



CHAPTER 5

AN ANALYSIS OF THE INFLUENCE OF HERBIVORES AND MAN ON VEGETATION STRUCTURE: A CASE STUDY IN MAPUTALAND, SOUTH AFRICA

Abstract

The Maputaland region is part of the Maputaland – Pondoland – Albany hotspot of biodiversity. In communal land human pressure places strain on the natural resources of the region, but recent studies have also indicated that in conservation land the measures applied in the early 1980s no longer have the desired effect as animal populations have increased to such levels that they might have an observable negative impact on vegetation structure. A size and height class analysis investigated the horizontal and vertical structure of 21 vegetation units in Maputaland. Similar vegetation units under different utilisation pressure (human utilisation, herbivore utilisation, no utilisation) were compared. The results clearly indicated changes in stem diameter size class distribution as a result of human and animal utilisation, although the vertical structure remained unchanged. The canopies of all vegetation units were more open in utilised areas. In human dominated areas, this led to an overabundance of smaller woody plants whereas in animal utilised areas under formal conservation, these agents appeared to control the regeneration of woody plant species and possibly lead succession towards a sparse woodland system. The absence of utilisation in woodlands increased stand density and canopy closure. For the rare Sand Forest vegetation, an increased diversity and possibly stimulated dynamics were observed in areas under animal utilisation. However, recent increases in animal populations, especially elephants, appeared problematic. Sand Forest in non-utilised areas appeared more homogenous. The study presents the first quantification of change in vegetation structure due to animals or people in northern Maputaland and the first indication of the speed at which natural processes may influence the vegetation in the region.

Keywords

Animal utilisation, horizontal structure, human utilisation Maputaland, size class distribution, Sand Forest, vertical structure, woodlands

Introduction

Disturbance of natural ecosystems by people and herbivores are at the centre of many conservation debates. People utilise vegetation and therefore, depending on



the level of utilisation it may lead to general vegetation change, degradation and fragmentation of ecosystems, or even extirpation of species (Kinnaird *et al.* 2003; Schmidt-Soltau 2003; Kupfer *et al.* 2004; Peteers 2005; Rudel 2006; Ndangalasi *et al.* 2007). While animals are usually the object of conservation measures, the effects of animal concentrations in confined areas can also be detrimental to vegetation in similar ways (Barnes 2001; Bond and Loffell 2001; Hornberg 2001; Tedonkeng Pamo and Tchamba 2001; Brits *et al.* 2002; Mapaure and Campbell 2002; Mosugelo *et al.* 2002; Shaw *et al.* 2002; Fashing and Mwangi Gathua 2004; Sheil and Salim 2004; Western and Maitumo 2004; Wiseman *et al.* 2004; Van Aarde and Jackson 2007; Western In Press). Yet, vegetation, animals and people have co-existed for millennia, and appear to be interdependent in terms of maintaining biodiversity, and ecosystem services (Kameri-Mbote and Cullet 1997; Laurance 1999; Perrings and Lovett 1999; Schmidt-Soltau 2003; Ticktin 2004b; Ward 2004; Ickowitz 2006; O'Connor *et al.* 2007). It is recognised that while disturbance is an essential factor to produce biodiversity rich matrix environments, too much disturbance reduces biodiversity through landscape destruction, while insufficient disturbance reduces biodiversity through homogenisation (Maisels *et al.* 2001; Moegenburg and Levey 2002; Gillson *et al.* 2003; Paul *et al.* 2004; Bell and Donnelly 2006; Chapman *et al.* 2006; Degen *et al.* 2006; Herrerias-Diego *et al.* 2006; Lindenmayer *et al.* 2006; Lindenmayer and Noss 2006; Spies *et al.* 2006; Stouffer *et al.* 2006; Ndangalasi *et al.* 2007). A problem therefore occurs when an agent, biological, anthropogenic or climatic, or a combination thereof, but also lack thereof, influences the vegetation in an unnatural way, leading to the above problems.

For conservation to be efficient, it is now accepted that reserve networks including large ecological reserves work best (Cabeza and Moilanen 2001; Reyers *et al.* 2002; Pressey *et al.* 2003; Lindenmayer *et al.* 2006; Rouget *et al.* 2006). However, due to the limited size of the world's conservation areas (12% of the world land surface) and social acceptance of conservation concepts by local people (Brooks *et al.* 2006; West and Brockington 2006), it is obvious that much, if not the majority of conservation efforts have to be devoted to non-conserved areas (Sutherland 2003; Lindenmayer *et al.* 2006; Smith *et al.* 2006). The latter is especially important to preserve a variety of natural habitats under anthropogenic disturbance regimes, to retain landscape heterogeneity, and to regain biodiversity in areas where disturbance led to habitat destruction, but also to improve the output of natural and managed systems, and control resource extraction (Perrings and Lovett 1999; Decocq *et al.* 2004; Ticktin 2004a; Ticktin 2004b; Degen *et al.* 2006; Lindenmayer *et al.* 2006; Rouget *et al.* 2006; Rudel 2006; Wagner *et al.* 2006; Naughton-Treves *et al.* 2007).



It is therefore important to establish the quality of natural systems and to detect changes at both landscape and local level, within and outside conserved areas (Lindenmayer *et al.* 2006). Understanding natural system dynamics will allow more informed decisions to be taken (Lawes and Obiri 2003; Boudreau *et al.* 2005; Wagner *et al.* 2006). Ideally this knowledge comes from long-term studies and monitoring (Condit *et al.* 1998) and when such longitudinal studies are not available, they should be initiated. Initially, management decisions will rest on the available knowledge but these can be adapted and refined as additional information is gleaned (Condit *et al.* 1998; Boudreau and Lawes 2005; Lindenmayer *et al.* 2006; Smith *et al.* 2006).

To evaluate plant community structure and condition, static stem size distribution profiles provide interesting and useful insight in many facets of tree population structure, but are of little use to accurately assess the future plant community growth (Condit *et al.* 1998; Niklas *et al.* 2003). However, this method is often used to assess the growth potential of a community because of its ease of use (Condit *et al.* 1998; Obiri *et al.* 2002; Boudreau *et al.* 2005), and because it is often the only information available about a specific plant community. A significant relationship has been established between the slope of a linear regression fitted to the size structure of a community or a population, and its ecological condition (Niklas *et al.* 2003). Communities with highly negative slope values have been significantly linked with growing populations, whereas the reverse is true for communities with flatter or less negative slopes values (Niklas *et al.* 2003). Additionally, a link has been established between the position of the mean diameter of the trees in a population, termed “centroid”, and the size class distribution midpoint. A centroid skewed to the left of the midpoint indicates a young and growing community, whereas one skewed to the right indicates an older, relatively undisturbed community (Niklas *et al.* 2003).

Two analyses are reported on in the present study. The first analysis, to evaluate the state of the vegetation units was a classic size class distribution regression analysis based on the spread of stem diameter values of woody plants in each unit evaluated (hereafter referred to as the SCD analysis or horizontal structure). The second regression analysis, to increase the usefulness of available data and hopefully complement the results from the SCD analysis, was based on the height class distribution of the trees in each vegetation unit. It is hoped that this latter analysis (hereafter referred to as the HCD analysis or vertical structure) will add another dimension to the study of the structure of each unit.

In this paper the horizontal and vertical vegetation structure at three sites within a similar environment were compared. One site, the Tembe Elephant Park (Tembe) is



under conservation rule and represents a situation where animals are the main disturbance. The Tshanini Community Conservation Area (Tshanini) is under as low human utilisation as is possible in the region due to its remoteness and difficulty of access and wild animals have been removed. The third site, the Manqakulane Rural Community (Manqakulane), is where people have relocated at a known date, and used the natural habitat since. While long-term studies of the area are unavailable, studying similar vegetation types within one geographical region but under different utilisation regimes allows us to gain an understanding of the processes operating at the different sites (Poorter *et al.* 1996; Chapman and Chapman 1997; Chapman *et al.* 1999), and hopefully bypasses some of the restrictions of classical size class distribution analyses (Condit *et al.* 1998; Boudreau *et al.* 2005).

Study area

Northern Maputaland is a region where long-term studies on vegetation dynamics are conspicuously absent (Gaugris 2004; Guldemond 2006; Matthews 2006; Smith *et al.* 2006). The region lies in the northern portion of the recently identified Maputaland - Pondoland - Albany hotspot of biodiversity (Smith *et al.* 2006). It harbours a rich range of endemic plant and animal species, many of which are rare and endangered (Van Wyk and Smith 2001; Matthews 2006). The region consists mainly of a sandy plain interspersed with ancient littoral dunes. It is covered by an open to closed woodland, with patches of Sand Forest and the Muzi Swamp running along the eastern boundary (Matthews *et al.* 2001; Gaugris *et al.* 2004).

Maputaland lies in a transition zone between the tropics to the north, and the subtropics to the south. The summers are hot, wet, and humid, while the winters are cool to warm and dry. Tembe received a mean annual rainfall of 721 mm in the period from 1981 to 2003 (Matthews 2006).

Tembe Elephant Park was created in 1983 to preserve the remnants of the Maputaland coastal African elephant *Loxodonta africana* (Blumenbach 1797) population as well as the rare Sand Forest vegetation (Morley 2005; Matthews 2006), and given to the then KwaZulu-Natal Bureau of Natural Resources to manage. Since 1983, little development occurred in the park and its main purpose was to preserve the region's rare wildlife (KwaZulu Natal-Nature Conservation Services 1997; Browning 2000). The park has also served as a barrier to protect the local people from elephants raiding their crops.

Due to poaching in Mozambique the northern boundary of the park was closed in 1989, thus preventing animals from moving out of the park. Animal populations



subsequently increased in numbers without the option of migrating along the Maputaland coastal plain seasonally (Morley 2005; Guldemon and Van Aarde In Press). There is now concern about the potential damage to the vegetation in the park due to the confined animal populations, especially elephants, a phenomenon observed elsewhere in southern Africa (Lombard *et al.* 2001; Guldemon and Van Aarde In Press; Van Aarde and Jackson 2007).

Tembe is the largest ecological reserve for northern Maputaland, and protects the largest share of the Sand Forest vegetation (Matthews 2006; Smith *et al.* 2006). However, the region around and south of the park is considered of high conservation value and most suitable for conservation purposes due to the low agricultural value of the land (Eeley *et al.* 2001; Matthews 2006; Smith *et al.* 2006). This intrinsic value is threatened by human population growth in the region, because of the pressure it exerts on natural resources, especially wood (Kloppers 2001; Peteers 2005; Gaugris *et al.* 2007). Although at present this demographic growth and its effect appear limited to areas along the road network (Brookes 2004), it is anticipated that it may lead to the utilisation of increasingly vast sections of land, thus endangering the natural ecological processes in this region (Brookes 2004; Matthews 2006; Smith *et al.* 2006).

The land of the community of Manqakulane is situated 6 km south of Tembe Elephant Park and in 2004 was comprised of 778 permanent residents (Peteers 2005). During the course of the year 2000, this community officially allocated a portion of their tribal land to become a game reserve now gazetted as the Tshanini Community Conservation Area. This area was described extensively in Gaugris (2004) and appears to be the most representative “pristine” fragment of original northern Maputaland vegetation outside a formal conservation area. In Tshanini utilisation of wood resources by man has been low to insignificant since 1992, a date when the community people relocated their village from the eastern boundary of Tshanini to its current position along the Muzi Swamp (Gaugris 2004). While this move released Tshanini from human utilisation, it transferred a considerable pressure on the habitat surrounding the new village location as people cleared land for households and fields (Gaugris 2004; Peteers 2005; Gaugris *et al.* 2007).

The effect of man on the vegetation in a rural community is evaluated within the village area of the Manqakulane community. Utilisation of resources within communal land is governed by tribal laws that restrict the use of resources to those that are available within the tribal land of that particular community (Gaugris *et al.* 2007). Tarr *et al.* (2006) and Gaugris *et al.* (2007) found that people from the rural communities in northern Maputaland use resources available nearest to their households, rarely



travelling further than 3 km to gather natural resources, which is consistent with other studies in KwaZulu-Natal and South Africa (Brookes 2004; Lawes *et al.* 2004; Boudreau *et al.* 2005; Peteers 2005; Gaugris *et al.* 2007; Madubansi and Shackleton 2007).

A total of 11 vegetation units (Table 1) were sampled within the three study areas. Whenever possible names follow the classification presented in Matthews *et al.* (2001). The Tall Sand Forest described in Matthews *et al.* (2001) and Gaugris *et al.* (2004) is here called Intermediate Sand Forest, as the Tall Sand Forest description is applied to a new type of Sand Forest unit recognised during the present sampling of Tembe and described in Chapter 4 of the present study. However, it does not occur in Manqakulane and Tshanini. Two additional communities viz. *Afzelia quanzensis* clumps and *Afzelia quanzensis* forest on sand were also described in the present study for the first time. These communities did not fit any of the established descriptions, and expert opinion was used to name them, despite the lack of data to prove their status adequately.

Material and Methods

Rectangular plots of varying length and width, depending on vegetation density, were used to obtain abundance and size class distribution data of woody species in the three sites studied. A total of 254 transects were conducted, of which 48 were in Tshanini, 42 in Manqakulane, and the remainder in Tembe. The data were captured by using Microsoft Excel and then compiled into a database in Microsoft Access.

Stem diameter measurements of woody plants were classified into 12 classes of varying diameter width for the SCD analysis (>0 to <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, ≥52 cm). The tree height measurements at the vegetation unit level were similarly classified into eight classes of varying heights (>0 to <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). The variations in diameter and height were used to accommodate approximately equal numbers of individuals in each class with increasing size because the number of individuals generally declines with size (Condit *et al.* 1998; Lykke 1998; Boudreau *et al.* 2005). The size and height classes were selected after a review of stem diameters and tree heights observed in the region (Pooley 1997; Matthews *et al.* 2001; Brookes 2004; Gaugris 2004). The number of individuals in each size or height class is divided by the width of the class (number of cm per class) to obtain a mean number of individuals per unit of measurement for each class (Condit *et al.* 1998) before calculating the density

Table 1: Vegetation units of the study area in Maputaland, northern KwaZulu-Natal, South Africa

Code	Abbreviation	Community Name	Synonym in other studies
1		Sand Forest association	
1.1	AQ	<i>Afzelia quanzensis</i> subassociation	Newly described in the present study
1.1.1	AQC	<i>Afzelia quanzensis</i> clumps	Newly described in the present study
1.1.2	AQF	<i>Afzelia quanzensis</i> forest	Newly described in the present study
1.2	SF	Sand Forest subassociation	
1.2.1	SSF	Short Sand Forest	Short Sand Forest in Matthews <i>et al.</i> (2001) and Gaugris <i>et al.</i> (2004)
1.2.2	ISF	Intermediate Sand Forest	Tall Sand Forest in Matthews <i>et al.</i> (2001) and Gaugris <i>et al.</i> (2004)
1.2.3	TSF	Tall Sand Forest	Newly described in the present study, replaces TSF of Matthews <i>et al.</i> (2001) and Gaugris <i>et al.</i> (2004)
2	CW	Closed Woodland association	
2.1.0	CWT	Closed Woodland Thicket	Described as such in Matthews <i>et al.</i> (2001) and as Closed Woodland in Gaugris <i>et al.</i> (2004)
2.2.0	CWC	Closed Woodland on Clay	Described as such in Matthews <i>et al.</i> (2001) and as Woodland on Clay in Gaugris <i>et al.</i> (2004)
2.3.0	CWS	Closed Woodland on Sand	Described as such in Matthews <i>et al.</i> (2001) and as Open Woodland on Sand in Gaugris <i>et al.</i> (2004)
3	OW	Open Woodland association	
3.1.0	OWS	Open Woodland on Sand	Described as such in Matthews <i>et al.</i> (2001) and as Sparse Woodland on Sand in Gaugris <i>et al.</i> (2004)
3.2.0	OWAH	Open Woodland on Abandoned Household sites	Newly described in the present study
4	SW	Sparse Woodland association	
4.1.0	SWS	Sparse Woodland on Sand	Described as such in Matthews <i>et al.</i> (2001)

(D_i) per size and height class per vegetation unit in each study site. The class midpoint (M_i) for each diameter and height size class was set as the halfway measurement for each size class (Condit *et al.* 1998).

Once D_i and M_i were established, normal logarithmic transformations (Condit *et al.* 1998) of the type $\ln(D_i+1)$ and $\ln(M_i+1)$ were used to standardize the data (Lykke 1998; Niklas *et al.* 2003; Boudreau *et al.* 2005) before calculating the least square linear regressions fitting the data. The value of 1 was added as some size class bins could be empty (Lykke 1998; Boudreau *et al.* 2005). For each vegetation unit a regression was calculated with $\ln(M_i+1)$ values as independent variable and $\ln(D_i+1)$ values as dependent variable (Condit *et al.* 1998; Lykke 1998; Boudreau *et al.* 2005). The slopes of these regressions are referred to as SCD slopes for the diameter-based regressions and HCD slopes for the height-based regressions.

Two regressions were calculated per analysis for each vegetation unit. The initial regression encompassed the full data set (hereafter referred to as the complete analysis), while the second regression was restricted to the last ten diameter size classes or seven height size classes (hereafter referred to as the restricted analysis), thus removing a potential bias from weather induced sudden seedling germination because not all surveys were conducted in the same year (Yeh *et al.* 2000; Niklas *et al.* 2003). For each regression, the location, year of sample, slope, intercept, r^2 -value, standard error, significance of F, numerator degrees of freedom, number of size classes over which the regression was calculated and the centroid are indicated. The centroid represents the mean diameter or height at the unit level, and the size/height class in which it is located is indicated.

An analysis of covariance (ANCOVA) F-test was used to compare the regression slopes and intercepts between comparable vegetation units on different sites by using the linear regression comparison tool in GraphPad PRISM 4 software (Windows version, GraphPad Software, San Diego California USA, www.graphpad.com). This analysis begins by comparing the slopes of the regressions, and should there be no significant difference between the slopes, it evaluates the degree of difference between the Y-axis intercepts. When the slopes are similar, a pooled slope value is given. Should there be no significant difference established at the Y-axis intercept comparison level, a pooled Y-axis intercept value is also presented. Should there be no significant difference at either slope or Y-axis intercept levels, the vegetation in the sites compared can be described through the pooled slope and pooled Y-axis intercept.



Results

Only seven of the 11 vegetation units identified were compared across the sites. The SCD and HCD slopes for all communities are presented in Tables 2 and 3 respectively. A total of 22 regressions were calculated on the complete SCD analysis, F was highly significant in all regressions, and the r^2 -values for 21 of these regressions was >0.80 , and 0.75 for the remaining regression. All regressions of the restricted SCD analysis were highly significant while a total of 18 regressions had r^2 -values >0.80 , the remaining values being 0.48, 0.70 and 0.77 (Table 2).

The complete HCD analysis performed weakly, with only four regressions where the r^2 -value was greater than 0.80 (Table 3). However, F remained significant for all but six of the regressions. The restricted HCD analysis performed better with 16 regressions with r^2 -values >0.80 , while only three regressions were not significant. Only the HCD analysis of the Closed Woodland Thicket in Tshanini could not be resolved satisfactorily with either method.

The SCD slopes and Y-axis intercepts of all Tshanini vegetation units were steeper/higher in the restricted analysis than in the complete analysis, reflecting a lower abundance of trees in size classes 1 and 2 than in the size classes following them. This was also the case for the Short and Tall Sand Forest in Tembe. All remaining SCD slopes and Y-axis intercepts were shallower/lower in the restricted analysis than in the complete analysis, thus reflecting a greater abundance of trees in size classes 1 and 2 than in the size classes following them (Table 2).

The opposite pattern held true for the HCD analysis, whereby all but two of the HCD slopes and Y-axis intercepts were steeper/higher in the restricted analysis than in the complete analysis. The two units for which the above did not hold true were the Short and Intermediate Sand Forest units of Tshanini, although the slope only differed marginally in the Intermediate Sand Forest case (Table 3). The latter two units had SCD slopes showing a dearth of small diameter trees, while the HCD slopes indicated the opposite. The Sand Forest units of Tembe and the woodland units of Tshanini showed a dearth of small size classes in both horizontal and vertical structures. However, the woodlands of Tembe and Manqakulane, and the *Azelia quanzensis* association of Tembe showed an abundance of small trees in the horizontal structure that was not reflected at the vertical level.

The SCD centroid of communities in Tshanini shifted by one size class upwards for all but the Short Sand Forest unit, where it shifted by two size classes upwards (Table 2) between the complete and restricted SCD analysis. The SCD centroid of all other communities shifted by two to four size classes from the complete to restricted

Table 3: Results of the height class distribution (HCD) analysis by vegetation unit for the full data set and data set restricted to the largest six classes (height class is abbreviated as HC)

VT	Vegetation unit (abbr.)*	Location	Year of sample	Number of individuals sampled	Regression analysis of HCDs by using the full data set							Regression analysis of HCDs by using a data set restricted to HC 2 to HC 8								
					Slope	Intercept	r ²	Standard error	F	Df _d	Centroid location	Slope	Intercept	r ²	Standard error	F	Df _d	Centroid location		
VT 01.1.1	AQC	TEP	2004	96	-0.48	5.77	0.03	3.02	0.17	-	6	HC 3	-2.28	9.38	0.94	0.57	77.90	**	5	HC 3
VT 01.1.2	AGF	TEP	2004	201	-1.52	8.85	0.69	1.08	13.47	*	6	HC 3	-2.11	10.03	0.94	0.52	78.58	**	5	HC 3
VT 01.2.1	SSF	TCCA	2001	2411	-2.76	10.53	0.62	2.31	9.68	*	6	HC 3	-2.67	10.37	0.52	2.52	5.40	-	5	HC 4
VT 01.2.1	SSF	TEP	2004	896	-1.67	8.94	0.54	1.65	6.97	*	6	HC 3	-2.42	10.45	0.80	1.18	20.29	**	5	HC 4
VT 01.2.2	ISF	TCCA	2001	2883	-1.69	8.15	0.52	1.71	6.58	*	6	HC 4	-1.68	8.14	0.44	1.88	3.87	-	5	HC 4
VT 01.2.2	ISF	TEP	2004	4632	-1.53	8.70	0.57	1.41	8.01	*	6	HC 3	-2.26	10.16	0.88	0.81	37.74	**	5	HC 3
VT 01.2.3	TSF	TEP	2004	1779	-0.82	8.26	0.21	1.67	1.62	-	6	HC 3	-1.79	10.22	0.94	0.46	72.04	**	5	HC 4
VT 02.1.0	CWT	TCCA	2001	4126	-1.46	6.72	0.27	2.53	2.27	-	6	HC 4	-1.97	7.74	0.35	2.61	2.74	-	5	HC 4
VT 02.1.0	CWT	TEP	2004	117	-1.11	6.01	0.12	3.25	0.79	-	6	HC 3	-2.97	9.75	0.87	1.12	33.75	**	5	HC 3
VT 02.1.0	CWT	MRC	2004	1170	-4.08	12.84	0.93	1.23	74.92	**	6	HC 2	-4.16	13.00	0.90	1.34	46.50	**	5	HC 2
VT 02.2.0	CWC	TEP	2004	2015	-2.11	8.56	0.70	1.46	14.25	**	6	HC 3	-2.81	9.96	0.89	0.98	39.86	**	5	HC 3
VT 02.2.0	CWC	MRC	2004	186	-2.27	9.58	0.83	1.08	30.10	**	6	HC 3	-2.91	10.87	1.00	0.19	1108.73	**	5	HC 3
VT 02.3.0	CWS	TCCA	2001	3915	-1.98	7.94	0.53	1.97	6.85	*	6	HC 4	-2.36	8.69	0.56	2.05	6.32	*	5	HC 4
VT 02.3.0	CWS	TEP	2004	1999	-1.68	8.06	0.43	2.06	4.50	*	6	HC 3	-2.68	10.08	0.80	1.33	19.45	**	5	HC 3
VT 02.3.0	CWS	MRC	2004	819	-2.44	9.45	0.86	1.07	35.55	**	6	HC 3	-3.00	10.58	0.97	0.56	140.46	**	5	HC 3
VT 03.1.0	OWS	TCCA	2001	4663	-2.57	7.94	0.71	1.76	14.47	**	6	HC 4	-2.93	8.65	0.71	1.82	12.47	*	5	HC 4
VT 03.1.0	OWS	TEP	2004	4202	-1.81	7.30	0.51	1.88	6.32	*	6	HC 3	-2.87	9.43	0.94	0.73	74.60	**	5	HC 3
VT 03.1.0	OWS	MRC	2004	149	-2.29	7.82	0.26	4.07	2.14	-	6	HC 3	-4.70	12.65	0.97	0.87	140.36	**	5	HC 3
VT 03.2.0	OWAH	MRC	2004	995	-2.55	8.71	0.89	0.97	47.11	**	6	HC 3	-3.10	9.80	0.98	0.39	309.87	**	5	HC 3
VT 04.1.0	SWS	TEP	2004	654	-2.76	8.46	0.75	1.69	18.21	**	6	HC 3	-3.76	10.47	0.99	0.31	726.33	**	5	HC 3
VT 04.1.0	SWS	MRC	2004	176	-2.11	6.56	0.31	3.38	2.65	-	6	HC 3	-4.13	10.62	0.99	0.49	339.70	**	5	HC 3

Notes: TCCA Tshanini Game Reserve
TEP Tembe Elephant Park
MRC Manqakulane Rural Community
(abbr.)* Abbreviated form, see Table 1 for details

** Highly significant ($p \leq 0.01$)
* Significant ($p \leq 0.05$)
- Not significant ($p > 0.05$)



analysis (Table 2). The greatest shift in size classes (four upwards) was observed in the *Afzelia quanzensis* clumps of Tembe, and in the open and sparse woodlands on sand of Manqakulane.

The HCD centroid of the complete and restricted analyses remained within the same height class for most units except the Sand Forest where it shifted upwards by one height class in the Short Sand Forest units of Tembe and Tshanini, and in the Tall Sand Forest unit of Tembe.

Because no significant differences were found between any of the sites regarding the HCD regressions, the regression results presentation will further only focus on the SCD regressions. Additionally, only the centroids of the restricted analyses will be used for the presentation of results, and therefore when the term centroid is used, the centroid for the restricted analysis is relevant.

The Short Sand Forest unit is present in Tembe and Tshanini. The slope and Y-axis intercepts of both SCD analyses in Tshanini were significantly steeper/greater than in Tembe (Table 2, 4). The SCD centroid was located in size class 4 in Tshanini and Tembe (Table 2), while the HCD centroid is located in height class 4 for both sites (Table 3). The graphical resolutions of the complete and restricted SCD analyses appear in Figure 1.

The Intermediate Sand Forest unit is also present in Tembe and Tshanini. The slopes of the regressions were similar in both sites for the complete and restricted SCD analyses (Tables 2, and 4), but the Y-axis intercept of the complete and restricted SCD analyses were significantly higher in Tembe than in Tshanini (Table 2). In effect, the SCD analysis of Tembe represented a greater abundance of trees of all sizes than in Tshanini (Figure 2). The SCD/HCD centroids in Tshanini were located within size/height class 4, but the SCD centroid was located within size class 5 and the HCD centroid within height class 3 in Tembe. The centroid positions showed a greater contribution of large diameter trees in Tembe, while there appeared to be a greater contribution from tall trees in Tshanini.

The Closed Woodland Thicket unit occurs on all three study sites. The three sites appeared similar in both SCD and HCD slopes and Y-axis intercepts (Tables 4 and 5, restricted analyses). However, when considering the abundance of the smaller diameter trees (complete SCD analysis), only Tembe and Tshanini were similar, while the slope and Y-axis intercepts of Manqakulane were significantly steeper/greater (Tables 2 and 4). The SCD centroid for Tshanini was located within size class 3, but within size class 5 for the two other sites (Table 2). The HCD centroid was located within height class 4 in Tshanini, height class 3 in Tembe and height class 2 in

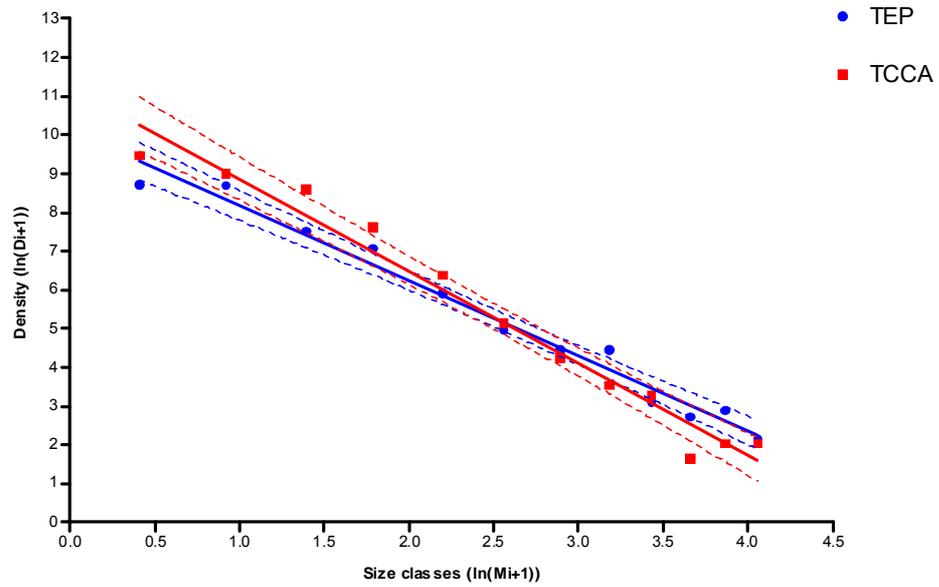
Table 4: The stem diameter class distribution (SCD) slopes and Y-axis intercepts for the comparable vegetation units of the three study sites, Maputland, South Africa

Comparison levels			Slope comparison					Y-axis intercept comparison					Final outcome
VT	Units (Abbr.)*	Sites compared	F value	Df _n	Df _d	P value	Pooled slope	F value	Df _n	Df _d	P value	Pooled Intercept	
FULL DATA SET													
VT 01.2.1	SSF	TEP / TCCA	7.59 **	1	20	0.01	-	-	-	-	-	-	Different
VT 01.2.2	ISF	TEP / TCCA	0.00 <i>ns</i>	1	20	0.92	-1.86	9.98 **	1	21	<0.01	-	Different
VT 02.1.0	CWT	TEP / TCCA / MRC	5.74 **	2	30	<0.01	-	-	-	-	-	-	Different
		TEP / TCCA	0.94 <i>ns</i>	1	20	0.34	-2.01	0.29 <i>ns</i>	1	21	0.60	9.14	Similar
		TCCA / MRC	6.06 *	1	20	0.02	-	-	-	-	-	-	Different
VT 02.2.0	CWC	TEP / MRC	8.25 **	1	20	0.01	-	-	-	-	-	-	Different
		TEP / MRC	0.54 <i>ns</i>	1	20	0.47	-2.02	0.01 <i>ns</i>	1	21	0.92	9.40	Similar
VT 02.3.0	CWS	TEP / TCCA / MRC	1.21 <i>ns</i>	2	30	0.31	-2.04	4.06 *	2	32	0.03	-	Different
		TEP / TCCA	2.38 <i>ns</i>	1	20	0.31	-2.00	9.80 **	1	21	0.01	-	Different
		TEP / MRC	1.93 <i>ns</i>	1	20	0.18	-2.01	0.07 <i>ns</i>	1	21	0.79	9.54	Similar
VT 03.1.0	OWS	TCCA / MRC	0.03 <i>ns</i>	1	20	0.87	-2.04	4.42 *	1	21	0.05	-	Different
		TEP / TCCA / MRC	13.90 **	2	30	<0.01	-	-	-	-	-	-	Different
		TEP / TCCA	5.36 *	1	20	0.03	-	-	-	-	-	-	Different
VT 03.1.0	OWS	TEP / MRC	19.52 **	1	20	<0.01	-	-	-	-	-	-	Different
		TCCA / MRC	10.69 **	1	20	<0.01	-	-	-	-	-	-	Different
		TEP / MRC	0.04 <i>ns</i>	1	20	0.84	-2.22	0.37 <i>ns</i>	1	21	0.55	8.86	Similar
RESTRICTED DATA SET													
VT 01.2.1	SSF	TEP / TCCA	11.15 **	1	16	<0.01	-	-	-	-	-	-	Different
VT 01.2.2	ISF	TEP / TCCA	2.60 <i>ns</i>	1	16	0.12	-2.01	7.52 **	1	17	0.01	-	Different
VT 02.1.0	CWT	TEP / TCCA / MRC	2.94 <i>ns</i>	2	24	0.07	-2.03	1.50 <i>ns</i>	2	26	0.25	1.31	Similar
VT 02.2.0	CWC	TEP / MRC	0.08 <i>ns</i>	1	16	0.78	-1.66	0.18 <i>ns</i>	1	21	0.67	8.23	Similar
VT 02.3.0	CWS	TEP / TCCA / MRC	3.26 <i>ns</i>	2	24	0.06	-1.96	5.78 *	2	26	<0.01	-	Different
		TEP / TCCA	5.70 *	1	16	0.03	-	-	-	-	-	-	Different
		TEP / MRC	0.18 <i>ns</i>	1	16	0.68	-1.85	2.29 <i>ns</i>	1	17	0.15	9.02	Similar
VT 03.1.0	OWS	TCCA / MRC	5.83 *	1	16	0.03	-	-	-	-	-	-	Different
		TEP / TCCA / MRC	6.96 **	2	24	<0.01	-	-	-	-	-	-	Different
		TEP / TCCA	18.64 **	1	16	<0.01	-	-	-	-	-	-	Different
VT 03.1.0	OWS	TEP / MRC	9.73 **	1	16	<0.01	-	-	-	-	-	-	Different
		TCCA / MRC	1.67 <i>ns</i>	1	16	0.21	-2.45	0.02 <i>ns</i>	1	17	0.99	9.62	Similar
		TEP / MRC	0.02 <i>ns</i>	1	16	0.88	-1.62	0.85 <i>ns</i>	1	17	0.37	6.92	Similar

Notes: ** Highly significant ($p \leq 0.01$)
 * Significant ($p \leq 0.05$)
ns Not significant ($p > 0.05$)
 (abbr.)* Abbreviated form, see Table 1 for details



(a) SSF complete SCD analysis



(b) SSF restricted SCD analysis

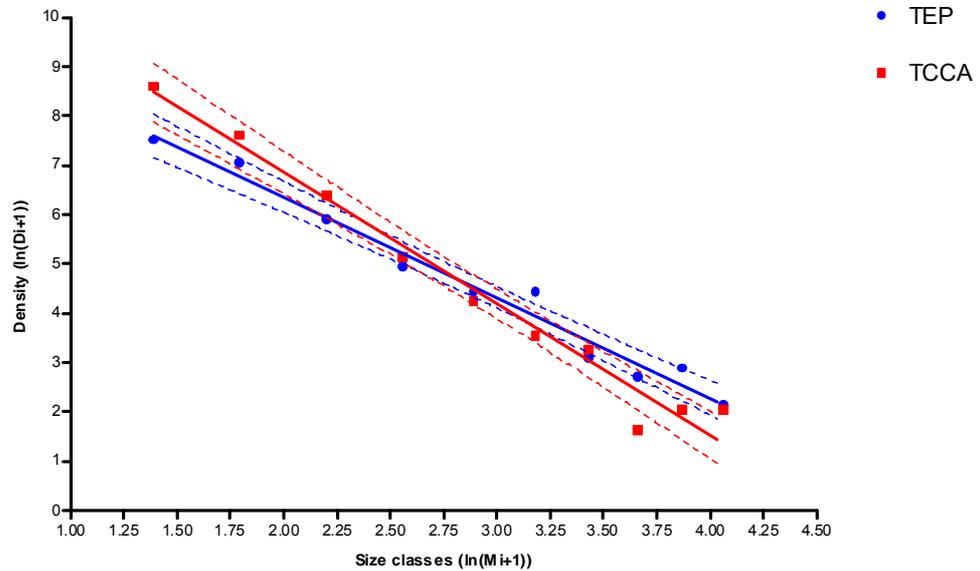
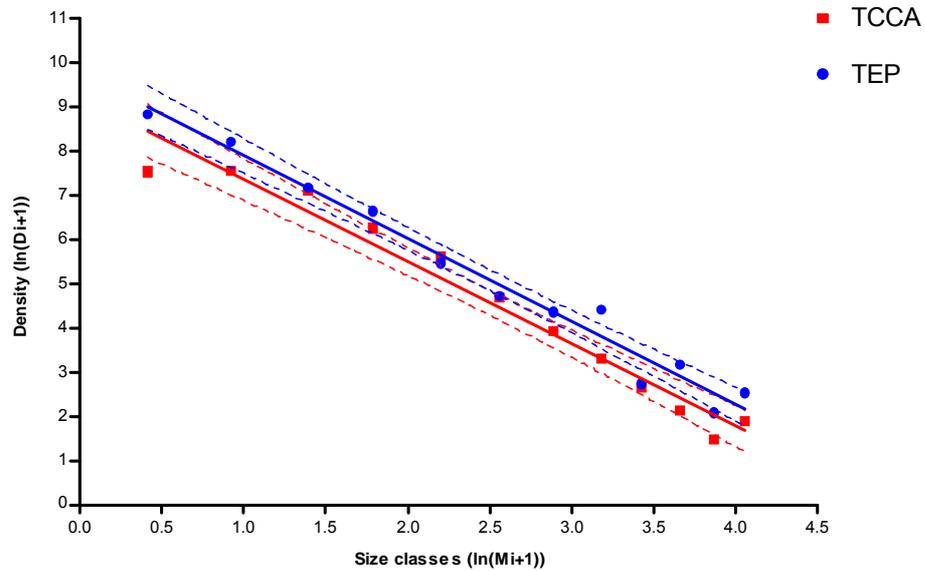


Figure 1: Stem diameter size class distribution in the Short Sand Forest (SSF) in Tembe Elephant Park (TEP) and Tshanini Community Conservation Area (TCCA). (a) A linear regression on all 12 size classes, (b) linear regression excluding the smallest two size classes. The dotted lines represent the 95% confidence intervals.

(a) ISF complete SCD analysis



(b) ISF restricted SCD analysis

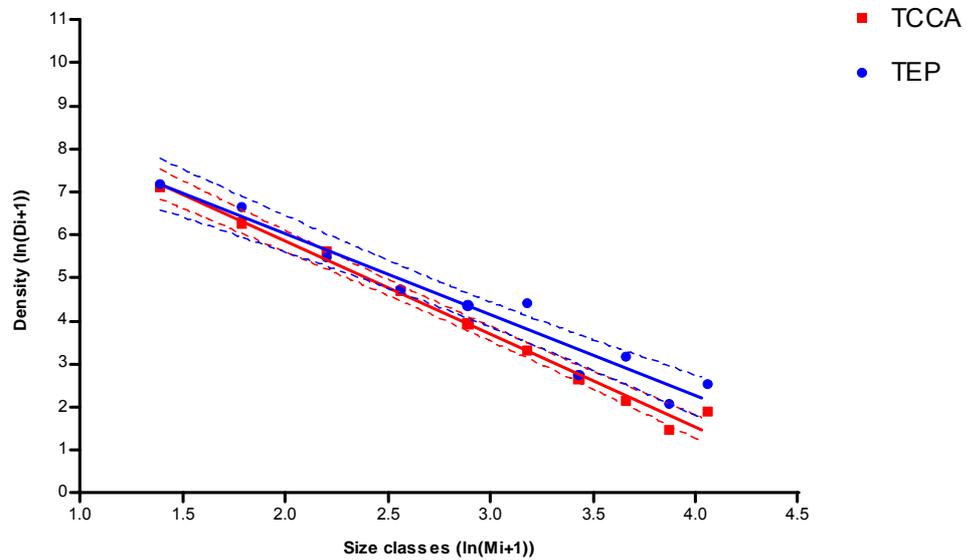


Figure 2: Stem diameter size class distribution in the Intermediate Sand Forest (ISF) in Tembe Elephant Park (TEP) and Tshanini Community Conservation Area (TCCA). (a) A linear regression on all 12 size classes, (b) linear regression excluding the smallest two size classes. The dotted lines represent the 95% confidence intervals.



Manqakulane (Table 3). The graphical resolution of the SCD analysis (Figure 3) confirmed that most of the difference lied in the smaller size classes, while the larger size classes were similar.

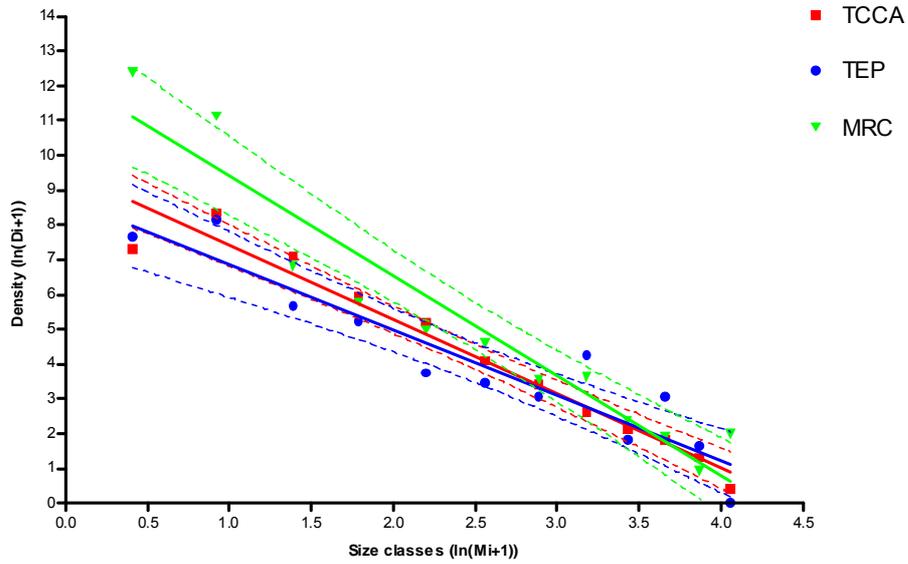
The Closed Woodland on Clay unit occurs only in Tembe and Manqakulane. The SCD slopes and Y-axis intercepts of Manqakulane and Tembe (Tables 4 and 5) did not differ significantly and the pooled slopes and Y-axis intercepts could therefore be used to describe the SCD curve shapes of both sites (Tables 4). The SCD centroid was located within size class 5 in both sites and the HCD centroid within height class 3 in both sites as well.

The Closed Woodland on Sand unit occurs on all three sites. The SCD slopes and Y-axis intercepts of Manqakulane and Tembe were similar, while the slope and Y-axis intercepts of Tshanini were significantly different from the two other sites (Table 4, Figure 4). The SCD centroids were located within size class 3 for Tshanini, size class 5 for Tembe and size class 4 for Manqakulane (Table 2). The HCD centroid of Tshanini was located within height class 4, while those of Tembe and Manqakulane were located within height class 3 (Table 3). In effect, density in larger size classes in Tshanini appeared lower than in both other sites while the smaller size classes appeared better represented.

The Open Woodland on Sand unit occurs on all three sites. The horizontal structure (SCD analysis) of the three sites showed that Tshanini and Manqakulane were similar (restricted analysis), while Tembe differed from both (Table 4, Figure 5). The steepest SCD slope and highest Y-axis intercept were found within Manqakulane, while the slope became progressively shallower and the Y-axis intercept lower in the Tshanini and Tembe sites successively (Table 2). The SCD centroids were located within size class 3 for Tshanini and within size class 5 for Tembe and Manqakulane (Table 2). The HCD centroid of Tshanini was located in height class 4, and those of Tembe and Manqakulane were located within height class 3 (Table 3). The Manqakulane site lacked individuals in the greater size classes, while the Tembe site seemed to have a greater abundance of larger trees than the Tshanini site (Figure 5).

The last comparison possible was within the Sparse Woodland on Sand unit found in Tembe and Manqakulane. The SCD analysis revealed that there were no differences between the two sites in either SCD or HCD levels (Tables 4 and 5). The SCD centroid of Tembe was located within size class 4 while that of Manqakulane was located within size class 5 (Table 2). The HCD centroids of Tembe and Manqakulane were both located within height class 3 (Table 3)

(a) CWT complete SCD analysis



(b) CWT restricted SCD analysis

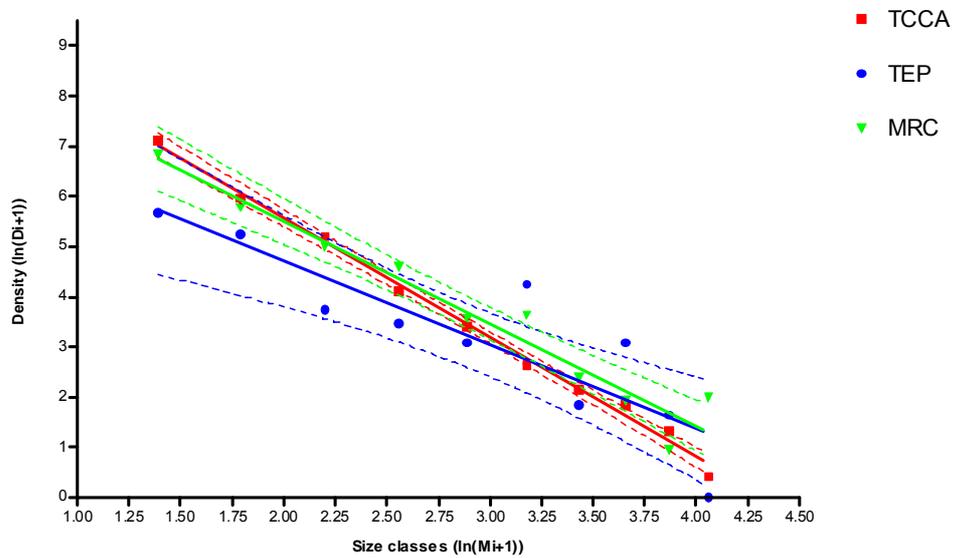


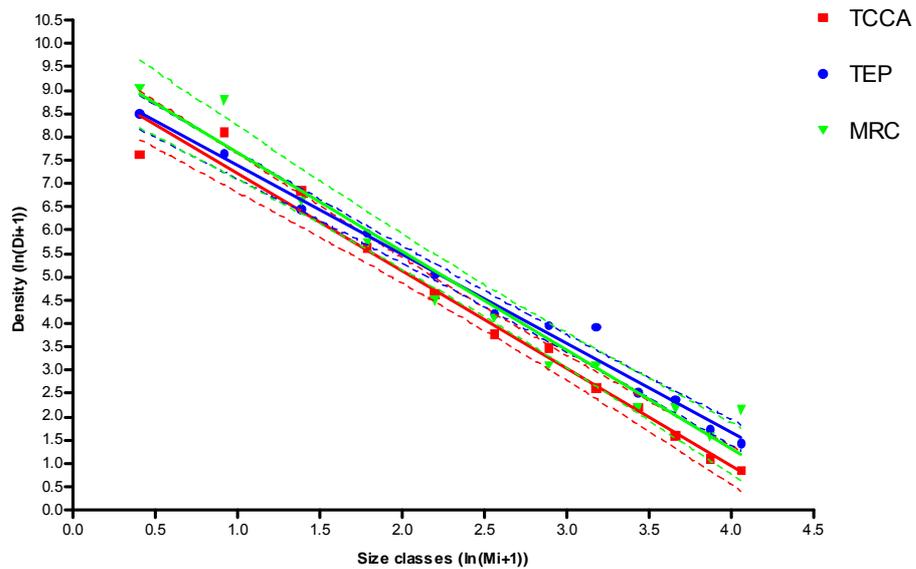
Figure 3: Stem diameter size class distribution in the Closed Woodland Thicket (CWT) in Tembe Elephant Park (TEP), Tshanini Community Conservation Area (TCCA) and the Manqakulane village zone area (MRC). (a) A linear regression on all 12 size classes, (b) linear regression excluding the smallest two size classes. The dotted lines represent the 95% confidence intervals.

Table 5: The height class distribution (HCD) slopes and Y-axis intercepts for the comparable vegetation units of the three study sites, Maputaland, South Africa

Comparison levels				Slope comparison					Y-axis intercept comparison					Final outcome
VT	Units (abbr.)*	Sites compared	Validity ^a	F value	Df _n	Df _d	P value	Pooled slope	F value	Df _n	Df _d	P value	Pooled Intercept	
FULL DATA SET														
VT 01.2.1	SSF	TEP / TCCA	X	1.00 <i>ns</i>	1	12	0.34	-2.21	0.01 <i>ns</i>	1	13	0.91	9.73	Similar
VT 01.2.2	ISF	TEP / TCCA	X	0.03 <i>ns</i>	1	12	0.86	-1.61	1.04 <i>ns</i>	1	13	0.33	8.43	Similar
VT 02.1.0	CWT	TEP / TCCA / MRC	-	2.91 <i>ns</i>	2	18	0.08	-2.21	2.60 <i>ns</i>	2	20	0.10	8.52	Similar
VT 02.2.0	CWC	TEP / MRC	X	0.05 <i>ns</i>	1	12	0.82	-2.19	1.68 <i>ns</i>	1	13	0.22	9.07	Similar
VT 02.3.0	CWS	TEP / TCCA / MRC	X	0.32 <i>ns</i>	2	18	0.73	-2.03	0.54 <i>ns</i>	1	20	0.59	8.48	Similar
VT 03.1.0	OWS	TEP / TCCA / MRC	-	0.12 <i>ns</i>	2	18	0.88	-2.22	0.05 <i>ns</i>	2	20	0.95	7.69	Similar
VT04.1.0	SWS	TEP / MRC	-	0.20 <i>ns</i>	1	12	0.66	-2.44	0.62 <i>ns</i>	1	13	0.45	7.51	Similar
RESTRICTED DATA SET														
VT 01.2.1	SSF	TEP / TCCA	-	0.04 <i>ns</i>	1	10	0.84	-2.54	0.21 <i>ns</i>	1	11	0.65	10.40	Similar
VT 01.2.2	ISF	TEP / TCCA	-	0.38 <i>ns</i>	1	10	0.55	-1.96	2.28 <i>ns</i>	1	11	0.16	9.14	Similar
VT 02.1.0	CWT	TEP / TCCA / MRC	X	1.77 <i>ns</i>	2	15	0.20	-3.03	1.84 <i>ns</i>	2	17	0.19	10.16	Similar
VT 02.2.0	CWC	TEP / MRC	-	0.05 <i>ns</i>	1	10	0.82	-2.85	4.31 <i>ns</i>	1	11	0.06	10.41	Similar
VT 02.3.0	CWS	TEP / TCCA / MRC	-	0.24 <i>ns</i>	2	15	0.79	-2.67	0.95 <i>ns</i>	1	17	0.41	9.78	Similar
VT 03.1.0	OWS	TEP / TCCA / MRC	X	3.38 <i>ns</i>	2	15	0.06	-3.49	1.49 <i>ns</i>	2	17	0.25	10.24	Similar
VT04.1.0	SWS	TEP / MRC	X	1.98 <i>ns</i>	1	10	0.19	-3.94	3.57 <i>ns</i>	1	11	0.09	10.54	Similar

Notes: ** Highly significant ($p \leq 0.01$)
 * Significant ($p \leq 0.05$)
ns Not significant ($p > 0.05$)
 Validity^a a X sign represents the data set where F was the most significant and r^2 -values reflected the best fit of the data, the X marked analysis should be selected for discussion
 (abbr.)* Abbreviated form, see Table 1 for details

(a) CWS complete SCD analysis



(b) CWS restricted SCD analysis

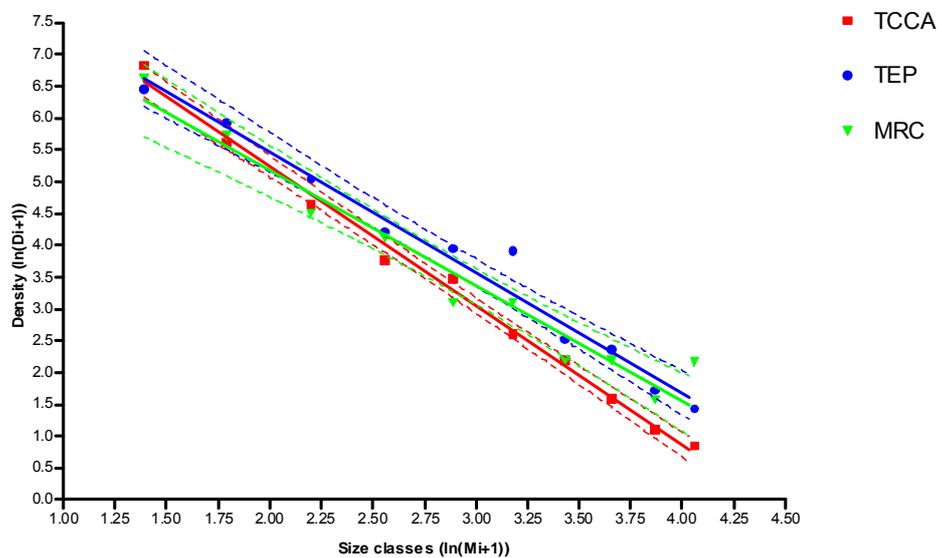
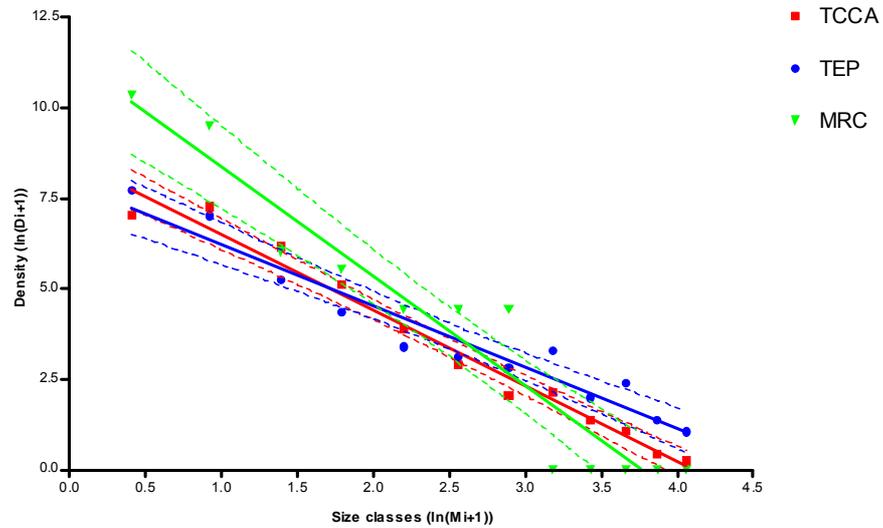


Figure 4: Stem diameter size class distribution in the Closed Woodland on Sand (CWS) in Tembe Elephant Park (TEP), Tshanini Community Conservation Area (TCCA) and the Manqakulane village zone area (MRC). (a) A linear regression on all 12 size classes, (b) linear regression excluding the smallest two size classes. The dotted lines represent the 95% confidence intervals.

(a) OWS complete SCD analysis



(b) OWS restricted SCD analysis

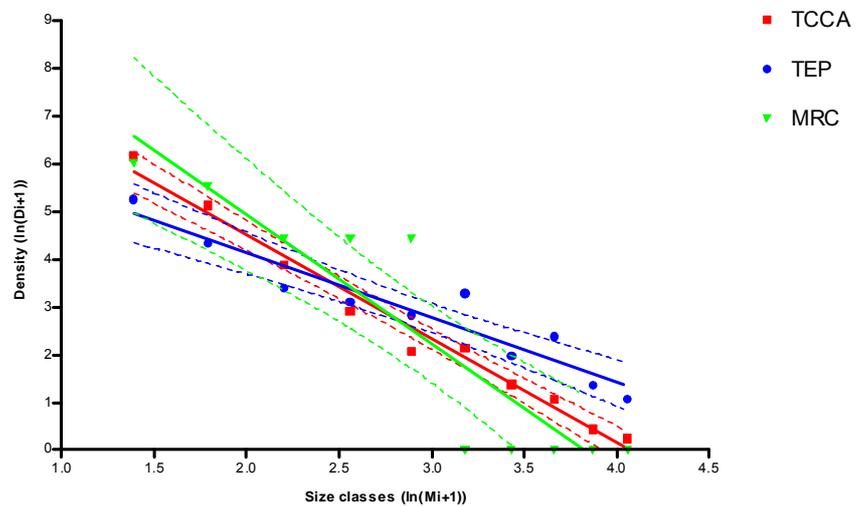


Figure 5: Stem diameter size class distribution in the Open Woodland on Sand (OWS) in Tembe Elephant Park (TEP), Tshanini Community Conservation Area (TCCA) and the Manqakulane village zone area (MRC). (a) A linear regression on all 12 size classes, (b) linear regression excluding the smallest two size classes. The dotted lines represent the 95% confidence intervals.



In essence, there appeared to be a clear difference in horizontal structure between the sites. From the five possible comparisons between Tembe and Tshanini, a similarity was only observed for the Closed Woodland Thicket unit. The woodlands of Tembe and Manqakulane were similar, except for the Open Woodland on Sand, while the three comparable woodlands of Tshanini and Manqakulane differed only in the Closed Woodland on Sand. The vertical structure of the three sites was not different.

Discussion

It is evident that the size class structure of vegetation units in Tshanini is markedly different from their counterparts in Tembe and Manqakulane. Gaugris *et al.* (2004) established a remarkable similarity in floristic composition between the Tembe and Tshanini sites but reported that cover-abundance of species varied significantly. Such heterogeneity among sites of similar vegetation types is not unknown, and is often linked to various modes of utilisation such as the presence/absence of animals, especially elephants (Sheil and Salim 2004; Babweteera *et al.* 2007), or the importance of traditional and commercial human activities (Poorter *et al.* 1996; Chapman and Chapman 1997; Chapman *et al.* 1997; Fashing and Mwangi Gathua 2004; Sheil and Salim 2004).

Besides the underlying geology and edaphic factors, vegetation in Africa is controlled by a fine balance of disturbances in the form of animal utilisation (Sheil and Salim 2004; Babweteera *et al.* 2007; O'Connor *et al.* 2007), climate (Lindenmayer *et al.* 2006; O'Connor *et al.* 2007), fire (Bond *et al.* 2003; Bond and Keeley 2005; Bond *et al.* 2005; Banda *et al.* 2006a) and people (Omeja *et al.* 2004; Boudreau and Lawes 2005; Banda *et al.* 2006b; Degen *et al.* 2006; Lindenmayer *et al.* 2006; Lindenmayer and Noss 2006; Ndangalasi *et al.* 2007). The balance between all of these elements varies continuously in time and place and represents the basis for the observed biodiversity (Gillson *et al.* 2003). While it appears that all elements are needed to maintain a high level of heterogeneity conducive to rich biodiversity (Perrings and Lovett 1999), the dominance of one or several of these elements can have the opposite effect (Chapman *et al.* 1997; Western and Maitumo 2004; Banda *et al.* 2006b; Western In Press). The overwhelming presence of man can have associated effects such as the confinement, reduction and even extirpation of animal populations (Babaasa 2000; Maisels *et al.* 2001; Babweteera *et al.* 2007).

To explain the differences in the present study, it is important to look at the above elements. Yeh *et al.* (2000) contend that when study sites are within a 7 km radius from a weather station, then the climate attributes of all sites within that area are



similar. In the present study the close proximity (6 – 7 km radius) of all three sites in space most likely rules out climatic factors particular to one site as an explanation for these differences. Additionally, there is no climatic event of catastrophic nature recorded since 1989, or even 1983 (Matthews 2006; Guldemond and Van Aarde In Press), and therefore the most likely answer lies in the influence of fire, herbivores and man.

Fire is a semi-controlled element in the woodlands of Tembe (Matthews 2006), but an uncontrolled and frequent event in Manqakulane and Tshanini, and is applied especially to stimulate grass re-growth for cattle grazing (Gaugris *et al.* 2004). Repeated fire leads to low fuel loads, which in the absence of animals, favour tree re-growth (Western and Maitumo 2004; Ickowitz 2006; Western In Press). In the presence of animals, the tree component in African woodlands is contained and the tree-grass balance is maintained. However, when the animal component exceeds the density that the system can sustain, especially grazers, the combination of fire and high animal density leads to a shift from closed to open or sparse woodlands (Salvatori *et al.* 2001; Walpole *et al.* 2004; Western and Maitumo 2004; Western In Press).

Rural people in Africa use trees mainly as sources of firewood, charcoal and building (Banks *et al.* 1996; Lawes *et al.* 2004; Boudreau *et al.* 2005; Banda *et al.* 2006b; Naughton-Treves *et al.* 2007; Ndangalasi *et al.* 2007), and will deforest areas for cultivation (Ickowitz 2006). Rural people usually deplete the stocks of various animal populations (Maisels *et al.* 2001; Banda *et al.* 2006b; Laurance *et al.* 2006), which can have further detrimental effects on vegetation dynamics (Maisels *et al.* 2001; Babweteera *et al.* 2007). The effect of people on vegetation through shifting cultivation is temporary, provided it remains non-commercial, and vegetation communities tend to recover after use, as long as the soil seed bank has remained and soil nutrients have not been depleted (Colón and Lugo 2006; Ickowitz 2006; Karlowski 2006). The above described effects are encountered in the Manqakulane area as well as in Tshanini. As such, the absence of wild animals in Manqakulane and Tshanini was diagnosed (Gaugris 2004; Gaugris *et al.* 2004; Guldemond and Van Aarde In Press), as well as the abandonment of fields on the eastern boundary of Tshanini (Gaugris 2004), where natural woodland vegetation appears to be coming back (Open Woodland on Abandoned Household site unit in the present study, see Table 1)

In the present study, differences between the three sites appear in three forms. The first noticeable difference is between complete and restricted analyses, in the horizontal and vertical structures. The most common case (case 1, 13 units) showed a shallower SCD slope in the restricted analysis than in the complete analysis;



associated with the opposite in the HCD analysis (the slope is steeper in the restricted analysis). The second most common case (case 2, six units) showed a steeper slope in the restricted analysis than in the complete analysis in both SCD and HCD analyses. The third case (case 3, two units) had a steeper restricted analysis SCD slope than the complete analysis, but a shallower restricted analysis HCD slope than in the complete analysis.

Case 1 implies an abundance of small trees, which are not found in the smallest height class of the HCD analysis. This represents an abundance of small but relatively tall trees. The latter is quite typical of an increased light availability where species compete for light by growing tall fast (Poorter *et al.* 1996; Myers *et al.* 2000; Paul *et al.* 2004). This pattern is only documented in the Tembe and Manqakulane sites, especially in the woodlands, but also in the *Azelia quanzensis* unit. While light availability could explain such a phenomenon in forest or thicket, in the woodlands it is most likely a result of growth of some woody species stimulated by the opening of the canopy by fire (Banda *et al.* 2006a; Karlowski 2006), large mammals (Western In Press), or people (Schwartz and Caro 2003; Boudreau *et al.* 2005) or a combination thereof.

In case 2, the dearth of small individuals found in the SCD is also found in the HCD and implies either removal of seedlings by animals, or a limited recruitment due to unfavourable conditions such as shading for light demanding pioneer species (Everard *et al.* 1994; Everard *et al.* 1995; Poorter *et al.* 1996; Obiri *et al.* 2002; Lawes and Obiri 2003; Schwartz and Caro 2003; Fashing and Mwangi Gathua 2004; Boudreau *et al.* 2005; Lawes and Chapman 2006). This particular case is found in Tembe's Sand Forest units and Tshanini's woodlands.

In case 3, there is a dearth of the smallest individuals in the horizontal structure that contrasts with an abundance of small individuals in the vertical structure. This particular case was associated with the abundance of semi-woody scrambling plants such as lianas, whereby size classes can be large, but height classes remain low (Fashing and Mwangi Gathua 2004; Lawes and Chapman 2006). This type of structure can limit the growth of seedlings and saplings of other species. Gaugris (2004) described in the Sand Forest units of Tshanini a ground layer of liana such as *Uvaria lucida* and *Uvaria caffra*, and vines such as *Rhoicissus revouillii* sprawling on the Sand Forest floor, which was not described for Tembe (Matthews *et al.* 2001). This particular feature suggests that in the absence of animals, a ground cover may develop in the Sand Forest



The next type of difference lies in the centroid's shift. To an extent this particular feature corroborates the above-mentioned differences in the SCD/HCD slopes. The centroid (or mean stem diameter/height location) is predicted to increase as the proportion of large individuals increases (Lawes and Obiri 2003; Niklas *et al.* 2003). In the present study the shift of the centroid position between the complete and restricted analyses was expected to represent the contribution of the smallest individuals in the size/height class distribution structure. While the change in SCD centroid location between the full and restricted analysis were largely within similar size or height classes at the different sites, the SCD centroid shift was lowest in Tshanini, therefore indicating a lower contribution of smallest individuals to the size class distributions than at other sites. The large SCD centroid shift at the other sites therefore indicates a greater contribution of the smaller individuals, and therefore a higher recruitment rate. One explanation is that vegetation units of Tshanini, especially the woodlands, are less disturbed than those of Manqakulane and Tembe (Gaugris 2004). Support of this explanation lies in the different years in which the sites in Tembe and Manqakulane (2004) and Tshanini were sampled (2001). Tshanini was sampled one year after abnormally high rainfall, which was expected to stimulate regeneration but did not, while Tembe and Manqakulane were sampled during a dry spell, which was expected to have the opposite effect (Brokaw and Busing 2000; Niklas *et al.* 2003; Babaasa *et al.* 2004; Matthews 2006).

Furthermore, in all but one instances, the restricted analysis SCD centroid of vegetation units in Tshanini are located within a lower size class than in Tembe and Manqakulane, while the HCD centroid is located in a higher size class (except short Sand Forest, where it is within the same size class). A logical deduction is that there is a greater abundance of tall trees with smaller diameters in Tshanini than in Tembe and Manqakulane. This particular aspect hints at a greater competition for light (Babaasa *et al.* 2004) in Tshanini, and therefore the assumption that canopies in Tembe and Manqakulane have more gaps than in Tshanini, following utilisation either by man or herbivores (Condit *et al.* 1998; Boudreau *et al.* 2005).

The final type of difference is expressed in the statistical comparisons of the SCD slopes and Y-axis intercepts between different sites. Both the complete and restricted analyses show remarkably well that Tshanini is different from both Tembe and Manqakulane and that the woodlands of the latter two sites appear remarkably similar. Only in the case of the Closed Woodland Thicket restricted analysis are the three sites similar. In the woodlands the following hypothesis is proposed: based on a review of literature, a combination of animal utilisation and fire management in Tembe,



and people utilisation through shifting agriculture and utilisation of trees for firewood and building wood in Manqakulane have modified the structure of Closed Woodland Thicket, Closed Woodland on Clay, Open Woodland on Sand, and Sparse Woodland on Sand. The large pools of smaller individuals, the steep slopes, and the SCD and HCD centroids generally skewed to the left of the size class distributions (towards smaller size classes) all hint at communities where disturbance is an active process (Condit *et al.* 1998; Niklas *et al.* 2003; Gaugris and Van Rooyen In Press), whereas these appear less clear cut for the Tshanini site.

The Sand Forest units offer a perplexing situation. The Short Sand Forest communities of the two sites are distinctly different, with that of Tshanini having a much steeper SCD slope and higher Y-axis intercept. It is therefore assumed that in Tshanini, Short Sand Forest is at an earlier successional stage than in Tembe (Denslow 1995; Babaasa *et al.* 2004). The Intermediate Sand Forests also differ but in the opposite direction and there appear to be a generally greater abundance of trees in all size classes in Tembe than in Tshanini. This particular aspect can possibly be linked to thinning, which in association with normal natural mortality in areas of low disturbance is recognised to lower tree density (Niklas *et al.* 2003). However, the latter does not totally conform to the theory, which would require a shift in the centroid to the right, as “average stem diameter increases with increasing maximum stem diameter” (Gaugris 2004). Moreover, since density of trees in the Intermediate Sand Forest of Tembe is higher than in Tshanini, it can be equally be assumed that the self-thinning limit has not yet been reached for Tshanini. Other alternatives are that the general lower density in Tshanini represents a less mature and more active vegetation community, or it may also represent a ghost of human harvesting activities before the 1992 move of the village in the east. The lack of old harvesting marks (Lindenmayer *et al.* 2006) does not weigh in favour of the latter theory, although it cannot be fully discarded.

Alternatively, the increase in numbers in the Intermediate Sand Forest in Tembe could be the result of disturbance in forests. Canopy gaps are created by elephants in the Sand Forest of Tembe (Shannon 2001; Matthews 2006) and it appears possible that increased light levels, or a greater light continuum (Van Rensburg *et al.* 1999; McGeogh *et al.* 2002) leads to an increased density of species throughout. The higher density of larger trees in Tembe can however not be explained satisfyingly in such manner as the time scales implied are much longer than those debated within the present study. The perceived fragility of Sand Forest in the current climatic context (Matthews 2006) implies that the larger the gaps, the more prone to fire and destruction the Sand Forest will become and theory indicates that larger gaps may



also favour species regeneration suites different from the current assemblage (Brokaw and Busing 2000; Babaasa *et al.* 2004; Karlowski 2006).

The current size of gaps in Sand Forest remains to be determined, although Shannon (2001) established the presence of two gap types, termed refuges, where elephants opened the Sand Forest canopy either severely or in a minor way. It is contended that until relatively recently the elephant population in Tembe might have contributed to a more diverse Sand Forest, however, the differences observed in other communities and a review of literature on the subject beg the question: until when (Van Rensburg *et al.* 1999; Matthews 2006)?

In conclusion, a difference at the unit level between similar vegetation types in three locations and under different utilisation regimes has been established for this part of Maputaland. It appears 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 thirty years. These results corroborate previous conclusions regarding the canopy opening and woody species modification effect of elephants on woodlands in Tembe (Guldmond and Van Aarde In Press) but go against other conclusions by the same authors. Most notably, there is an effect of herbivores on Sand Forest and all woodland units, not restricted to the open woodlands, but also areas outside conserved areas under human influence are most likely to be in a highly disturbed state. More importantly these results present the first systematic quantification of changes between vegetation communities under different utilisation regimes in Maputaland and provide the first estimate of the time scale at which processes take place.

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