stress
52	Tree dead - intact - dead from shading
53	Tree dead - intact - dead from high light
54	Tree dead - killed by combination of moisture stress and branch removal
55	Tree dead - killed from combination of shading and branch removal
56	Tree dead - killed by fire
60	Tree dead - totally uprooted
70	Top kill - drought dieback
71	Top kill - frost dieback
72	Top kill - dieback from debarking
80	Windfall
90	Live – deciduous leaf loss
91	Dying some branches still alive
92	Hedge growth from human utilisation
93	Tree dead, pushed over and broken, not uprooted

Agent (Agt.) of utilisation	
1	Elephant
2	Giraffe
3	Kudu
4	Eland
5	Black rhinoceros
6	Nyala
7	Impala
8	Bushbuck
9	Grey duiker
10	Red duiker
11	Suni
12	Unidentifiable mega browsers (elephant, giraffe)
13	Unidentifiable large/medium size browsers (kudu, nyala, eland, etc)
14	Unidentifiable medium/small size browsers (impala, bushbuck, duiker etc)
15	Moisture stress
16	Flooding
17	Shading
18	High light intensity
19	Fire
21	Wind
22	Accidental
23	Unknown
24	Human
25	Insects
26	Cane rat
27	Lightning
28	Cattle
29	Porcupine
30	Goats

Type of utilisation observed	
1	Whole plant (canopy and roots) utilized
2	Whole canopy utilized (roots still intact in ground)
3	Leaves and small twigs removed
4	Leaves, twigs, small branches, and large branches removed
5	Branch ends bitten off
6	Leaves plucked off
7	Leaves stripped
8	Parts of leaves removed
9	Only young leaves and leaf buds removed
10	Only mature leaves removed
11	Only senescent leaves removed
12	Bark removed
13	Roots removed
14	Flowers removed
15	Fruit / seeds removed
16	Dieback of main vertical branches/stems from top down
17	Dieback of horizontal branches/branch ends
18	Main stem/s cut
20	Accidental damage
21	No use / not damaged
22	Fire
23	Lightning
24	Pushed over and main stem broken
25	Pushed over and main stem intact

Growth responses (G.R.) to branch removal, stem breaking and debarking	
1	Coppice growth
2	Wound regrowth
3	Main stem resprouting
4	No coppice or regrowth - vigour appears unaffected
5	No coppice or regrowth - vigour appears reduced (tree dying)
6	Hedge growth
7	Mostly hedge growth with some normal growth
8	Mostly normal growth with some hedge growth
9	Tree dead

Age of utilization (Age)		Debarking – circumference (Brk.)		
1	< 1 month	1	1 % - 10 %	of the circumference of the stem removed
2	> 1 – 2 months	2	11 % - 25 %	
3	> 2 – 4 months	3	26 % - 50 %	
4	> 4 – 6 months	4	51 % - 75 %	
5	> 6 – 12 months	5	76 % - 90 %	
6	> 12 – 24 months	6	91 % - 99 %	
7	> 24 months	7	100%	
8	Continuous Regular Use			

Canopy volume removal		Debarking - stem height (Brk.)		
			Percentage of Stem Height	
1	1 % - 10 %	0.1	1 % - 10 %	of the height of stem removed
2	11 % - 25 %	0.2	11 % - 25 %	
3	26 % - 50 %	0.3	26 % - 50 %	
4	51 % - 75 %	0.4	51 % - 75 %	
5	76 % - 90 %	0.5	76 % - 90 %	
6	91 % - 99 %	0.6	91 % - 100 %	
7	100%	0.7	Whole stem plus branches	

The coding is derived from a code database used for other studies in KwaZulu-Natal, Northern Maputaland, South Africa, and only the codes relevant to the present study are displayed

Figure 1. Copy of the data capture coding sheet used for the study

3.2 Data Analysis

Plants were assigned to one of eight height classes (< 0.1 m, 0.1 to < 0.5 m, 0.5 to < 1.5 m, 1.5 to < 3.0 m, 3.0 to < 5.0 m, 5.0 to < 8.0 m, 8.0 to < 12 m, ≥ 12 m) representative of vegetation structure (Gaugris & van Rooyen, 2011). Utilisation events affecting only canopy volume were distinguished from those representing overall utilisation events (including canopy removal, bark damage, stem or branch breakages, uprooting and other types of damage). Canopy volume removal events were separated between recent events (12 months prior to fieldwork), and old events, for all older events.All analyses were conducted for each agent category for each vegetation unit:

- Large browsers (giraffe)
- Medium browsers (kudu, eland, black rhinoceros)
- Small browsers (suni, red duiker, common duiker, nyala, impala, bushbuck)
- Man
- Natural damage: considered as all instances where elephant or otheragent'sutilisation couldbe excluded and where a natural cause (wind, drought, fire, lightning or light conditions …) could be considered as most likely reason for observed damage.

The range of height classes available to an agent was all height classes where any utilisation event was documented for that agent during our study. It was calculated as the sum of height classes for all woody species with potential for use per vegetation unit for the agent. For example if six woody species were sampled and known to be used by the agent, and all eight height classes known to have been used by the agent for these species during our study, 48 size classes are considered as available in the vegetation type. However, if the agent can only access the lower four size classes, only 24 size classes were available to the agent.

Available canopy volume and canopy volume removal per height class per woody species per vegetation unit were estimated using Walker's method of 1976. The number of height classes where canopy removal events by an agent was observed was counted at vegetation unit level and expressed as a percentage of total number of height classes available to that agent. The number of height classes where at least 50% of the canopy volume was removed was calculated similarly per agent at vegetation unit level.

4. Results

The Sand Forest classification in Gaugris and van Rooyen (2008) was followed. A total of 168 species were encountered (84% of Tembe's documented woody species) through measurement of 12,915 woody plants.

4.1 Sand Forest Association

In the Sand Forest association and *Afzeliaquanzensis* clumps, medium and small browsers affected 20 to 76% of woody species during the recent period (Table 1). The older canopy removal values showed that natural damage affected the greatest number of woody species (40 to 78% of species). Utilisation marks appeared less noticeable after 12 months for medium (40 to 60% less species appearing as used) and small browsers (88 to 100% less species appearing as used).

Table 1. The number of woody species utilised by various agents in the vegetation associations of Tembe Elephant Park

Vegetation Unit			*Afzeliaquanzensis* clumps (VT 01.1.1)		Short Sand Forest (VT 01.2.1)		Tall Sand Forest (VT 01.2.2)		Mature Sand Forest (VT 01.2.3)	
No. of Species sampled			25		60		71		53	
No. of Species used by	Age	Type	No	(%)	No	(%)	No	(%)	No	(%)
Large Browsers	Recent	CV	0	0.0	0	0.0	0	0.0	0	0.0
	Old	CV	0	0.0	1	1.7	0	0.0	1	1.9
	All ages	O U	0	0.0	1	1.7	0	0.0	1	1.9
Medium Browsers	Recent	CV	5	20.0	25	41.7	33	46.5	20	37.7
	Old	CV	3	12.0	11	18.3	20	28.2	8	15.1
	All ages	O U	5	20.0	28	46.7	37	52.1	27	50.9
Small Browsers	Recent	CV	19	76.0	25	41.7	35	49.3	20	37.7
	Old	CV	0	0.0	2	3.3	4	5.6	0	0.0
	All ages	O U	19	76.0	25	41.7	38	53.5	22	41.5
Man	Recent	CV	0	0.0	0	0.0	0	0.0	0	0.0
	Old	CV	0	0.0	2	3.3	4	5.6	0	0.0
	All ages	O U	0	0.0	2	3.3	5	7.0	0	0.0
Natural Damage	Recent	CV	0	0.0	12	20.0	17	23.9	5	9.4
	Old	CV	10	40.0	47	78.3	51	71.8	28	52.8
	All ages	O U	10	40.0	51	85.0	52	73.2	29	54.7

Values are given for canopy removal (number of species where a percentage of canopy volume (CV) was removed) for the two periods evaluated (Recent: within 12 months prior to the study and Old: > 12 months prior to the study) and for the overall utilisation (O U), including all utilisation events, but time was undetermined.

The overall utilisation analysis showed that small browsers are the greatest users in the *Afzeliaquanzensis* clumps. However, in the Sand Forest association, marks from natural damage appeared to affect more woody species than any other agents (Table 1). Human activity signs were old.

During the recent period, medium browsers utilised up to 25.91% of height classes available to them (Table 2). Small browsers used the greatest part of the canopy available to them in Sand Forest (up to 60.47% of height classes available). Canopy removal by natural damage was low. In the old period, canopy removal marks from small and medium browsers appeared to disappear with time (Table 2). Human-linked canopy removal took place in the past (Table 2). Signs of canopy removal by natural damage accumulated over time, and up to 55% of available height classes were "used" in Short Sand Forest.

Table 2. The number and percentage of height classes (HC) utilised by the various agents in the Sand Forest association of Tembe Elephan t Park

				Vegetation Units									
				Afzeliaquanzensis clumps (VT 01.1.1)					Short Sand Forest (VT 01.2.1)				
Agent	Range of height classes used	Age	Type	NHCS*	Total HC utilisation		HC use where> 50 % of HC used		NHCS*	Total HC utilisation		HC use where> 50 % of HC used	
					(No)	(%)	(No)	(%)		(No)	(%)	(No)	(%)
Large Browsers	03 - 06	Recent	CV	36	0	0.00	0	0.00	125	0	0.00	0	0.00
		Old	CV	36	0	0.00	0	0.00	125	1	0.80	0	0.00
		All ages	O U	36	0	0.00	0	0.00	125	1	0.80	0	0.00
Medium Browsers	02 - 06	Recent	CV	45	5	11.11	1	2.22	146	32	21.92	1	0.68
		Old	CV	45	3	6.67	1	2.22	146	12	8.22	1	0.68
		All ages	O U	45	5	11.11	4	8.89	146	35	23.97	12	8.22
Small Browsers	01 - 05	Recent	CV	43	26	60.47	0	0.00	130	43	33.08	1	0.77
		Old	CV	43	1	2.33	0	0.00	130	0	0.00	0	0.00
		All ages	O U	43	27	62.79	26	60.47	130	43	33.08	21	16.15
Man	02 - 07	Recent	CV	48	0	0.00	0	0.00	154	0	0.00	0	0.00
		Old	CV	48	0	0.00	0	0.00	154	1	0.65	1	0.65
		All ages	O U	48	0	0.00	0	0.00	154	2	1.30	0	0.00
Natural Damage	01 - 08	Recent	CV	49	0	0.00	0	0.00	163	15	9.20	1	0.61
		Old	CV	49	14	28.57	1	2.04	163	90	55.21	2	1.23
		All ages	O U	49	14	28.57	13	26.53	163	96	58.90	78	47.85
				Tall Sand Forest (VT 01.2.2)					Mature Sand Forest (VT 01.2.3)				
				NHCS*	Total HC utilisation		HC use where> 50 % of HC used		NHCS*	Total HC utilisation		HC use where> 50 % of HC used	
					(No)	(%)	(No)	(%)		(No)	(%)	(No)	(%)
Large Browsers	03 - 06	Recent	CV	164	0	0.00	0	0.00	90	0	0.00	0	0.00
		Old	CV	164	0	0.00	0	0.00	90	1	1.11	0	0.00
		All ages	O U	164	0	0.00	0	0.00	90	1	1.11	0	0.00
Medium Browsers	02 - 06	Recent	CV	193	50	25.91	2	1.04	109	26	23.85	2	1.83
		Old	CV	193	28	14.51	2	1.04	109	8	7.34	2	1.83
		All ages	O U	193	64	33.16	17	8.81	109	40	36.70	21	19.27
Small Browsers	01 - 05	Recent	CV	173	68	39.31	1	0.58	96	30	31.25	0	0.00
		Old	CV	173	4	2.31	0	0.00	96	0	0.00	0	0.00
		All ages	O U	173	72	41.62	32	18.50	96	32	33.33	23	23.96
Man	02 - 07	Recent	CV	206	0	0.00	0	0.00	114	0	0.00	0	0.00
		Old	CV	206	7	3.40	1	0.49	114	0	0.00	0	0.00
		All ages	O U	206	8	3.88	1	0.49	114	0	0.00	0	0.00
Natural Damage	01 - 08	Recent	CV	224	27	12.05	0	0.00	121	5	4.13	0	0.00
		Old	CV	224	123	54.91	3	1.34	121	46	38.02	0	0.00
		All ages	O U	224	128	57.14	90	40.18	121	49	40.50	33	27.27

NHCS* = Number of height classes sampled in the range used by the agent;

HC = Height Classes;

No. = Number.

The number of height classes utilised is represented range utilised by the agent, the number of height classes in that range where utilisation of at least 50% of the height class was observed for at least one species. Values are given for canopy removal utilisation events (CV) for the two periods evaluated (Recent: within 12 months prior to the study and Old: > 12 months prior to the study) and for the overall utilisation (O U), including all utilisation events, but time was undetermined.

In terms of overall utilisation, values mirrored those of old canopy removal, although the percentage of height classes used was usually higher for all agents (Table 2), especially when considering the number of height classes where utilisation affected ≥ 50% of a height class canopy volume. More than 25% of height classes lost > 50% of their volume through natural damage.

4.2 Woodland Vegetation Group

Recent woody species use was greatest for small and medium browsers (Table 3). Small browsers used more species in Closed Woodland Thicket and Sparse Woodland on Sand than any other agent, and used ≥ 50% of woody species available in all woodland units. Natural damage affected less woody species than other agents in most instances. When considering old canopy removal, utilisation signs by medium and small browsers were disappearing. However, > 50% of woody species showed old natural damage signs in three woodland vegetation types.

Table 3. The number of woody species utilised by the various agents in the vegetation associations of Tembe Elephant Park

Vegetation Unit			Closed Woodland Thicket (VT 02.1.0)		Closed Woodland on Clay (VT 02.2.0)		Closed Woodland on Sand (VT 02.3.0)		Open Woodland on Sand (VT 03.1.0)		Sparse Woodland on Sand (VT 04.1.0)	
No of Species sampled			29		116		115		92		40	
No of Species used by	Age	Type	No	(%)	No	(%)	No	(%)	No	(%)	No	(%)
Large Browsers	Recent	CV	0	0.0	1	0.9	5	4.3	11	12.0	0	0.0
	Old	CV	0	0.0	1	0.9	0	0.0	4	4.3	0	0.0
	All ages	O U	0	0.0	3	2.6	5	4.3	14	15.2	1	2.5
Medium Browsers	Recent	CV	8	27.6	66	56.9	60	52.2	43	46.7	11	27.5
	Old	CV	5	17.2	35	30.2	37	32.2	23	25.0	4	10.0
	All ages	O U	8	27.6	89	76.7	78	67.8	60	65.2	15	37.5
Small Browsers	Recent	CV	16	55.2	79	68.1	76	66.1	72	78.3	21	52.5
	Old	CV	1	3.4	2	1.7	4	3.5	2	2.2	2	5.0
	All ages	O U	16	55.2	82	70.7	80	69.6	73	79.3	22	55.0
Man	Recent	CV	1	3.4	1	0.9	3	2.6	0	0.0	0	0.0
	Old	CV	0	0.0	0	0.0	1	0.9	0	0.0	1	2.5
	All ages	O U	1	3.4	2	1.7	4	3.5	0	0.0	1	2.5
Natural Damage	Recent	CV	1	3.4	28	24.1	20	17.4	38	41.3	7	17.5
	Old	CV	8	27.6	56	48.3	63	54.8	43	46.7	14	35.0
	All ages	O U	8	27.6	59	50.9	67	58.3	52	56.5	16	40.0

Values are given for canopy removal (number of species where a percentage of canopy volume (CV) was removed) for the two periods evaluated (Recent: within 12 months prior to the study and Old: > 12 months prior to the study) and for the overall utilisation (O U), including all utilisation events, but time was undetermined.

The overall woody species utilisation showed that the medium browsers used mainly the Closed Woodlands on Clay and Sand and the Open Woodland on Sand (more than 50% of available woody species). Overall utilisation by small browsers was consistently > 50% of sampled woody species in all woodland units. Natural damage affected > 50% of woody species in three woodland units. Recent signs of human utilisation appeared in Closed

Woodlands.

Small browsers affected the greatest number of height classes (Table 4) followed by natural damage and medium browsers. Utilisation by large browsers was seldom encountered. Natural damage affected a substantialnumber of height classes where canopy removal was ≥ 50% in the Closed Woodland on Sand and Clay, the Open Woodland on Sand and the Sparse Woodland on Sand. Old canopy removal events followed similar trends as Sand Forest, whereby signs of utilisation by medium and small browsers tended to disappear. Natural damage canopy removal affected approximately a third of height classes throughout the Woodlands.

Table 4. The number and percentage of height classes (HC) utilised by the various agents in the Woodland association of Temb e Elephant Park

Agent	Range of height classes used	Age	Type	Vegetation Units									
				Closed Woodland Thicket (VT 02.1.0)					Closed Woodland on Clay (VT 02.2.0)				
				NH CS*	Total HC utilisation		HC use where > 50 % of HC used		NHCS*	Total HC utilisation		HC use where > 50 % of HC used	
					(No)	(%)	(No)	(%)		(No)	(%)	(No)	(%)
Large Browsers	03 - 06	Recent	CV	41	0	0.00	0	0.00	261	1	0.38	0	0.00
		Old	CV	41	0	0.00	0	0.00	261	1	0.38	0	0.00
		All ages	O U	41	0	0.00	0	0.00	261	3	1.15	0	0.00
Medium Browsers	02 - 06	Recent	CV	50	16	32.00	0	0.00	333	131	39.34	5	1.50
		Old	CV	50	11	22.00	0	0.00	333	55	16.52	5	1.50
		All ages	O U	50	14	28.00	9	18.00	333	189	56.76	105	31.53
Small Browsers	01 - 05	Recent	CV	43	24	55.81	0	0.00	321	150	46.73	0	0.00
		Old	CV	43	1	2.33	0	0.00	321	2	0.62	0	0.00
		All ages	O U	43	26	60.47	18	41.86	321	156	48.60	74	23.05
Man	02 - 07	Recent	CV	50	1	2.00	0	0.00	342	1	0.29	0	0.00
		Old	CV	50	0	0.00	0	0.00	342	0	0.00	0	0.00
		All ages	O U	50	1	2.00	0	0.00	342	2	0.58	1	0.29
Natural Damage	01 - 08	Recent	CV	51	2	3.92	0	0.00	364	48	13.19	6	1.65
		Old	CV	51	16	31.37	0	0.00	364	107	29.40	8	2.20
		All ages	O U	51	17	33.33	9	17.65	364	119	32.69	50	13.74

Agent	Range of height classes used	Age	Type	Closed Woodland on Sand (VT 02.3.0)				
				NHCS*	Total HC utilisation		HC use where > 50 % of HC used	
					(No)	(%)	(No)	(%)
Large Browsers	03 - 06	Recent	CV	262	5	1.91	0	0.00
		Old	CV	262	0	0.00	0	0.00
		All ages	O U	262	5	1.91	2	0.76
Medium Browsers	02 - 06	Recent	CV	317	115	36.28	2	0.63
		Old	CV	317	56	17.67	2	0.63
		All ages	O U	317	145	45.74	60	18.93
Small Browsers	01 - 05	Recent	CV	317	145	45.74	1	0.32

		Old	CV	317	4	1.26	1	0.32
		All ages	O U	317	153	48.26	78	24.61
Man	02 - 07	Recent	CV	332	3	0.90	0	0.00
		Old	CV	332	1	0.30	0	0.00
		All ages	O U	332	4	1.20	0	0.00
Natural Damage	01 - 08	Recent	CV	373	36	9.65	8	2.14
		Old	CV	373	132	35.39	12	3.22
		All ages	O U	373	134	35.92	74	19.84

Agent	Range of height classes used	Age	Type	Open Woodland on Sand (VT 03.1.0)					Sparse Woodland on Sand (VT 04.1.0)				
				NHCS*	Total HC utilisation		HC use where > 50 % of HC used		NHCS*	Total HC utilisation		HC use where > 50 % of HC used	
					(No)	(%)	(No)	(%)		(No)	(%)	(No)	(%)
Large Browsers	03 - 06	Recent	CV	188	12	6.38	0	0.00	48	1	2.08	0	0.00
		Old	CV	188	4	2.13	0	0.00	48	0	0.00	0	0.00
		All ages	O U	188	15	7.98	1	0.53	48	1	2.08	0	0.00
Medium Browsers	02 - 06	Recent	CV	246	91	36.99	0	0.00	72	18	25.00	4	5.56
		Old	CV	246	40	16.26	0	0.00	72	4	5.56	1	1.39
		All ages	O U	246	122	49.59	44	17.89	72	20	27.78	8	11.11
Small Browsers	01 - 05	Recent	CV	243	145	59.67	3	1.23	73	34	46.58	0	0.00
		Old	CV	243	14	5.76	0	0.00	73	5	6.85	0	0.00
		All ages	O U	243	148	60.91	71	29.22	73	34	46.58	26	35.62
Man	02 - 07	Recent	CV	254	0	0.00	0	0.00	74	0	0.00	0	0.00
		Old	CV	254	0	0.00	0	0.00	74	1	1.35	0	0.00
		All ages	O U	254	0	0.00	0	0.00	74	1	1.35	0	0.00
Natural Damage	01 - 08	Recent	CV	273	85	31.14	6	2.20	77	12	15.58	8	10.39
		Old	CV	273	109	39.93	10	3.66	77	23	29.87	4	5.19
		All ages	O U	273	132	48.35	63	23.08	77	32	41.56	22	28.57

NHCS* = Number of height classes sampled in the range used by the agent;

HC = Height Classes;

No = Number.

The number of height classes utilised is represented in three ways, a total number of height classes utilised within the range utilised by the agent, the number of height classes in that range where utilisation of at least 50% of the height class was observed for at least one species. Values are given for canopy removal utilisation events (CV) for the two periods evaluated (Recent: within 12 months prior to the study and Old: > 12 months prior to the study) and for the overall utilisation (O U), including all utilisation events, but time was undetermined.

Overall utilisation values were generally higher than those for canopy removal and the percentage of height classes where at least 50% of the individuals' available canopy was used was noticeably higher, especially from natural damage (19.48%) in Sparse Woodland on Sand (Table 4).

5. Discussion

While utilisation of trees by elephant is easily observed and has previously been informedfor Tembe (Guldemond & van Aarde, 2007), medium and small mammalsbrowsing, less easily observed, had not yet been considered. Results indicate that utilisationproved quite intense, although this should not be surprising. A long term study in Zululand in Ithala Game reserve (Ithala) observed that browsers and "natural damage" generate three times more impact than elephants, and that the combined impact, over a period of eight years changed both woody species composition and population structures (Wiseman et al., 2004). In all Tembe's Woodlands and to a lesser extent in Sand Forest, small and medium browsers utilised a sizeable portion of available height classes (generally 1/3 to 2/3 of height classes available). Considering these animals' size, the height classes utilised are the smaller ones, which are important for recruitment, such as seedlings and saplings. In Ithala, the combination of elephants and browsers pressure was such that plant species composition changed from species with climax state lifecycle traits (long lived, low recruitment) to more pioneer like species (high recruitment, shorter lifespans) and also promoted the recruitment of less desirable browse species (Wiseman et al., 2004). Other studies have shown that small mammals herbivory is usually not a limiting factor on its own, although it slows regeneration in cases of high densities (Barnes, 2001; Walpole et al., 2004; Western & Maitumo, 2004; Western, 2006). In Kenya's Masaai Mara National Reserve, 73% of woody species were utilised by small browsers, which changed species composition and abundance andfacilitated some invasive species (Walpole et al., 2004). In Botswana, small to medium browsers were considered responsible for changing vegetation morphology (Styles & Skinner, 2001). The overall utilisation levels by small and medium browsers in Tembe are approaching Kenyan values or even exceeding them in some vegetation types. Therefore, the risk that further small and medium browser population increases would lead to homogenisation of some vegetation units cannot be discarded. Utilisation of woodlands in Tembe already showed that elephants homogenised Open Woodlands, with a risk of forcing succession towards Sparse Woodlands (Guldemond & Van Aarde, 2007). We consider that elephant utilisation assisted by the heavy smaller browser utilisation in Tembe's woodland conditions seenhere is likely to push succession from dense woodlands to sparse ones. This is likely to progressin much the same ways as happenedin East Africa (Western & Maitumo, 2004; Birkett & Stevens-Wood, 2005) unless a management action is taken to limit herbivore populations.

The question of mark accumulation appears quite straightforward. In an unfenced situation, natural migratory movements of animal populations, following rainfall and food availability afford plants time to recover after utilisation events (van Aarde & Jackson, 2007; Wiseman et al., 2004). Likewise, low animal population numbers make repeated use a rare event, and not the norm. However, in Tembe, fences restrict migratory movements, and the size of the park does not allow simulated migratory movements (van Aarde & Jackson, 2007), therefore, repeated utilisation events appear unsurprising unless it exceeds what can be considered as normal considering woody decay rates (Sheil & Salim, 2004). Medium and small browsers utilise many height classes but their actions appear to leave little durable signs of utilisation, which is logical as they tend to defoliate rather than break. Comparatively, elephants, which usually defoliate by breaking branches, stems, or even uprooting whole trees (Wiseman et al., 2004; O'Connor et al., 2007) leave a long-lasting imprint on vegetation that would be observed for long periods. Natural damage marks accumulation is, however, a puzzle.

"Natural damage" intensity was generally a concern. This includes all natural phenomenon that can potentially "damage" or even kill trees (wind, fire, lightning, moisture conditions, drought, light conditions, disease, etc.), which are part of a natural system under normal conditions or subsequent to catastrophic events (Lindenmayer et al., 2006). In Tembe's forests and woodlands, natural damage affects a considerable number of species (27 to 58% of species in woodlands and 40 to 85% of species in Sand Forest) in an obvious manner (32 to 41% of height classes available in woodlands and 28 to 59% of height classes available in Sand Forest). This aspect was also established in Ithalawhere natural damage was considered to represent 37% of all utilisation events (Wiseman et al., 2004). Of concern here is that marks appear to also accumulate over time (Tables 1, 2, 3, 4) at a rate that must exceed what it should be for a natural system in the absence of a natural disturbance in both Sand Forest and woodlands. While it is acknowledged that marks observation is influenced by wood decay rate (Sheil & Salim, 2004) and that in slow decay areas, marks can be observed for much longer periods and therefore falsely give impression that marks accumulate, in Short Sand Forest, 85% of woody species are affected by "natural damage" and 55.00% of available height classes displayed evidence of canopy removal (Table 2). This appears extremely high for a vegetation type where fire hardly occurs and where wind should have not much effect because of large tall trees absence (Izidine et al., 2003; Matthews, 2006). As the plants abundance and Short Sand Forest vegetation height make it particularly suited to elephant utilisation, akin to thickets in Addo Elephant Park (Lombard et al., 2001),in the present study, considering utilisation levels, we hypothesise that "natural damage" marks observed may be by default promoted by elephant browsing in the vegetation type.

6. Conclusion

In conclusion, as demonstrated for other areas, small and medium mammalian browsers appear to have a considerable influence on all vegetation types of Tembe. Although this impact appears to rarely last for more than a year in terms of canopy volume removal (defoliation), observed levels of use are close to levels measured elsewhere that were followed by a retrogression sequence with significant associated vegetation changes. As elephant impact is also considered significant in Tembe (Gaugris & van Rooyen, 2011; Gaugris et al., 2012), a clear danger exists of forcing Tembe's vegetation into a phase of rapid changes. Subsequent to the present study field work in 2004, larger carnivores (Lions and wild dogs) were reintroduced in Tembe, which should be a key step to restore natural limits to herbivore populations' growth. A follow up study to evaluate whether utilisation decreased as a result would be a worthwhile effort to consider the effectiveness of higher order predators' reintroduction to control herbivore impact on vegetation state and vegetation dynamics.

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Notes

Note 1. Hypothesis based on combination of known group count, total area count and informed guess.

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