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ScienceDirect
South African Journal of Botany xx (2009) xxx–xxx
SOUTH AFRICAN JOURNAL OF BOTANY
www.elsevier.com/locate/sajb

Woody vegetation structure in conserved versus communal land in a biodiversity hotspot: A case study in Maputaland, South Africa

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Received 7 April 2009; received in revised form 15 November 2009; accepted 16 November 2009

Abstract

This study evaluated the effects of humans and herbivores on woody vegetation structure in the woodlands and forests of Maputaland. The woody vegetation structure of plant communities at three sites within a similar environment but under different utilisation regimes since the early 1990s was evaluated by means of a stem diameter and tree height class analysis. The effects of human utilisation were evaluated on the land of the rural Manqakulane community; herbivore utilisation was evaluated in the Tembe Elephant Park; and because of the low levels of utilisation since 1992 the vegetation in the Tshanini Community Conservation Area was used as a benchmark for the comparisons. In both woodlands and sand forests, utilisation regime resulted in changes in stem diameter size class distributions, although the height structure remained unchanged. In communal land human-associated disturbance promoted the presence of small woody plants. In general, conserved land under animal utilisation, had the least small diameter woody plants, but most of the large trees, whereas in the absence of utilisation intermediate densities of small diameter woody plants were found but low densities of large trees. This study presents the first quantification of significant changes in the woody vegetation structure in Maputaland due to human utilisation, herbivore utilisation, or lack of utilisation. It also provides a timeframe within which land use can cause significant changes in vegetation structure.

Keywords: Animal utilisation; Diameter class distribution; Height class distribution; Herbivory; Human utilisation; Sand forest; Woodlands

1. Introduction

Disturbance of natural ecosystems by people and herbivores are at the centre of many conservation debates. Yet, vegetation, animals and people have co-existed for millennia, and are interdependent in terms of maintaining biodiversity and ecosystem services (Ickowitz, 2006; O'Connor et al., 2007). Vegetation in Africa is controlled by a fine balance of disturbances in the form of animal utilisation (O'Connor et al., 2007), climate (Lindenmayer et al., 2006), fire (Bond and Keeley, 2005) and people (Ndangalasi et al., 2007). The balance between these elements varies continuously in time and space and represents the basis for the observed biodiversity (Gillson et al., 2003). While all elements are needed to maintain a high level of heterogeneity conducive to high levels of biodiversity (Perrings and Lovett, 1999), the dominance of one or several of these elements can have the opposite effect (Western and Maitumo, 2004), whereas insufficient disturbance also reduces biodiversity through homogenisation (Lindenmayer and Noss, 2006).

Rural people in Africa, as in Maputaland, use trees mainly as sources of firewood and building material and will deforest areas for cultivation. They also deplete the wildlife (Laurance et al., 2006), which can further disturb the natural vegetation dynamics (Babweteera et al., 2007). The effect of people on vegetation through shifting cultivation is temporary, as vegetation communities tend to recover after use, provided the soil seed bank has remained intact (Ickowitz, 2006). High levels of human utilisation may, however, lead to general vegetation change, degradation and fragmentation of ecosystems, or even extirpation of species (Schmidt-Soltau, 2003; Ndangalasi et al., 2007). While animals

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doi:10.1016/j.sajb.2009.11.007

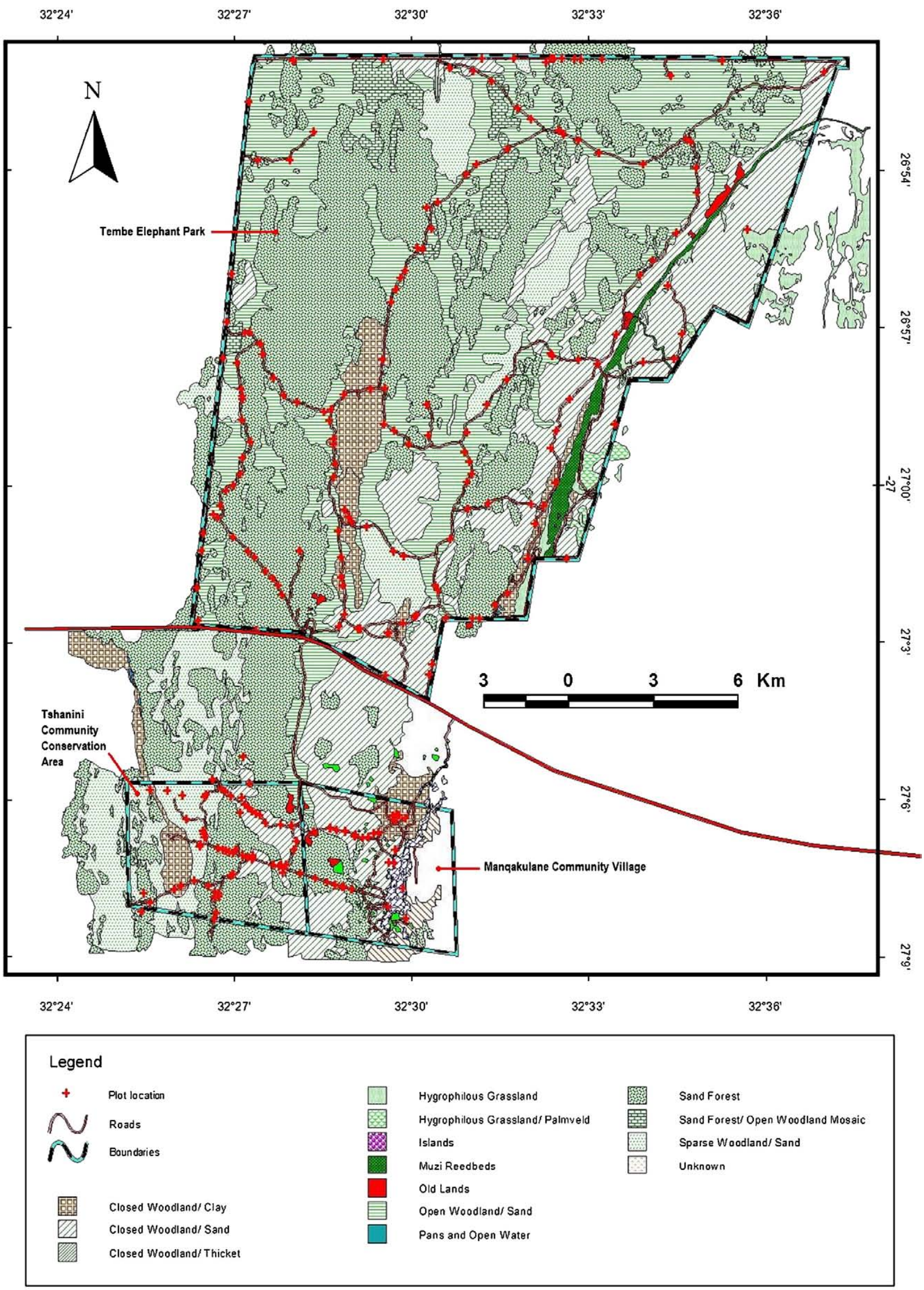

Fig. 1. The study area in Maputaland, South Africa, with Tembe Elephant Park, Tshanini Community Conservation Area and the Manqakulane Village.

Please cite this article as: Gaugris, J.Y., Van Rooyen, M.W., Woody vegetation structure in conserved versus communal land in a biodiversity hotspot: A case study in Maputaland, South Africa, S. Afr. J. Bot. (2009), doi:10.1016/j.sajb.2009.11.007

are usually the object of conservation measures, the effects of animal densities in confined areas can be detrimental to vegetation in similar ways (Western and Maitumo, 2004).

For conservation to be efficient, reserve networks including large ecological reserves work best. However, due to the limited size of the world's conservation areas and social acceptance of conservation concepts by local people (West and Brockington, 2006), it is obvious that much, if not the majority of conservation efforts, have to be devoted to non-conserved areas (Smith et al., 2006). The latter is especially important to preserve a variety of natural habitats under anthropogenic disturbance regimes, to retain landscape heterogeneity, to regain biodiversity in areas where disturbance led to habitat destruction, and also to improve resource use (Lindenmayer et al., 2006; Naughton-Treves et al., 2007).

It is therefore important to firstly establish the quality of natural ecosystems and secondly to quantify differences at both landscape and local level, between conserved and non-conserved areas (Lindenmayer et al., 2006). Understanding natural ecosystem dynamics, and the disturbance cycles that govern them, will allow for more informed management decisions to be taken.

The aims of this study were therefore: (a) to determine the woody vegetation structure of plant communities at three sites within a similar environment but under different disturbance regimes since the early 1990s, and (b) to relate the differences in the vegetation to the impacts of the disturbance agents operating at the three sites. To quantify the differences in the vegetation structure between the sites the stem diameter size class distribution as well as height size class distribution were compared between the sites. Because long-term studies of the area are not available, it is hoped that studying similar vegetation types under different utilisation regimes within one geographical region will allow us to understand the natural ecosystem dynamics at the different sites.

2. Study area

Maputaland lies in the Maputaland–Pondoland–Albany biodiversity hotspot. It harbours a wide variety of plant and animal species, many of which are endemic, rare or endangered. The focus area is located between the Muzi Swamp on the eastern side and the Pongola River on the western side (Fig. 1). The geology of the Maputaland plain, where the three study sites are located, is homogenous (Matthews et al., 2001; Matthews, 2006). The topography, water drainage, soil structure and depth of the area are remarkably similar and consistent along the north–south and east–west axes (Matthews et al., 2001; Matthews, 2006).

The study area is characterised by a sandy plain interspersed with north–south trending ancient littoral dune cordons covered by a mosaic of open to closed woodland, with patches of sand forest. Maputaland's woodlands and sand forests show high levels of similarity in terms of species composition (Matthews et al., 2001; Gaugris et al., 2004).

The region lies in a transition zone between the tropics and subtropics. Summers are hot, wet, and humid, while winters are cool to warm and dry. The mean annual rainfall for the region, as measured at the Sihangwane weather station at the entrance of the Tembe Elephant Park, is 700 mm (Gaugris, 2008).

Tembe Elephant Park (Tembe) was proclaimed in 1983 to preserve the rare sand forest vegetation and the remaining elephant population (Matthews, 2006). The park was fully fenced in 1989, thus preventing natural animal migration along the Maputaland coastal plain (Matthews, 2006; McCracken, 2008). Wildlife numbers subsequently increased (Table 1) and there is now concern that the park's vegetation may be compromised. Tembe protects the largest portion of sand forest vegetation in South Africa (Smith et al., 2006). The region surrounding the park has a low agricultural potential, but is highly suitable for conservation (Eeley et al., 2001). This land is threatened by the regional human population growth and the pressure it exerts on natural resources, especially wood as a source of fuel or building material (Gaugris et al., 2007). Although, at present, human population growth and its effects appear limited to areas along the road network, it is anticipated to lead to the use of increasingly vast sections of land, thus endangering natural ecological processes in the region (Brookes, 2004).

The community of Manqakulane occupies 5000 ha situated 6 km south of Tembe. In 2000, this community set aside half of their tribal land as a conservation area, the Tshanini Community Conservation Area (Tshanini). This tract of land can be considered as the most representative "pristine" fragment of original vegetation outside a conservation area in this part of Maputaland (Gaugris et al., 2004; Gaugris and Van Rooyen, 2008). Resource utilisation in Tshanini has been low to insignificant since 1992, when the people relocated their village from Tshanini's eastern boundary to its current position along the Muzi Swamp (Gaugris, 2004). While this move released Tshanini

Table 1
Changes in animal numbers in the Tembe Elephant Park between 2000 and 2005 (Matthews, 2005).

Species	Scientific name	2000 census	2005 census
African elephant	*Loxodonta africana*	130	>200 (266) [a]
White rhinoceros [b]	*Ceratotherium simum*	35	43
Black rhinoceros [b]	*Diceros bicornis*	22	20
Giraffe [b]	*Giraffa camelopardalis*	100	131
Hippopotamus	*Hippopotamus amphibius*	14	20
Plain's zebra [b]	*Equus quagga*	200	176
Eland [b]	*Tragelaphus oryx*	40	0
Buffalo	*Syncerus caffer*	60	100
Kudu [b]	*Tragelaphus strepsiceros*	290	532
Blue wildebeest [b]	*Connochaetes taurinus*	130	434
Waterbuck [b]	*Kobus ellipsiprymnus*	360	419
Impala [b]	*Aepyceros melampus*	600	694
Nyala	*Tragelaphus angasii*	300	1800
Bushbuck	*Tragelaphus scriptus*	Unknown	40
Reedbuck	*Redunca arundinum*	880	268
Grey duiker	*Sylvicapra grimmia*	Unknown	200
Red duiker	*Cephalophus natalensis*	Unknown	400
Suni	*Neotragus moschatus*	Unknown	>500
Warthog	*Phacochoerus africanus*	260	300
Bush pig	*Potamochoerus porcus*	Unknown	Unknown

[a] Combination of known group count, total area count and informed guess, the number in brackets indicates the maximum number based on growth as calculated in 2002.

[b] Indicates species that were re-established in the area.

from the use of natural resources by people, it transferred considerable pressure on the habitat surrounding the new village as people cleared land for homesteads and fields (Peteers, 2005).

In this study Tshanini was used as a benchmark because of the low levels of utilisation since 1992. In general, people in northern Maputaland rarely travel further than 3 km to harvest natural resources (Boudreau et al., 2005; Gaugris et al., 2007). Therefore the effect of man on the woody vegetation was evaluated within the village area of the Manqakulane community, which was occupied by 784 permanent residents at the time of the study. The effect of herbivores, on woody vegetation structure was evaluated in Tembe.

3. Material and methods

Eleven vegetation units were sampled within the three study areas: these included two *Afzelia quanzensis* communities; three Sand Forest communities; three Closed Woodland communities; two Open Woodland communities and one Sparse Woodland community. The classification of the communities follows Matthews et al. (2001), Gaugris et al. (2004) and Gaugris and Van Rooyen (2008).

Rectangular plots of varying length (15–100 m) and width (4–10 m) were used to obtain size class distribution and herbivore utilisation data of the woody species. A total of 254 plots were surveyed, of which 48 were in Tshanini (2420 ha), 42 in Manqakulane (2500 ha), and the remainder in Tembe (30 000 ha) (Fig. 1). Plot length and width in the Sand Forest and Closed Woodland were adjusted based on vegetation density in order to survey a minimum of 150 plants per plot. In the Open and Sparse Woodland the maximum plot size was used. All woody plants (i.e. plants with an erect to scrambling growth form and with a ligneous trunk, thus including lianas) ≥ 0.4 m height and ≥ 1.0 cm stem diameter, encountered in the plots, were identified to the species and measured, while those of dimensions below these cut-offs were only measured along one half of the plot area. Stem diameters of larger trees were measured at 100 cm above ground, while for smaller plants the measurements were taken above the basal swelling. For multi-stemmed individuals, while the plant was recorded as multi-stemmed, only the largest stem diameter was recorded. Tree height was either directly measured by using gradated plastic rods with a total length of 6 m, or estimated by using these rods for higher trees.

The stem diameter measurements were classified into 12 classes of varying diameter width for the size class distribution (SCD) analysis (<1 cm, 1 to <2 cm, 2 to <4 cm, 4 to <6 cm, 6 to <10 cm, 10 to <14 cm, 14 to <20 cm, 20 to <26 cm, 26 to <34 cm, 34 to <42 cm, 42 to <52 cm, and ≥ 52 cm). The tree height measurements were classified into eight classes of varying height intervals (<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, and ≥ 12 m). Data of all individuals for all replicate plots of the same vegetation type were pooled for each site. The number of individuals in each size or height class was divided by the width of the class to obtain a mean number of individuals per unit of measurement for each

Table 2
Analysis of height class distribution by vegetation unit at three sites indicating the year of sampling, number of individuals sampled, the slope, *Y*-axis intercept, r^2-value and significance of the regression and mean height.

Vegetation unit	Site	Year of sample	Number of individuals sampled	Regression analysis				Mean
				Slope	Intercept	r^2	Significance	Height (m) H_1/H_2 [a]
Afzelia quanzensis clumps	TEP	2004	96	−0.48	5.77	0.03	–	1.02/1.02
Afzelia quanzensis forest	TEP	2004	201	−1.52	8.85	0.69	*	0.73/0.76
Short Sand Forest	TCCA	2001	2411	−2.76	10.53	0.62	*	0.92/2.55
Short Sand Forest	TEP	2004	896	−1.67	8.94	0.54	*	1.47/2.44
Tall Sand Forest	TCCA	2001	2883	−1.69	8.15	0.52	*	1.87/3.08
Tall Sand Forest	TEP	2004	4632	−1.53	8.70	0.57	*	1.16/2.56
Mature Sand Forest	TEP	2004	1779	−0.82	8.26	0.21	–	1.50/2.62
Closed Wdld Thicket	TCCA	2001	4126	−1.46	6.72	0.27	–	2.58/2.64
Closed Wdld Thicket	TEP	2004	117	−1.11	6.01	0.12	–	0.98/0.98
Closed Wdld Thicket	MRC	2004	1170	−4.08	12.84	0.93	**	0.22/0.35
Closed Wdld on clay	TEP	2004	2015	−2.11	8.56	0.70	**	0.97/1.01
Closed Wdld on clay	MRC	2004	186	−2.27	9.58	0.83	**	0.60/0.63
Closed Wdld on Sand	TCCA	2001	3915	−1.98	7.94	0.53	*	2.08/2.36
Closed Wdld on Sand	TEP	2004	1999	−1.68	8.06	0.43	*	1.22/1.23
Closed Wdld on Sand	MRC	2004	819	−2.44	9.45	0.86	**	0.79/0.87
Open Wdld on Sand	TCCA	2001	4663	−2.57	7.94	0.71	**	1.57/1.96
Open Wdld on Sand	TEP	2004	4202	−1.81	7.30	0.51	*	0.87/1.23
Open Wdld on Sand	MRC	2004	149	−2.29	7.82	0.26	–	0.52/0.52
Open Wdld on Abandoned Fields	MRC	2004	995	−2.55	8.71	0.89	**	0.63/0.68
Sparse Wdld on Sand	TEP	2004	654	−2.76	8.46	0.75	**	0.57/0.57
Sparse Wdld on Sand	MRC	2004	176	−2.11	6.56	0.31	–	0.50/0.50

TCCA = Tshanini Community Conservation Area; TEP = Tembe Elephant Park; MRC = Manqakulane Rural Community; Wdld = Woodland; ** = Highly significant ($p<0.01$); * = Significant ($p<0.05$)*t*; – = not significant ($p>0.05$).

[a] H_1 represents the mean height when all height classes are considered, H_2 represents the mean height when the first two (seedlings and saplings) size classes have been removed from the sample.

Table 3
The height class distribution (HCD) compared within vegetation types across the three study sites, Maputaland, South Africa.

Vegetation types	Sites compared	Slope comparison		Intercept comparison		Final outcome
		p-value	Pooled slope	p-value	Pooled slope	
Short Sand Forest	TEP/TCCA	0.34	−2.21	0.91	9.73	Similar
Tall Sand Forest	TEP/TCCA	0.86	−1.61	0.33	8.43	Similar
Closed Woodland Thicket	TEP/TCCA/MRC	0.08	−2.21	0.10	8.52	Similar
Closed Woodland on Clay	TEP/MRC	0.82	−2.19	0.22	9.07	Similar
Closed Woodland on Sand	TEP/TCCA/MRC	0.73	−2.03	0.59	8.48	Similar
Open Woodland on Sand	TEP/TCCA/MRC	0.88	−2.22	0.95	7.69	Similar
Sparse Woodland on Sand	TEP/MRC	0.66	−2.44	0.45	7.51	Similar

ns = not statistically significant.

class (Condit et al., 1998) before calculating the density (D_i) per size and height class per vegetation unit in each site. The class midpoint (M_i) for each diameter and height class was set as the halfway measurement for each size class. Natural logarithmic transformations of the type $\ln(D_i+1)$ and $\ln(M_i+1)$ were performed before calculating least square linear regressions for each vegetation unit (Condit et al., 1998; Lykke, 1998; Niklas et al., 2003; Gaugris and Van Rooyen, 2007). The double logarithmic transformation was used as this generally best represents the shape of size class distribution data (Condit et al., 1998). Moreover, because sample plot areas were small (<1 ha), it was assumed that our dataset would not depart from log–log linearity (see Niklas et al., 2003) nor be biased by habitat heterogeneity and species diversity from the sample of the vegetation community (see Niklas et al., 2003).

The mean diameter of all individuals per vegetation unit was calculated as follows:

$$Mean = \sum(D_i \times M_i)/\sum D_i,$$

where i ranges from 1 to 12, D_i is the mean density per size class, and M_i is the class midpoint per size class. This value is referred to as the centroid by Niklas et al. (2003). Mean height of all individuals in each vegetation unit was similarly calculated. The mean diameter or height of a community will increase if the number of large individuals in a community increases or the number of small individuals decreases, which usually occurs when a community develops into more mature stages. Mean diameter and mean height were calculated twice, the first set of calculations were based on the full data set (labelled as D_1 and H_1), while the second calculation was performed without the first two size classes (labelled as D_2 and H_2), thereby removing the potential bias from seedlings and saplings on the mean, but also providing a further indication of where the bulk of individuals lie. If the two calculations provide similar results, it is clear that the bulk of the population is towards the smaller size classes. An ANOVA was used to compare the mean diameters and heights of the various vegetation groups without the effects of seedlings and saplings (on D_2 and H_2).

An analysis of covariance (ANCOVA) F-test was used to compare the regression slopes and intercepts between comparable vegetation units across sites using GraphPad PRISM 4 (GraphPad Software, San Diego California USA, www.graphpad.com). This software compares regression slopes, and should there be no significant difference in the slopes, it proceeds to compare the Y-axis intercepts. If no significant difference is found, a pooled slope and Y-axis intercept is calculated to present the combined data.

It should be noted that inferring vegetation dynamics from size class distributions from single surveys is not recommended (Condit et al., 1998; Boudreau and Lawes, 2005). While we acknowledge the shortcomings of such studies, we feel that by using three sites that have been under different regimes over a similar period of time, we have the possibility to evaluate structural changes caused by different disturbance agents and infer the consequences on the dynamics of the vegetation in Maputaland.

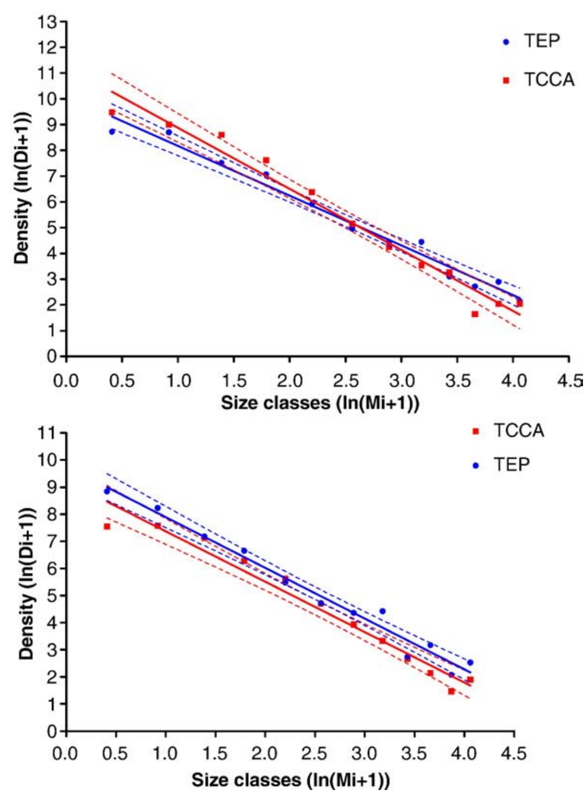

Fig. 2. A linear regression on stem diameter size classes in the Sand Forest communities. (a) Short Sand Forest and (b) Tall Sand Forest in Tembe Elephant Park (TEP) and Tshanini Community Conservation Area (TCCA). The dotted lines represent the 95% confidence intervals.

4. Results

Surveys were conducted in all vegetation units but because not all units occurred on all sites, only seven of the 11 units could be compared across sites. In the case of the height class distribution (HCD) analysis no significant differences were found between any of the sites regarding the HCD regressions (Tables 2 and 3).

For the Short Sand Forest there were more small trees and fewer large trees in Tshanini than in Tembe (Fig. 2a) resulting in a significantly steeper slope in Tshanini than in Tembe (Tables 4 and 5). Mean stem diameter in the Short Sand Forest in Tshanini and Tembe was 5.54 cm and 5.81 cm respectively (D_2), whereas the corresponding mean height values were 2.55 m and 2.44 m respectively (H_2).

For the Tall Sand Forest the SCD analysis showed a greater abundance of trees of all sizes in Tembe compared to Tshanini (Fig. 2b). This was reflected in the significantly higher *Y*-axis intercept for Tembe than for Tshanini but similar slope values (Tables 4 and 5). The mean stem diameter in Tshanini was lower than in Tembe (4.38 cm as against 6.24 cm), whereas the mean height showed the opposite trend (3.08 m as against 2.56 m). These results showed a greater contribution of large diameter trees in Tembe, while there was a greater contribution from tall trees in Tshanini.

Diameter size class distributions in the Closed Woodland Thickets of Tembe and Tshanini were similar, but the high abundance of small trees in Manqakulane resulted in a significantly steeper slope than that of the other two sites (Fig. 3a; Tables 4 and 5). Mean stem diameters in the Closed Woodland Thicket in Tshanini, Tembe and Manqakulane were 4.79 cm, 8.35 cm and 5.75 cm respectively, which indicated the most of large individuals in Tembe. The mean plant heights in this community were 2.64 m, 0.98 m and 0.35 m for Tshanini, Tembe and Manqakulane respectively indicating taller trees in Tshanini.

No significant differences were detected in the stem diameter distributions of the Closed Woodland on Clay between Manqakulane and Tembe (Tables 4 and 5) with mean stem diameter and mean plant height values also quite similar.

The Closed Woodland on Sand in Manqakulane had more small trees than in Tembe and Tshanini and this was reflected in the significantly higher *Y*-axis intercept (Fig. 3b; Tables 4 and 5). The mean stem diameter in this community however, indicated that woody plants in Tshanini were the smallest (4.88 cm in Tshanini as against 5.67 cm for Manqakulane and 6.57 cm for Tembe). However, mean plant height indicated that Tshanini had more tall trees (mean of 2.36 m against means of 0.87 m and 1.23 m for Manqakulane and Tembe respectively) in this vegetation unit than the other two sites (Tables 4 and 5).

The SCD analysis for Open Woodland on Sand showed differences between all sites (Tables 4 and 5). The overabundance of small plants and absence of woody plants in the three largest size classes in Manqakulane was reflected in the steep

Table 4
Analysis of stem diameter class distribution by vegetation unit at three sites indicating the year of sampling, number of individuals sampled, the slope, *Y*-axis intercept, r^2-value and significance of the regression and centroid locations.

Vegetation type	Site	Year of sample	Number of individuals sampled	Regression analysis				Mean stem
				Slope	Intercept	r^2	Significance	D^a (cm) D_1/D_2[b]
Afzelia quanzensis clumps	TEP	2004	96	−1.77	8.59	0.89	**	0.91/7.52
Afzelia quanzensis forest	TEP	2004	201	−1.55	8.49	0.84	**	1.14/8.49
Short Sand Forest	TCCA	2001	2411	−2.37	11.24	0.97	**	2.68/5.54
Short Sand Forest	TEP	2004	896	−1.93	10.11	0.98	**	2.14/5.81
Tall Sand Forest	TCCA	2001	2883	−1.86	9.21	0.97	**	1.89/4.38
Tall Sand Forest	TEP	2004	4632	−1.87	9.77	0.98	**	1.92/6.24
Mature Sand Forest	TEP	2004	1779	−1.62	10.02	0.95	**	3.06/7.29
Closed Wdld Thicket	TCCA	2001	4126	−2.13	9.54	0.96	**	2.12/4.79
Closed Wdld Thicket	TEP	2004	117	−1.87	8.73	0.88	**	1.88/8.35
Closed Wdld Thicket	MRC	2004	1170	−2.87	12.28	0.92	**	0.75/5.75
Closed Wdld on clay	TEP	2004	2015	−1.87	8.99	0.98	**	1.67/6.65
Closed Wdld on clay	MRC	2004	186	−2.17	9.80	0.75	**	1.05/7.71
Closed Wdld on Sand	TCCA	2001	3915	−2.09	9.31	0.98	**	1.90/4.88
Closed Wdld on Sand	TEP	2004	1999	−1.90	9.28	0.99	**	1.74/6.57
Closed Wdld on Sand	MRC	2004	819	−2.11	9.77	0.96	**	1.30/5.67
Open Wdld on Sand	TCCA	2001	4663	−2.09	8.59	0.98	**	1.84/4.59
Open Wdld on Sand	TEP	2004	4202	−1.69	7.94	0.94	**	1.57/8.20
Open Wdld on Sand	MRC	2004	149	−3.02	11.38	0.93	**	0.90/6.09
Open Wdld on Abandoned Fields	MRC	2004	995	−2.16	8.91	0.93	**	1.16/5.28
Sparse Wdld on Sand	TEP	2004	654	−2.26	8.82	0.89	**	1.01/5.36
Sparse Wdld on Sand	MRC	2004	176	−2.18	8.88	0.86	**	0.95/6.63

TCCA = Tshanini Community Conservation Area; TEP = Tembe Elephant Park; MRC = Manqakulane Rural Community; Wdld = Woodland; ** = Highly significant ($p<0.01$); * = Significant ($p<0.05$)*t*; – = not significant ($p>0.05$).

[a] D = Diameter.

[b] D_1 represents the mean stem diameter when all size classed are considered, D_2 represents the mean stem diameter when the first two size classes (seedlings and saplings) are removed from the sample.

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Table 5
The stem diameter class distribution (SCD) compared within vegetation types across the three study sites, Maputaland, South Africa.

Vegetation type	Sites compared	Slope comparison		Intercept comparison		Final outcome
		p-value	Pooled slope	*p*-value	Pooled slope	
Short Sand Forest	TEP/TCCA	0.01	–	–	–	Different
Tall Sand Forest	TEP/TCCA	0.92	−1.86	<0.01	–	Different
Closed Woodland Thicket	TEP/TCCA/MRC	<0.01	–	–	–	Different
	TEP/TCCA	0.34	−2.01	0.60	9.14	Similar
	TCCA/MRC	0.02	–	–	–	Different
	TEP/MRC	0.01	–	–	–	Different
Closed Woodland on clay	TEP/MRC	0.47	−2.02	0.92	9.40	Similar
Closed Woodland on Sand	TEP/TCCA/MRC	0.31	−2.04	0.03	–	Different
	TEP/TCCA	0.31	−2.00	0.01	–	Different
	TEP/MRC	0.18	−2.01	0.79	9.54	Similar
	TCCA/MRC	0.87	−2.04	0.05		Different
Open Woodland on Sand	TEP/TCCA/MRC	<0.01	–	–	–	Different
	TEP/TCCA	0.03	–	–	–	Different
	TEP/MRC	<0.01	–	–	–	Different
	TCCA/MRC	<0.01	–	–	–	Different
Sparse Woodland on Sand	TEP/MRC	0.84	−2.22	0.55	8.86	Similar

** = Highly significant ($p<0.01$); * = Significant ($p<0.05$)*t*; – = not significant ($p>0.05$).

SCD slope and high *Y*-axis intercept (Fig. 4). Mean stem diameter was 4.59 cm, 8.20 cm and 6.09 cm, and mean tree height of 1.96 m, 1.23 m and 0.52 m for Tshanini, Tembe and Manqakulane respectively. Here, Manqakulane had the most of short trees, Tembe the most large diameter ones, but Tshanini had more tall trees.

For the Sparse Woodland on Sand, no differences between Tembe and Manqakulane in either SCD or HCD analyses could be demonstrated (Tables 3 and 5).

An ANOVA calculated on the mean diameter (D_2) ($F=9.58$, $P=0.001$, $df=2/18$) and height (H_2) ($F=14.30$, $P<0.001$, $df=2/18$) without the interference of seedling and sapling stages showed significant differences between the three sites in that respect. Tshanini has a higher mean height than Tembe and Manqakulane, which indicates and abundance of taller trees. The mean diameter of trees in Tembe is greater than that of Manqakulane and Tshanini.

5. Discussion

Despite a remarkable floristic similarity between Tshanini and Tembe (Gaugris et al., 2004; Gaugris and Van Rooyen, 2008) the

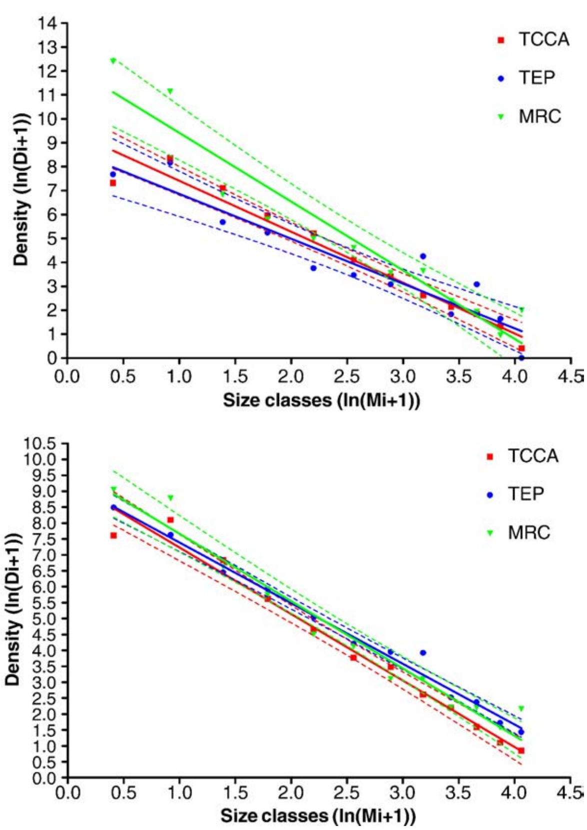

Fig. 3. A linear regression on stem diameter size classes in the closed Woodland communities. (a) Closed Woodland Thicket and (b) Closed Woodland on Sand in Tembe Elephant Park (TEP), Tshanini Community Conservation Area (TCCA) and the Manqakulane village zone area (MRC). The dotted lines represent the 95% confidence intervals.

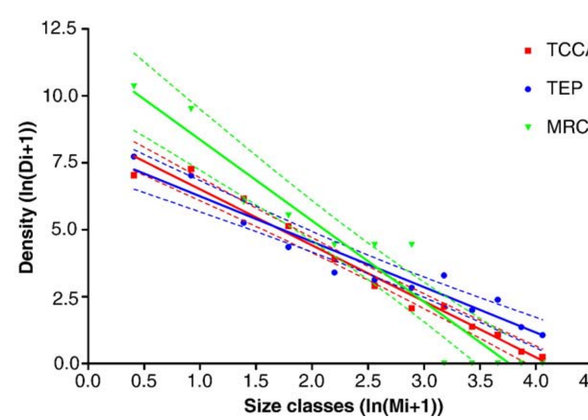

Fig. 4. A linear regression on stem diameter size classes in the Open Woodland on Sand in Tembe Elephant Park (TEP), Tshanini Community Conservation Area (TCCA) and the Manqakulane village zone area (MRC). The dotted lines represent the 95% confidence intervals.

Please cite this article as: Gaugris, J.Y., Van Rooyen, M.W., Woody vegetation structure in conserved versus communal land in a biodiversity hotspot: A case study in Maputaland, South Africa, S. Afr. J. Bot. (2009), doi:10.1016/j.sajb.2009.11.007

size class structure of the vegetation units in Tshanini was markedly different from equivalent units in Tembe and Manqakulane. From five possible comparisons between Tembe and Tshanini, a similarity was observed only for the Closed Woodland Thicket. The woodlands of Tembe and Manqakulane were similar in two out of four comparisons (Closed Woodland on Sand and Sparse Woodland on Sand) while all three woodland types comparable between Tshanini and Manqakulane differed.

Such heterogeneity among sites of similar vegetation types is not unknown, and is often linked to different modes of utilisation such as the presence/absence of animals, especially elephants (Babweteera et al., 2007), or human traditional and commercial activities (Fashing and Mwangi Gathua, 2004). To explain the differences in the vegetation between the three sites, the main drivers of vegetation dynamics, i.e. climate, fire, herbivory and people have to be considered. In our study area, the spatial proximity of the three sites most likely rules out climatic factors as a driver. Weather station data are considered representative of an area within a radius of 20 km (Yeh et al., 2000), and because the study area stretches across 33 km from north to south the entire study area would be encompassed within one such zone. Therefore the most likely answer lies in the influence of fire, herbivores or man. Edaphic factors were ruled out due to the remarkable similarity in soils and their water retention abilities throughout the area (Matthews et al., 2001).

African savanna ecosystems are classified as non-equilibrium systems (Sankaran et al., 2005), which are in need of fire and herbivory to maintain a tree-grass balance. Fire is a semi-controlled, relatively infrequent element in the woodlands of Tembe (Matthews, 2006), but a relatively frequent event in Manqakulane and Tshanini, where it is used to stimulate grass re-growth for cattle grazing (Gaugris et al., 2004). Fire affects the vegetation primarily in the 0–3 m height interval above ground level (Levick et al., 2009) and repeated fire can maintain the woody vegetation in a juvenile state by top-killing seedlings and sapling (Higgins et al., 2000, 2007; Bond et al., 2003). In their study Levick et al. (2009) found that herbivory exerted a greater influence on vegetation structure than fire and that the effects could be mainly attributed to megaherbivores. The effects of grazers depend on their density with woody cover being depressed at low grazer biomass, but when a threshold grazer biomass is exceeded woody growth is favoured (Sankaran et al., 2005, 2008; Ickowitz, 2006). In the presence of wild browsers, the tree component in African woodlands is generally contained and the tree-grass balance is maintained. However, when the animal component exceeds the density that the system can sustain, the combination of fire and high animal density can transform closed woodland into open woodland (Western and Maitumo, 2004). In our case study, the mean annual rainfall is consistent with canopy closure by the tree component being possible, while our results also appear consistent with the presence/absence of herbivores and human utilisation being the main drivers for vegetation changes rather than fire. In Tshanini the mean height of the woodland vegetation ranges from just under 1.96 m (H_2 for Open Woodland) to 2.64 m (H_2 for Closed Woodland Thicket), which is significantly higher than in Tembe or Manqakulane, consistent with a wooded landscape heading towards canopy closure (Sankaran et al., 2005) and on the upper range of the “fire trap” (Bond and Keeley, 2005; Karlowski, 2006). Moreover, the absence of herbivores to graze or browse is no longer buffering the system from moving towards canopy closure (see Sankaran et al., 2005).

Vegetation structure in this part of Maputaland could be grouped into four forms: Case 1 represented a dearth of plants with both small and large diameters and was found only in Tshanini where it occurred in all woodland vegetation types as well as in the Tall Sand Forest, but not in the Short Sand Forest. In the past 15 years the vegetation in Tshanini has been less disturbed by either herbivores or man than those of Manqakulane and Tembe (Gaugris, 2004). In general, the communities in Tshanini were differentiated from their counterparts at the other sites by having taller plants with smaller stem diameters. The latter is quite typical of increased competition for light (Babaasa et al., 2004) under a closed canopy, where species compete for light by growing tall fast (Paul et al., 2004). While light availability could explain such a phenomenon in forest, thicket or closed woodland, this would not be the case for the open woodland. Niklas et al. (2003) contend that mean stem diameter of a community indicates community age and can be used to highlight disturbance. One explanation could therefore be that the vegetation of Tshanini, especially the woodlands, are less mature than those in Tembe.

Case 2, a dearth of small diameter plants together with an abundance of large diameter plants, was found only in Tembe and occurred in all woodland types as well as the Short Sand Forest, but not in the Tall Sand Forest. In spite of these vegetation types having more large individuals than the same vegetation types in Tshanini, the mean height of the vegetation was lower. Such a vegetation structure could result from either removal of seedlings by animals, or limited recruitment opportunities due to unfavourable light conditions (Fashing and Mwangi Gathua, 2004; Boudreau et al., 2005). At high ungulate densities a reduction in seedling or sapling densities often occurs. This is reported to have a marked effect on the age and size structure of woodland, reducing or even eliminating cohorts of young trees for many years (Gill, 2006). In general, Tembe’s vegetation seems to represent the most mature stage (sensu Niklas et al., 2003) of all sites.

Case 3, an abundance of small diameter plants associated with a dearth of large diameter plants was encountered primarily in Manqakulane, e.g. Open Woodland on Sand, but also in the Short Sand Forest of Tshanini. In the Closed Woodland Thicket and Closed Woodland on Sand in Manqakulane a similar structure was found although the lack of large plants was not as pronounced. Furthermore, in the Closed Woodland Thicket of Manqakulane an under representation of the intermediate size classes was noticeable, which could possibly be ascribed to selective harvesting of these size classes. The steep slope in the Short Sand Forest of Tshanini is not so much the result of a large contribution of small individuals as it is due to the lack of very large individuals. The Short Sand Forest in Tshanini could therefore be at an earlier successional stage than in Tembe or the low density of large trees in Tshanini is a ghost of human harvesting activities before the community was translocated. However, the lack of old harvesting marks (Lindenmayer et al.,

2006) does not weigh in favour of this theory. In the absence of almost any disturbance by animals or man since 1992 in Tshanini, a ground cover composed of semi-woody scrambling plants such as liana has developed in the Short Sand Forest of Tshanini (Gaugris, 2004) but is absent in Tembe (Matthews et al., 2001). Such a ground layer could potentially limit the growth of seedlings and saplings of other species (Lawes and Chapman, 2006). In Manqakulane a Case 3 structure was possibly the result of the recurrent fire restricting plant growth in the “fire trap” (Bond and Keeley, 2005; Karlowski, 2006) or high numbers of domestic livestock (Sankaran et al., 2005). The large pools of small individuals and the steep slopes in Manqakulane indicate young communities where disturbance is an active process.

Case 4 represented an abundance of both small and large diameter plants and was observed in the Tall Sand Forest of Tembe. The large numbers of small plants in these forests and woodlands are probably the result of the opening of the canopy, which creates opportunities for enhanced recruitment. In the Tall Sand Forest of Tembe canopy gaps are primarily created by elephants. Shannon (2001) described the presence of two gap types, termed refuges, where elephants opened the canopy either severely or in a minor way. Large gaps may favour species with regeneration suites different from the current assemblage (Karlowski, 2006). The impact of large herbivores on ecosystem dynamics and functioning depends on many factors, the most important being the density of the herbivores (Pastor et al., 2006). High herbivore densities have led to detrimental effects on diversity (Western and Maitumo, 2004; Western, 2007), and therefore, as has been observed in east Africa before, it is contended that the elephant and other large herbivores population in the closed system of Tembe and the present levels of utilisation, far higher than in the past, will soon be compromising diversity. Gaugris (2008) observed the disappearance of several tree species in Tembe in both their juvenile and adult stages (most notably: *Albizia adianthifolia*, *Albizia versicolor* and *Garcinia livingstonei*), which reinforces our assumption.

The current study’s results indicate that the three different utilisation regimes have led to different outcomes in terms of structure within a similar time period. In the woodlands, a combination of animal utilisation and fire management in Tembe, and people utilisation through shifting agriculture, harvesting for firewood and construction material, cattle grazing and recurrent fires in Manqakulane have modified the vegetation structure.

Both sand forest types differed distinctly in size class structure between Tembe and Tshanini. Two factors could be contributing towards such a structure: the lower number in the large size classes in Tshanini could possibly be traced back to higher levels of human utilisation in the past and the increased numbers of small individuals in Tembe could be the result of the creation of canopy gaps. Moreover, elephant impact could be demonstrated in the Sand Forest as well as all Woodland communities and was not restricted to the Open Woodlands as indicated by Guldemond and Van Aarde (2007).

The 1989 to 2004 period represented a 15-year management cycle that was sufficient to drive Maputaland’s vegetation in our study area towards a changed state. Since 1989, Tembe has been under steadily mounting animal pressure (Gaugris, 2008), Tshanini was suddenly released from human use and the Manqakulane village area, a then mostly unused area (Peteers, 2005), was increasingly subjected to land clearing for human purposes. It is clear that people and animals influence the vegetation in a distinctive and rapid manner as the differences presented here are expected to represent the changes in vegetation unit structure over a period of less than twenty years.

Acknowledgments

Dedicated to Irmie Gaugris. Acknowledgements are expressed to Sabelo Mthembu and Caroline Vasicek for fieldwork assistance; Ezemvelo KwaZulu-Natal Wildlife for research facilities use; and the Centre for Wildlife Management of the University of Pretoria for financial support. We are grateful to Bruce Page and Rob Slotow of the School of Biological and Conservation Sciences of the University of KwaZulu-Natal, Durban, South Africa, for supporting the official administration of the project. The South African National Research Foundation supported this research (Grant Number 2053522).

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Edited by ED Witkowski