

Herbivores and human impact on woody species dynamics in Maputaland, South Africa

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Summary (200 words)

Maputaland's woodlands are under utilisation pressure inside and outside conserved areas, due to mounting densities of mammals in the former, and increasing human utilisation of vegetation in the latter. Conservation of this biodiversity hotspot requires a better understanding of vegetation dynamics. To this purpose, woodland vegetation structure was evaluated at three sites through size class distribution analysis and grain determination, a forestry concept here applied to woodlands. Three sites represented animal disturbance, human disturbance, and no disturbance, under their respective utilisation regimes for comparable periods.

Results showed clear utilisation patterns with woodlands over-utilised by man in rural areas, and damaged by large herbivores in confined conserved areas. Worryingly, common species occurrence changed subsequent to the three land use forms applied. The woodlands were mostly fine-grained forest-like vegetation units, and followed fine-grained forests dynamics closely. The grain model performed successfully for the region's woodlands and proved a good tool to improve vegetation dynamics understanding.

In general, people and herbivores led to local extirpation of species and threatened both ecological structure and function of Maputaland's woodlands. However, the fine grain status was considered positive, as it facilitated future management options by reducing time frames and scale of management actions to be applied.

Keywords

Grain, human utilisation, herbivores, rural community, vegetation dynamics

Introduction

Savanna woodlands, a dominant feature of the African landscape, evolved under a delicate mixture of fire, animal and people-related disturbance in association with climate (Bond et al., 2005). Under low human demographic pressure and where wildlife roams freely, woodlands are resilient (Walpole et al., 2004) and able to support large, but temporary, surges of utilisation. However, woodland ecosystems tend to change where demographic pressure is high, such as high human population density or in confined conservation areas where animal densities have increased to levels that exceed the ecological capacity of the reserve.

Under intense wildlife utilisation, especially by African elephant *Loxodonta africana* Blumenbach, the transformation of woodland into grassland has been documented (Western, 2007), while under a low utilisation intensity and if the rainfall allows, woodlands become denser and can potentially be replaced by forests (Walpole et al., 2004). The response to human utilisation is more complex. It is widely acknowledged that woodlands in Africa are a valuable, if not essential, resource for rural people in Africa (Shackleton et al., 2007). Where people are few, agriculture limited to shifting cultivation, and where wildlife is absent from the landscape, woodlands have changed into forests (Ickowitz, 2006). Where human density is high, wildlife is usually hunted to local extinction and clear gradients of plant utilisation develop away from villages (Schwartz and Caro, 2003). In these areas there is usually a wealth of seedlings and saplings but larger trees show a gap in pole-sized

classes. While the gap in size classes may become a sustainability issue, there is often sufficient regeneration to perpetuate the woodland type, albeit with a changed structure (Luoga et al., 2002). Problems occur when commercial harvesting pressure is added (Caro et al., 2005). In those instances, selective harvesting can lead to local extirpation of all commercially valuable woody species, thus changing species composition (Naughton-Treves et al., 2007, Ticktin and Nantel, 2004).

Woodlands and forests in Maputaland are intricately interwoven, diverse vegetation units, which share many species. In protected areas, it is documented that both Sand Forest and woodlands are deteriorating due to high animal densities (Gaugris, 2008), while outside conserved areas, numerous questions have been raised with regards to the potential destruction of these ecosystems by people (Smith et al., 2006).

To avoid further woodland destruction, management strategies need to be developed that will maintain the integrity of ecosystems in Maputaland. To achieve this goal information is needed on the current state of the vegetation and the underlying drivers of vegetation dynamics within conserved as well as human dominated landscapes. The approach followed in this study was to evaluate and compare the woody vegetation structure by means of a size class distribution analysis on three geographically related sites of similar potential and species composition but under three distinct utilisation regimes for a comparable period of time (from 1989 to 2004):

- Site 1: Sparse to closed woodlands under the influence of rising herbivore density, without anthropogenic pressure,
- Site 2: Sparse to closed woodlands under the influence of anthropogenic activities, without herbivore pressure,
- Site 3: Sparse to closed woodlands under neither anthropogenic activities nor herbivore pressure.

A range of techniques have been devised to derive as much knowledge as possible from once-off surveys to gain an understanding of the population dynamics of the species (Boudreau and Lawes, 2005; Boudreau et al., 2005, Lawes and Obiri, 2003; Niklas et al.,

2003). Based on the three sites studied and the influences that prevail on each of the sites, we expect to encounter broad scenarios as follow:

- Site 1: Mega herbivore lead to the removal of typical structural elements of the woodlands and small to large herbivore pressure reduces the recruitment of new individuals, an overall opening of the woodland vegetation is expected.
- Site 2: Household establishment, shifting agriculture and wood harvesting by people create large open patches under the shade of the marginal trees of the original woodlands. These “open” areas once abandoned are colonised by a range of disturbance adapted woodland species normally found at much lower densities on undisturbed sites.
- Site 3: The absence of anthropogenic and herbivore pressure is expected to lead to a densification of the woodlands, with possibly a transition into forest in some instances.

The aim of the present paper was therefore to evaluate these three woodland sites in Maputaland and to evaluate and interpret the effects of the different disturbance agents on woody species' population structure and dynamics, and further provide some management implications. .

Study area

The three study sites were in close proximity to each other within the central Maputaland coastal plain (Figure 1). Ancient littoral dune cordons aligned in a north – south direction form the sandy backbone of this region, which is bounded by the Muzi Swamp along the eastern side and the Pongola River on the western side. The region is subtropical, with hot, wet summers, cool and dry winters, and a mean annual rainfall of 700 mm (Gaugris, 2008). The rainy period occurs from October to April, with a maximum usually in January and February when mean monthly rainfall exceeds 100 mm. From May to September, rainfall can be absent, however humidity usually remains >65% during these cooler months (Gaugris et al., 2004).

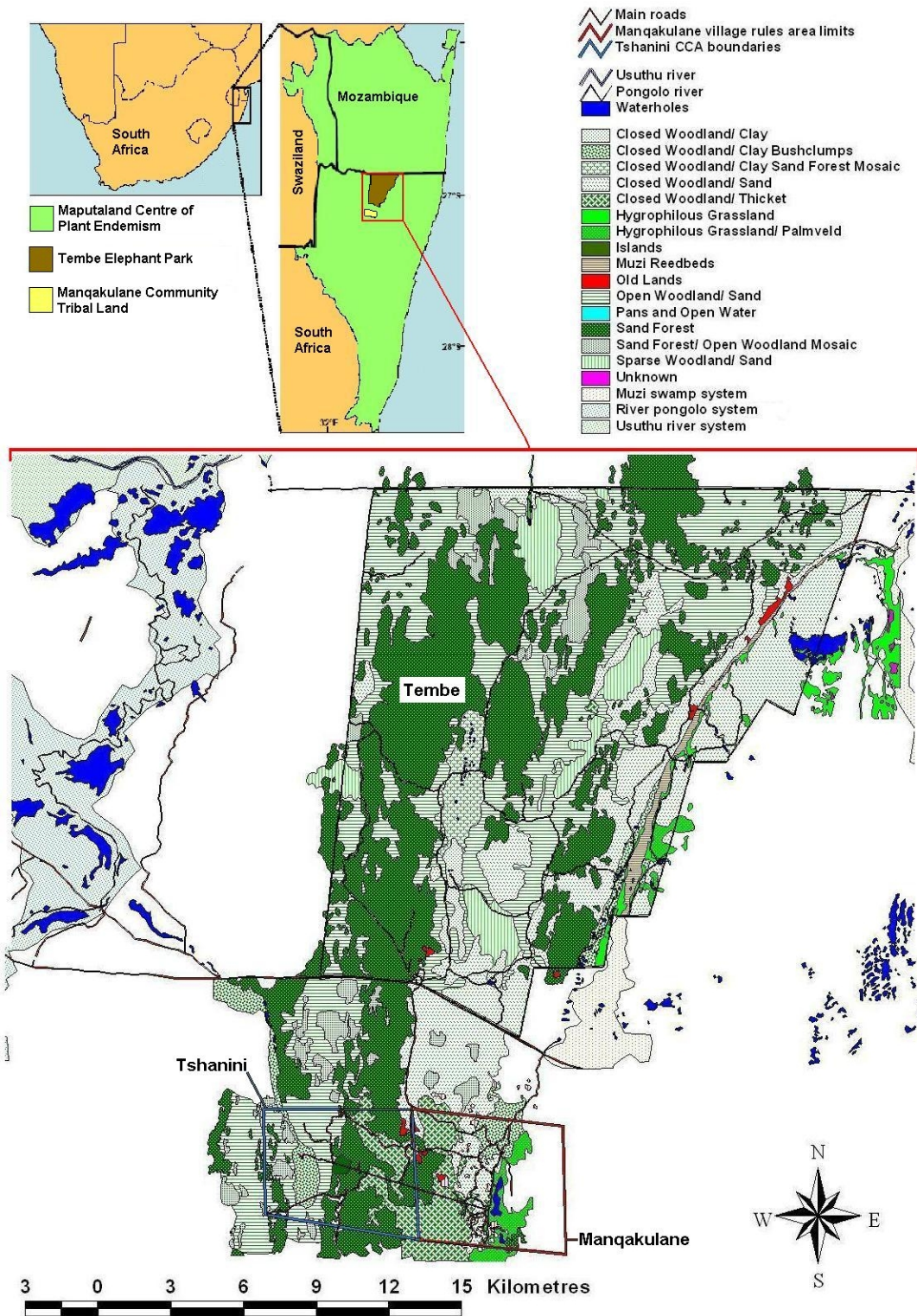


Figure 1 The geographic localisation of the three study sites in KwaZulu-Natal, South Africa. Map adapted from Gaugris *et al.* (2007b).

The vegetation consists of sparse to closed woodlands dotted with patches of Sand Forest (Gaugris and Van Rooyen, 2008). The woodlands are classified as “Coastal Sandveld” vegetation (Morgenthal et al., 2006), characterised by sandy soil with a clay fraction <10%. Fire plays an important role in vegetation changes in Maputaland (Matthews et al., 2001). Regular and frequent fires occur in most parts of Maputaland’s woodlands, and are nearly exclusively anthropogenic in origin (Matthews et al., 2001). Fire appears to promote the tree component of the woodlands (Matthews et al., 2001). Woodlands of this region produce an exceptionally species rich seed bank dominated by herbaceous species, especially weeds, along with some tree species (Kellerman and Van Rooyen, 2007). The seed bank diversity and species composition along with distribution of seeds in the soil profile supports the theory that these woodlands are frequently disturbed. Seasonal variation in the size of the seed bank is large and more important than spatial variation. The similarity between seed bank and standing vegetation was low, thereby making the seed bank composition a poor indicator of potential vegetation. It is hypothesized that woodlands tree species recruit through successful germination and establishment within a short period after the seed rain, provided that suitable conditions prevail.

Tembe Elephant Park (hereafter referred to as Tembe) was proclaimed in 1983 to conserve the region’s remaining wildlife and protect Sand Forest vegetation. The park’s 30 000 ha were fully fenced in 1989. Subsequent to fencing, thanks to conservation efforts and the lack of significant populations of large predators, herbivore populations grew and repopulated the park’s extent. Some animal populations increased considerably, especially large herbivores (nyala *Tragelaphus angasi* increased by >600%, kudu *Tragelaphus strepsiceros* increased by >400%) and mega herbivores (elephants increased by >60%) (Matthews, 2005) to levels that may be exceeding the park’s ecological capacity for these species (Morley, 2005; Gaugris, 2008). Tembe is considered as site 1 and treatment 1, where general herbivore density increased progressively and where, one year after the survey were conducted, in 2005, elephant density was believed to exceed Tembe’s ecological capacity for that species (Morley, 2005; Gaugris, 2008). Animal populations’

management in Tembe has been required since 2000, with an annual removal of 500 medium to large browsers through culling (Gaugris, 2008). Fire management in Tembe attempts to imitate natural cycles and sections are burnt every 2 to 4 years during the dry season (Matthews et al., 2001; Matthews, 2006). However, these fires tend to be of a high intensity due to the accumulation of a large fuel load.

The Manqakulane village (hereafter referred to as Manqakulane) represents the land east of Tshanini (ca. 2 500 ha) (Figure 1), and comprises the village zone and the portion of land between the village and Tshanini. In 2004, a total of 778 residents lived in 124 households in Manqakulane. In contrast to the regional population trend, this population remained relatively stable over the past 10 years, (Peteers, 2005, Gaugris and Van Rooyen, 2010). In general, however, Maputaland's recent human population growth means that land clearing for homesteads and fields is increasing, and is further fuelled by rural society modernisation and immigration linked to Maputaland becoming a favourite tourism destination (Peteers, 2005). Manqakulane is considered as site 2 and treatment 2, where human influence occurs through land clearing for shifting cultivation, herbivores hunting, cattle grazing and related regular low intensity fires in open areas, harvesting of pole-sized trees (3.0 – 10.0 cm diameter, see Gaugris et al., 2007a) and firewood harvesting.

The Tshanini Community Conservation Area (hereafter referred to as Tshanini) is a remarkable achievement of the Manqakulane rural community. In 1992, the community set aside 2 420 ha as a conservation area. Before that time, people used the land for collecting building material, firewood, food gathering, cattle grazing, hunting, and some cultivation. In 1992, following installation of a water supply, people moved eastwards (Gaugris et al., 2007a). Tribal laws have protected Tshanini since 1992 and little human utilisation took place. Tshanini is considered as site 3 and treatment 3, and represents the most suitable control site available where neither human nor herbivore utilisation took place. The legacy of past utilisation by people prior to 1992 is expected to appear for some species. However, due to the density of human population and the traditional way of building construction and living prior to 1992, utilisation is unlikely to have been high (Peteers, 2005; Gaugris et al.

2007a). The utilisation of poles for construction in Manqakulane was estimated (in 2004) at around four poles per ha per year with diameters ranging from 3.0 to 10.0 cm (Gaugris et al., 2007a). Because population density was lower prior to 1992 (historical records show a population of less than 600 people for 1995), it is likely that wood use for house construction was even lower in Tshanini. Fire occurrence in Tshanini is low, although cattle grazing oriented low intensity fires occur on an annual basis in open areas.

Methods

Data used for the present study were initially collected to determine utilisation levels (in terms of biomass removed / utilised), as a basis for a management plan to ensure sustainable utilisation of Maputaland's vegetation (Gaugris, 2008). Analyses conducted in the present study were therefore undertaken to complement the utilisation study (Gaugris, 2008). The following six vegetation units were sampled (Figure 2):

- Closed Woodland Thicket (found in all three sites)
- Closed Woodland on Clay (found in Tembe and Manqakulane)
- Closed Woodland on Sand (found in all three sites)
- Open Woodland on Sand (found in all three sites)
- Open Woodland on Abandoned Fields (found only in Manqakulane)
- Sparse Woodland on Sand (found in Tembe and Manqakulane)

A total of 105, 42 and 30 plots were located through a stratified random sampling approach in the woodland units of Tembe, Manqakulane and Tshanini respectively. Plot number was proportional both to the total area of the sites and to woodland vegetation area in these sites. Plots were placed at least 50 m away from management tracks and at least 100 m away from tourist tracks. Plot size varied in length and width (25 - 100 m long and 5 –10 m wide) depending on woody plants

a)



b)



c)



Figure 2 A visual guide to assist in differentiating the physiognomic differences between closed, open and sparse woodland, as described for the Maputaland vegetation. a) Presents closed woodlands, b) shows open woodlands, while c) shows typical sparse woodlands from the region.

density and was adjusted to ensure that at least 150 individual plants were surveyed per plot. The plots were bisected along their length and walked in two lengthwise subplots.

While walking along the first length, all woody plants (i.e. plants with an erect to scrambling growth form and with a ligneous trunk, thus including lianas) encountered in the plots were identified to the species and measured. When walking back along the other subplot, only woody plants ≥ 0.4 m height and ≥ 1.0 cm stem diameter, were measured. For all plants, stem diameters measurements were taken above the basal swelling, at the point where stem dimensions become regular, for large trees stem diameters were measured at 100 cm above ground.

Stem diameter measurements of woody plants were classified into 12 size classes of varying diameter width (<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). Multi-stemmed plants were considered as a single individual, and in order to illustrate largest stem size attained, for these plants only the largest stem diameter was used. These dimensions were selected after a review of the available literature to represent biologically meaningful classes (Lykke, 1998). Increasing diameter class widths were used to balance the decreasing stem density with increasing stem diameter, and to provide for finer divisions in the smaller stem diameters (Condit et al., 1998).

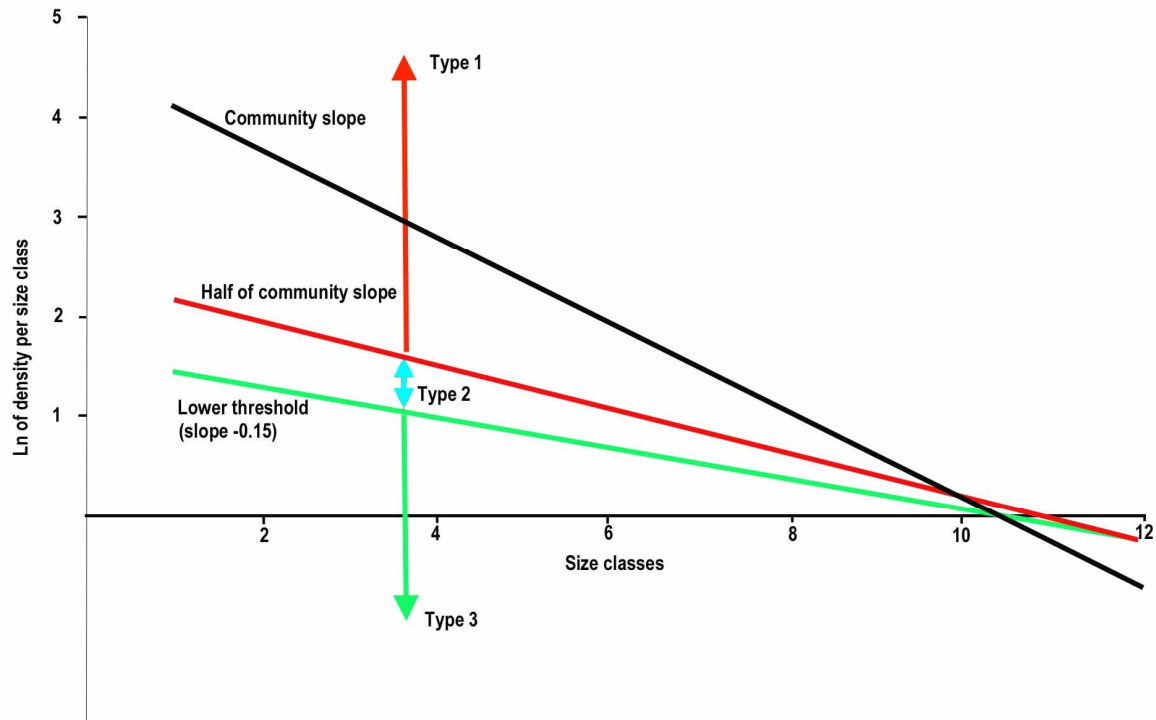
Because size classes bins vary in size, the number of individuals per diameter class was divided by the class width (in cm) to obtain a comparable measure of density on a per cm of diameter basis for all size classes (Condit et al., 1998). Thereafter plant density (D_i) per ha per diameter class per species per vegetation unit in each study site was calculated as: (corrected abundance of individuals per cm per diameter class)/(area in ha of all plots per vegetation unit in a site). The diameter class midpoint (M_i) was calculated as the mean of the upper and lower limit of each diameter size class (Condit et al. 1998). Logarithmic transformations of the type $\ln(D_i+1)$ and $\ln(M_i+1)$ (the value of +1 was added because some size classes' bins were empty) were used to standardize the data (Lykke, 1998; Niklas et al., 2003) before performing least square linear regressions where the size class midpoint dimension was used as independent variable, while the density value was used as dependent variable. This species level size class regression analysis on the spread of stem

diameter values (hereafter referred to as the SCD analysis) was conducted in each vegetation unit. All diameter classes up to the largest class with individuals present were included in the regressions; larger, empty classes were omitted. The minimum number of individuals to perform a reliable regression analysis was set at 30 (hereafter referred to as full analysis) (Niklas et al., 2003). Regressions were also calculated for species where 10 to 29 individuals were sampled (hereafter referred to as limited analysis) as some authors consider it a sufficient sample size (Condit et al., 1998). However, these species are treated separately. The same methodology was used to conduct vegetation unit level size class regression analyses based on all individuals sampled within all plots specific to the vegetation unit, to be used as guidelines to evaluate species behaviour.

The slope of these regressions is considered the most valuable attribute to summarise the shape of the size class distribution and provided a sufficient number of individuals was sampled is able to explain most (>80%) of the data (Condit et al., 1998; Niklas et al., 2003). Moreover, regression slopes provide a direct and objective numerical measure which is less sensitive to personal interpretation than curve shape analysis. The sample plot areas were generally small (<0.1 ha) and therefore the dataset was not expected to depart from log-log linearity (see Niklas et al. 2003) nor to be biased by habitat heterogeneity. The regressions slopes are referred to as SCD slopes.

Depending on the steepness of the size class regression slope, species were classified into three types (Figure 3):

- Type 1: these are species with slopes steeper or equal to half that of the vegetation unit (calculated for all individuals of all species). Because vegetation community slopes in the study area were strongly negative, this category includes species with strongly negative slopes that typically represent regenerating populations (Condit et al., 1998). In this case it is assumed that the deaths of larger individuals will be offset by the



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- Figure 3: Idealised representation of the classification of regression slopes in three types; the equations representing each of the situations appear on the graph. Slopes that fit within the slope limits defined by the arrows can be classified within these respective Types. Note that this is a slope-based classification and that straightforward adjustments must be made to accommodate variations linked to Y-axis intercepts (i.e. a regression with the following equation " $y = -0.2x + 8$ " should still be classified as Type II based on its slope, not on its Y-axis intercept).

successful recruitment and growth of an individual from a healthy pool of small individuals able to grow in the shade under the canopy. These species are usually considered as shade tolerant. In successional terms they can be considered both as pioneer species able to rapidly colonise a gap, and as established dominant mature species (Burslem and Whitmore 1999).

- Type 2: these are species with slopes shallower than half that of the vegetation unit, but steeper than a lower threshold slope coefficient of -0.15. This threshold generally

represent species populations with stable to limited regeneration through pulses of recruitment dependent on canopy gaps or disturbance but where the frequency of recruitment should ensure persistence provided that cycles that drive their dynamics do not exceed the lifespan of these usually shade intolerant organisms. In successional terms, these species can usually be considered as typical to secondary to late secondary stages (Condit et al., 1998; Lykke, 1998, Burslem and Whitmore 1999).

- Type 3: these are species with slopes coefficients shallower than -0.15 or even positive ones. These slopes are considered as flat or positive, and are generally deemed to represent species with populations that have limited to no regeneration under the prevailing conditions, whether it be caused by natural events or through harvesting (Condit et al., 1998; Lykke, 1998; Niklas et al., 2003). Large individuals may be present in landscape, flower and produce fruits, yet prevailing conditions are no longer suitable for recruitment. This may be the case for long lived early successional species finding themselves outcompeted at the recruitment stage by more adapted later successional species. Seedling predation or harvesting may also be responsible for the lack of recruitment. Finally this could also be the case of long lived mature climax species that may not require large pools of seedlings to recruit (Condit et al., 1998; Burslem and Whitmore 1999).

The Y-axis intercept is a new parameter which we use to improve our understanding of species population dynamics. When it is high, it can be reasonably assumed that a large pool of small individuals is available, whereas the closer it gets to zero, the less small individuals are present (Everard et al., 1994). Should it be a negative intercept value associated with a positive size class regression slope, it may indicate that few to no young individuals were found. This could represent either a natural recruitment problem (unsuitable prevailing conditions for recruitment or predation) or anthropogenic activities such as harvesting of smaller size classes. It was considered that this parameter would be of particular use in assisting the interpretation of Type 3 SCD slopes.

Both the slopes and Y-axis intercepts of the regressions were compared for species occurring within the same vegetation unit under different utilisation regimes (treatment 1 to 3) by means of an analysis of covariance (ANCOVA) using GraphPad PRISM 4 (GraphPad Software, San Diego, California, USA, www.graphpad.com). Should there be no significant difference in slope or Y-axis intercept, the species was described through a pooled slope and Y-axis intercept.

Two mean values were calculated for the stem diameter distribution of each species. The 'centroid' was calculated as the arithmetic mean value of the stem diameter for all individuals in a species in a vegetation unit per site. The 'midpoint of stem diameter range' was calculated as the mean of the upper and lower limits of the diameter range included in the diameter class distribution of a species. A link has been shown between the position of the centroid and the midpoint of the diameter class range for each species (Niklas et al. 2003). It is assumed that a centroid value larger than (or to the right of) the midpoint value shows an increase in the number of large stemmed individuals, or a decrease in the number of small stemmed individuals. This is generally considered as an indicator of a mature to old and comparatively undisturbed population. A centroid value smaller than (or to the left of) the midpoint value shows an increase in the proportion of small stemmed individuals or a reduction in the number of large stemmed individuals. The latter may therefore indicate a young and growing population (Niklas et al., 2003). This is considered a result of an inverse relationship between mean stem diameter and plant density at both species and community levels. In general, as mean stem diameter increases the density decreases, in such a way that an increasing part of the biomass is found in fewer individuals (Niklas et al., 2003). This reflects the cumulative response behaviour of all the species that form a community as the succession process takes place. In the absence of disturbance, mature plants of an early successional species grow larger and outcompete smaller stems of that species. Progressively a reduction in density of that species occurs while the species' centroid shifts towards the right of the size class distribution midpoint. If all species behave similarly, then the community's centroid shifts similarly (Niklas et al., 2003). A centroid was therefore also

calculated at the community level, and is referred to as the vegetation community centroid. Because the community behaviour is supposed to reflect the combined behaviour of all its species, it is important to cross-check the community behaviour and species behaviour (Niklas et al., 2003). This differentiation could further allow the separation of species typifying the current situation and species representing remnants of past conditions.

The spatial grain of regeneration is a commonly used forestry concept to describe the “coarseness in texture or granularity of spatial elements composing an area” (Lawes and Obiri, 2003) and is typically used to describe grain at forest level, rather than species level. Species have been defined as fine, intermediate and coarse grained, as have forests depending on the scale of regeneration of the dominant tree species (Lawes and Obiri, 2003). In essence if a forest is dominated by species of fine-grain character, then the balance of probability is in favour of the forest as a whole having fine-grained dynamics. Species grain evaluation is performed through evaluating the relative abundance (expressed as density) of the subcanopy component and the canopy component of the species that reach what can be considered the canopy of the vegetation unit under consideration (Lawes and Obiri, 2003). In other words, species grain evaluation can be summarised as determining whether large and small trees of the same species co-occur or not (Everard et al., 1995). The study by Everard et al. (1995) further established a link between grain and disturbance, whereby in fine-grained forests common canopy species were shade-tolerant, recruiting predominantly through the growth of existing, shade-tolerant species in the absence of large scale disturbance. Comparatively, in coarse-grained forest, the canopy is dominated by shade-intolerant species that recruit predominantly through colonization and rapid growth of shade-intolerant species in larger gaps made by larger scale disturbance.

In the present study, the scatter plot graphical model of Lawes and Obiri (2003) to determine species grain by plotting canopy density (X-axis) and subcanopy density (Y-axis), was used (Figure 4). In the present study, subcanopy and canopy densities were calculated for each species as follow: subcanopy density per species represented the sum of densities for size classes 3 to 6 (i.e. 2 to <14 cm), thereby removing all saplings from the analysis, and

canopy density constituted the group of size classes 7 to 12 (i.e 14 cm and above). Species canopy and subcanopy densities are plotted in the scatter plot. Their position in the plot is judged in reference to what are considered “lower limits” defining the minimum density required in order to ensure two elements (Lawes and Obiri, 2003):

- For canopy elements, sufficient adult trees are present to ensure reproduction can lead to recruitment
- For subcanopy elements, sufficient juvenile individuals are present to ensure that over the course of its lifecycle one of the adults in the canopy may be replaced by a juvenile plant of the subcanopy.

The scatter plot is further partitioned in two sectors by the line that represents equal subcanopy and canopy densities. Because this model rests on common species defining the vegetation unit, a final element taken into consideration is frequency of occurrence of the species in the landscape. At the vegetation unit level, species should be found in at least 50% of plots in order to be considered in this model (Lawes and Obiri, 2003).

In the present study, because the study area is in regions that were studied by Lawes and Obiri (2003), identical critical lower bounds for the canopy and subcanopy density (10 and 30 individuals per ha respectively) and frequency levels (minimum of 50% frequency of occurrence) as Lawes and Obiri (2003) were applied for Closed Woodlands as the latter have a forest-like structure (Gaugris, 2004). However, for Open and Sparse Woodlands, canopy boundaries were relaxed to 5 and 3 individuals per ha respectively and frequency of occurrence was regarded with less importance due to the clumped nature of vegetation in these woodlands. Moreover, shrubby species seldom reach canopy size classes and can therefore not easily be accommodated in the grain model.

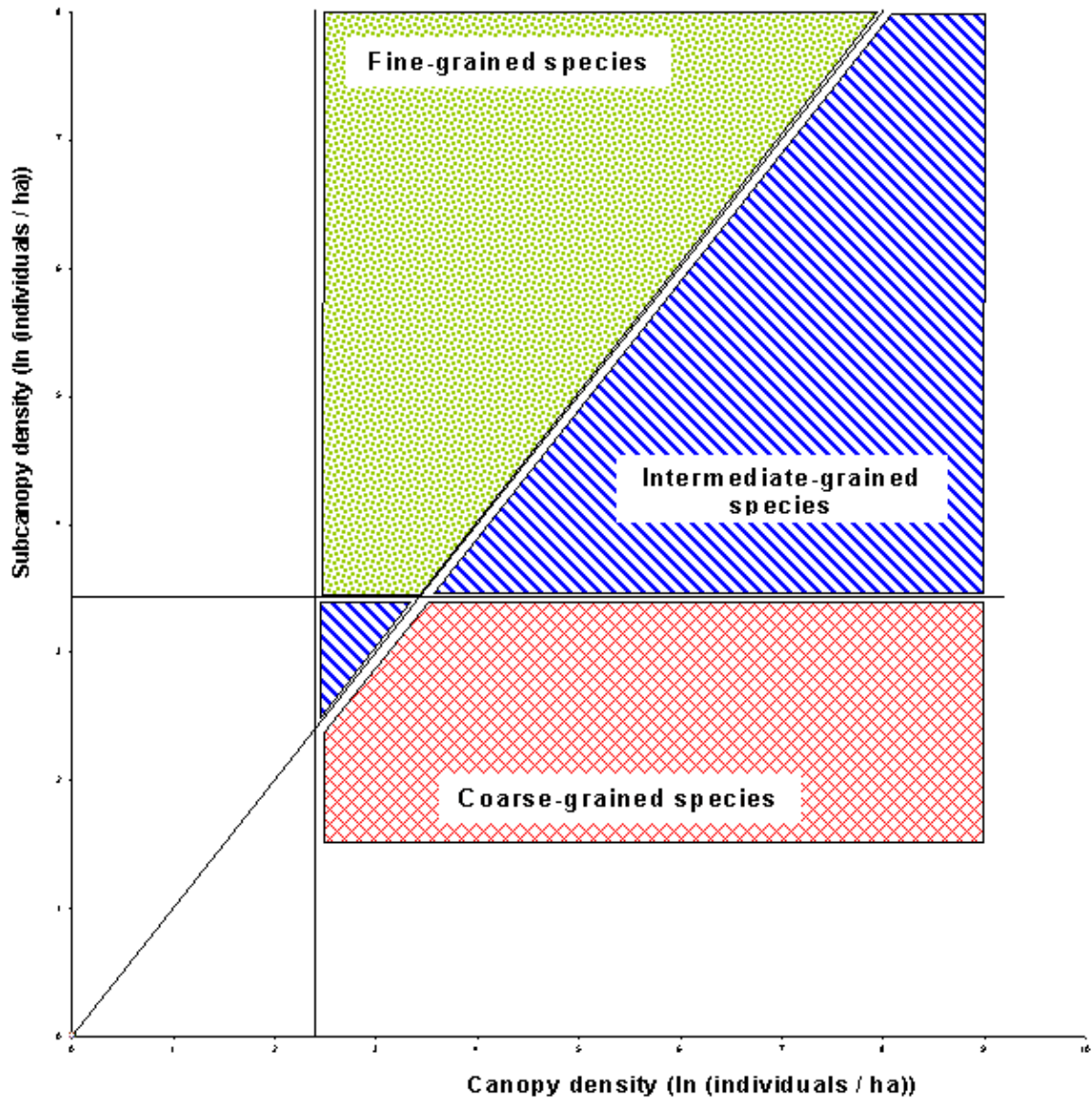


Figure 4 The graphical grain determination model based on canopy density (X-axis) and subcanopy density (Y-axis) used to evaluate tree species grain in the three study sites in KwaZulu-Natal, South Africa. Values are ln-transformed to improve readability. The model is adapted from Lawes and Obiri (2003).

Results

Closed Woodland Thicket

In Tembe only three species (Table 1), all classified as Type 1 (Table 2), had enough individuals sampled for analysis purposes. In Tshanini, 44 species were evaluated. The

majority were classified as Type 1 in the full analysis, whereas most were classified within Type 3 in the limited analysis. The type 3 classification could indicate that such species have populations of large trees with limited recruitment, or that such populations do not need to recruit often to survive in that particular vegetation unit. Manqakulane was represented by 24 species, all classified as Type 1. The subcanopy density indicated that a plentiful supply of young individuals was available to replace senescent ones (Table 1). The mean centroid position was noticeably lower in Manqakulane than at other sites, indicating an overabundance of small individuals there.

INSERT TABLES 1 AND 2 HERE

A total of 18 species regression slopes and y-axis intercepts comparisons could be made between the three sites and half showed different population structures (Table 3). Of the thirteen species that could be compared between Tshanini and Manqakulane seven differed in population structure, whereby Tshanini populations had shallower slopes and lower Y-axis intercepts than their Manqakulane counterparts, thus indicating that less young individuals were found in Tshanini than in Manqakulane. The sole species that could be compared between Tembe and Manqakulane had similar slopes and Y-axis intercepts. Between Tembe and Tshanini only one of the three species compared displayed a similar population structure at both sites.

INSERT TABLE 3 HERE

Closed Woodland on Clay

This vegetation unit occurred only in Manqakulane and Tembe. Some 50 species were evaluated in Tembe (Table 4) but in Manqakulane only five species met the criteria for SCD analysis. Most species at both sites were classified as Type 1 (Table 2), with some,

mostly in the restricted analysis, as Type 2 and 3. Mean centroid positions indicated a larger contribution of small size classes in Manqakulane than in Tembe.

INSERT TABLE 4 HERE

In Tembe the canopy density of a number of species was higher than the subcanopy density. In Manqakulane, the shade giving *Dialium schlechteri* was present at fairly high densities both in the subcanopy and canopy.

The two species that could be compared (*Dialium schlechteri* and *Euclea natalensis*) had similar population structures in the two sites (Table 3).

Closed Woodland on Sand

A total of 43, 39 and 28 species were evaluated in Tembe, Tshanini and Manqakulane respectively (Table 5). At all sites the majority of species were Type 1, but the percentages were highest in Manqakulane, followed by Tembe, and then Tshanini (Table 2). The abundance of small individuals in Manqakulane was apparent by the position of the centroid in size class 2, whereas it occurred within size class 3 in both Tembe and Tshanini.

INSERT TABLE 5 HERE

Quite a range of trees reached large to very large sizes in the canopy of this vegetation unit in both Tembe and Tshanini. Dominant species in Manqakulane's subcanopy included fruit bearing species such as *Strychnos spinosa* and *Strychnos madagascariensis* but also species typical of bush encroachment such as *Dichrostachys cinerea*, and *Terminalia sericea* (Table 5). Most large individuals sampled in Manqakulane were either trees providing shade (*Acacia burkei* and *Acacia robusta*) or trees bearing edible fruit (*Sclerocarya birrea* and *Strychnos madagascariensis*).

Twenty-three species were compared between sites (Table 3). The slopes were usually steepest in Manqakulane, followed by Tembe, and then shallowest in Tshanini. Most differences were at the Y-axis intercept level, where it followed the same order. Twelve species could be compared between Tshanini and Manqakulane of which seven differed in population structure. Of the six species that could be compared between Tembe and Manqakulane, equal numbers of species had similar and different population structures. Between Tembe and Tshanini nine species were compared of which five displayed a similar population structure at both sites.

Open Woodland on Sand

A total of 42 and 33 species were evaluated in Tembe and Tshanini (Table 6) respectively, but only one species in Manqakulane.

INSERT TABLE 6 HERE

In Tembe most species were Type 1 (Table 2). In Tshanini the majority of species were Type 1 in the full analysis, however 50% of species in the limited analysis were Type 3. Centroid positions were similar at the two sites for the full analysis.

In Tembe's canopy, some large to very large trees occurred. Some species showed anomalous population structures in Tembe such as *Albizia adianthifolia* which had a low frequency of occurrence and was absent in the subcanopy and scarce in the canopy. In comparison, in Tshanini this species was abundant and occurred in most plots. Another two species with canopy density much higher than subcanopy density and low frequency of occurrence in Tembe, were *Garcinia livingstonei* and *Sclerocarya birrea*.

Some 21 species were compared between Tembe and Tshanini and of these 13 displayed similar population structures. Most noticeably, *Albizia adianthifolia* had a shallower slope and a lower Y-axis intercept in Tembe than in Tshanini.

Open Woodland on Abandoned Fields

This vegetation type occurred only in Manqakulane. A total of 20 met the criteria for analysis (Table 7), the majority of which were Type 1 (Table 3). The position of the mean centroid indicated an abundance of small individuals.

INSERT TABLE 7 HERE

Only some large fruit bearing trees occurred (Table 13), such as *Sclerocarya birrea*, *Strychnos madagascariensis* and *Strychnos spinosa*, along some shade providing *Dialium schlechteri* and *Trichilia emetica*. *Dichrostachys cinerea*, *Strychnos spinosa* and *Acacia burkei* dominated the subcanopy.

Sparse Woodland on Sand

This vegetation unit occurred only in Tembe and Manqakulane. In Tembe eight species were analysed (Table 8) and most were Type 1 (Table 2). In Manqakulane only three species were evaluated and all were Type 1. The mean centroid position indicated a wealth of saplings in Tembe.

INSERT TABLE 8 HERE

In Manqakulane the potentially encroaching *Dichrostachys cinerea* dominated the subcanopy while the fruit bearing *Sclerocarya birrea* was present in the canopy and subcanopy at equal densities.

Dichrostachys cinerea was the only species that could be compared among sites and displayed a similar population structure (Table 3).

In a general manner across woodland vegetation communities, the majority of species for which at least 30 individuals were sampled displayed Type 1 patterns, whereas species for which less than 30 individuals were sampled displayed Type 3 patterns.

Grain of species and communities

The species grain was established by using the model presented in Figure 4. The detail for each species is provided in Gaugris (2008) and accessible electronically. Most species were fine-grained (Tables 1, 4 - 8), and therefore most vegetation units sampled were considered fine-grained (Table 9). However, the Closed Woodland on Clay and Open Woodland on Sand of Tembe were intermediate-grained vegetation units, as was the Open Woodland on Abandoned Fields in Manqakulane. In contrast to the methodology proposed by Lawes and Obiri (2003), the species for which grain could be established, but for which frequency of occurrence should have precluded their classification, were also considered to determine woodland communities' grain. This was considered because in woodlands the frequency of occurrence tends to be patchy rather than homogenous, and therefore expecting frequencies of occurrence as in forests was not considered as judicious.

INSERT TABLE 9 HERE

Discussion

In general, it appears that anthropogenic activity/disturbance induced an increase in regeneration (demonstrated by steeper slopes) and a shortening of the curve range (spanning less size classes). This could most likely be attributed to the selective and consistent removal of larger usable trees. These results are consistent with reports for other African environments under human influence (Ickowitz, 2006). In Manqakulane, woody regrowth was not affected by large herbivores, as most species larger than rodents were extirpated (Guldmond and Van Aarde, 2007), nor by livestock because their numbers were too low for such an impact (Peteers, 2005). A similar situation has been described for east

African savannas where wood and charcoal harvesting occurs (Luoga et al., 2002). Interestingly, many large fruit-bearing or shade-providing trees remained in Manqakulane, probably due to reluctance to cut such trees. This facilitation has also been commonly reported elsewhere in Africa (Luoga et al., 2002). A gap between small (<3.0 cm) and larger (>10.0 cm) size classes appeared, corresponding to size classes utilised (3.0 to 10.0 cm diameter) for homestead building in Manqakulane (Gaugris et al., 2007a). Indeed, significant differences in species population structures between sites were identified for species preferred for construction (*Psydrax locuples*, *Hymenocardia ulmoides*, *Terminalia sericea*), firewood (*Acacia spp.*, *Strychnos spp.*, *Dialium schlechteri*) or used as fruit crops (*Strychnos spp.*, *Sclerocarya birrea*).

In Tembe, the influence of mammalian herbivores was more subtle. In general, the centroid was either in the same size class or located one size classes higher in Tembe than in Tshanini. The position difference was primarily the consequence of a lower number of individuals sampled in large size classes in Tshanini rather than an overabundance of small individuals in Tshanini. The more centrally located centroid in Tembe meant that many large individuals contributed to the population structure and indicated a mature population status (Niklas et al., 2003). In Tembe this could also reflect herbivores utilising a range of smaller size classes. Fire could have a similar effect and remove smaller size classes (Bond and Keeley, 2005). However, fire occurs both in Tshanini and Tembe, although at a higher frequency in Tshanini (Gaugris et al., 2004; Gaugris, 2008). As such, the healthy population structures of Tshanini, despite regular fires, indicate that fire is not a limiting agent, and therefore that animals are most likely the shaping agent in Tembe (Gaugris and Van Rooyen, 2010). This interpretation was supported by comparisons of species preferred by elephant. For example, *Albizia adianthifolia* was particularly preferred by elephant (Gaugris, 2008) and approaching local extirpation in Tembe, whereas populations of the same species in Tshanini were healthy. *Garcinia livingstonei* and *Vanqueria infausta* seemed to be heading towards a similar problem situation. The reverse situation (declining species in Tshanini but healthy in Tembe) was not yet noted. Should this trend continue, Tembe faces the risk that

herbivores will bring some species to local extinction through continuous repeated utilisation (Gaugris, 2008; O'Connor et al., 2007). These changes in Tembe were reflected in two intermediate-grained vegetation units, which were fine-grained in Tshanini. Grain is known to change from fine to intermediate with increased disturbance levels (Lawes and Obiri, 2003).

In general, species in Tshanini were healthy and regenerating well. Even Type 3 species occurred at high densities in both the subcanopy and canopy and often grew into large trees. These species were usually documented from the limited analysis, although this could be a consequence of the smaller number of plots surveyed in Tshanini. Large, long-lived woody species are known to establish a strong canopy presence and a sufficient but somewhat episodic recruitment through the subcanopy (Burslem and Whitmore, 1999). This indicates both long-term regeneration scales and mature species populations and could explain flat or even positive slopes (Niklas et al., 2003). By nature, such species have small population sizes, as only a few large trees are necessary to form a closed canopy (Burslem and Whitmore, 1999). This is also consistent with the canopy closure observed in Tshanini as a result of vegetation being on the upper side of the fire trap (see Sankaran et al., 2005; Bond and Keeley, 2005).

A major concern lies in what could not be compared. Our sampling strategy favoured common species over rare ones. The percentage of species that met the criteria for analysis and were shared between the sites was low. Gaugris et al. (2004) compared Tembe and Tshanini in terms of species composition and established a similarity in the range of >25 – 50% of all species shared. In the current study, the number of woody species shared was usually lower than 30%. Among the species that could be compared the number of species with different population structures were more or less equal to those with similar structures, except for the Open Woodland on Sand where 62% of species had similar structures. In light of this result, it can be argued that three different sets of common species now occur on three sites that were originally remarkably similar in species composition and abundance (Gaugris et al., 2004). Therefore, it appears that from one state, three different situations arose, linked to three different land use forms. This represents a typical case of savannah in

multiple states depending on treatments received (Sankaran et al., 2005). In all cases where such comparisons were possible, Tshanini appears as the bridge between Tembe and Manqakulane, being more similar in terms of species shared and population structure to Tembe than Manqakulane is to Tembe, and vice versa. We therefore believe that Tshanini is probably the closest to the region's original vegetation state in 1989. These differences in species composition between the sites are concerning from a woodland management perspective. Indeed, a 50 year study in Kenya's Amboseli National Park showed a gradual decline of erstwhile common species, associated with the loss of the woodlands and a move towards grasslands as a result of herbivore utilisation (Western, 2007). The changes described here may therefore have far reaching implications in terms of landscape structure and function of northern Maputaland ecosystems.

Selective harvesting or utilisation by people or animals, appear as the most obvious culprits of landscape structure modification. Preferred common species are selectively removed from the landscape, and replaced by a competitor, which is less desirable to the utilisation agent. With intense selective utilisation, changes can be rapid, and drastic, as documented in east Africa (Walpole et al., 2004, Western, 2007). This selective harvesting was primarily detected by differences in species abundance. Often a species was sampled, but too few individuals occurred to allow analysis at one site's plots although enough occurred on another study site's plots. Species such as *Cleistanthus schlechteri*, *Combretum* spp., *Hymenocardia ulmoides*, *Ptaeroxylon obliquum*, *Pteleopsis myrtifolia*, *Terminalia sericea* are utilised by people in Manqakulane either for building or as firewood (Gaugris et al., 2007a; Gaugris and Van Rooyen, 2009) and were absent or showed a low abundance in Manqakulane, whereas these species were present and displayed healthy population structures in nearby Tshanini. Although some species appeared to thrive in Manqakulane but not in Tshanini (*Carissa* spp. *Clausena anisata*, *Deinbolia oblongifolia*, *Diospyros dichrophylla*, *Searsia gueinzii*, *Xylothea kraussiana*), these species were those that were little utilised, but benefit from changed canopy conditions.

The results therefore clearly illustrate the shaping influence of man on Maputaland's woodlands. This confirms the findings of a study conducted at the vegetation unit level where it could be demonstrated that people and animals influenced vegetation in a distinct and rapid manner with differences at vegetation unit level becoming apparent within a period of less than twenty years (Gaugris, 2008, Gaugris and Van Rooyen, 2008). These findings also confirm to a large extent the hypotheses we proposed to evaluate in the introduction. While we still consider the vegetation units to be woodlands and comparable, each of these sites now as a different set of common species that has been defined by treatment application over a period of 15 years. In Tembe's case, we have observed the expected extirpation of some favoured species and somewhat limited recruitment through herbivore pressure. In Manqakulane, the open patches under the shade of large structural trees were indeed confirmed and the abundance of a set of species normally present at much lower densities was observed. Finally in Tshanini, the relative "health" and number of species with a Type 3 SCD slopes indicated of some woodland units may be reaching maturity and that through canopy closure, a transition into a forest stage could be initiated.

The application of species grain undertaken in the present study complemented the size class distribution analysis. However, the species grain concept was developed for forests and limitations of the model as used in the present study must be stated. Although the model has been applied to woodlands previously (Gaugris et al., 2007b, Gaugris 2004), the validity of its general application to woodlands remains to be established. In addition, vegetation unit grain was here defined regardless of the frequency of occurrence suggested by Lawes and Obiri (2003). Furthermore, unit grain relied on the few species for which grain was determined, which begs the question of the representativeness of this group of species as a surrogate for the entire vegetation community grain.

Fine-grained forest communities are defined mostly by Type 1 species occurring equally at both subcanopy and canopy levels (Everard et al., 1995). Therefore, the fine-grained character of some vegetation units evaluated here could be conclusively shown (Tables 2 and 9). In fine-grained forests, natural regeneration of shade-tolerant species is

based on small-scale processes, and therefore regular small-scale disturbances are required to maintain vegetation structure (Lawes and Obiri, 2003). Coarse-grained species regenerate poorly under frequent small-scale disturbance regimes, but require larger scale disturbance (i.e. large clearings) at lower occurrence frequency, to maintain populations (Lawes and Obiri, 2003). Without disturbance, coarse-grained forests progressively become fine-grained ones as shade-tolerant species replace shade-intolerant species over time (Everard et al., 1995).

The Closed Woodland units of Maputaland were recognised as forest-like (Gaugris, 2008), and therefore the classical grain model was applied with confidence. However, for the Open and Sparse Woodland units, the gap concept driving grain theory is irrelevant. The gap concept relies on the assumption that gap-demanders that are characterised by light sensitive germination, fast growth, regular fruiting schedules, and a dormant seed bank, coexist with non-gap-demanders with light insensitive germination, slow growth, irregular fruiting schedules, and a sapling bank (Burslem and Whitmore, 1999). However, Open and Sparse Woodlands are not gap-limited. The grain concept there may indicate the frequency and intensity at which disturbances (fire, herbivory and human activity) that trigger a different set of regeneration conditions in rainfall unlimited (mean rainfall >650 mm per annum, see Sankaran et al., 2005) woodlands occur. Fine-grained woodlands would require a low intensity disturbance (fire, anthropogenic pressure or herbivore pressure) to be maintained, whereas coarse-grained woodlands would require episodic bursts of disturbance or utilisation to be maintained.

In terms of management and conservation, an intermediate to fine-grain status simplifies matters. In Tembe, the Closed Woodland on Clay and Open Woodland on Sand are now intermediate-grained communities, whereas the Tshanini or Manqakulane equivalents are fine-grained. It can be hypothesised that elephants may have opened the canopy to such an extent that the species composition of these woodlands is changing towards a coarse-grained composition – a case of large scale disturbance benefiting coarse grained species and detrimental to fine-grained ones.

In Manqakulane most vegetation units were classified as fine-grained (Table 9). Under constant human use (Gaugris et al., 2007a), the canopy remains relatively intact, but the undergrowth is utilised. As the subcanopy is constantly disturbed, the ground layer benefits from added space and/or light and the result is a noticeably increased regeneration pattern, although due to selective removal of desired and formerly abundant species the new group or “healthy” looking species may be more pioneer like and less diverse (Babaasa et al., 2004, Backeus et al., 2006). The Open Woodland on Abandoned Fields was classified as intermediate-grained. Woodlands clearing for cultivation and homesteads entirely destroys canopies and this state is maintained by recurrent human activity. Once human activity ceases, shade-intolerant species would be first to re-colonise the sites, followed by the shade-tolerant cohort (Karlowski, 2006). Re-colonisation appears relatively rapid as intermediate-grained woodland regenerated in less than 20 years. However, the species composition at present has a large component of species with alternative uses, especially fruit-bearing and shade-providing trees, mingled with species of little interest. An exception with *Terminalia sericea* merits further attention. This species has only recently become used in construction, due to the lack of other suitable species nearby (Gaugris et al., 2007a), it is therefore highly likely that the healthy population observed in the abandoned fields sites represents a species that was little used at the time, and that built up a healthy population structure.

The Closed Woodland Thicket was fine-grained at all three sites (Table 9). The fine grain was well corroborated by Type 1 species dominance in Tembe and Manqakulane, although it was not that clear in Tshanini. The spread of species in the various groups in Tshanini is reminiscent of mature tree populations in the absence of disturbance (Burslem and Whitmore, 1999). Without disturbance since 1992, the canopy closure favoured shade-tolerant species regeneration. It is also possible that the closed Woodland Thicket is in a transition towards a Short Sand Forest state. The hypothesis is reinforced by the fact that some forest species regenerate well in the thicket’s subcanopy (*Cleistanthus schlechteri*,

Dialium schlechteri, *Hymenocardia ulmoides*, *Pteleopsis myrtifolia*), but also occur in the canopy.

Conclusions

The effects of herbivores and man reported in this study can be described as “classical”. Similar effects have been documented for other regions in Southern, Eastern, and Central Africa. From a management point of view this represents a critical window of opportunity to act. Indeed, where wildlife overutilization occurred, reductions in herbivore populations, especially elephants, were followed by a spectacular woodland recovery within a short time span (Western and Maitumo, 2004), and therefore a prompt management action in that sense may at this stage help in avoiding the decline phase that appears to be a classical response to high herbivore densities. This action could be through the increase of selective removal of animal populations considered to be too high and sale of the products. Opening of fences towards natural dispersion areas north of the park, where human presence is low and may tolerate this increased abundance of wild herbivores is another option. The re-introduction of significant populations of large carnivores able to hunt and rapidly control herbivore populations could also be considered.

With regards to human utilisation, the issue is complex, as development is an inalienable right of rural people. However, many rural communities support the conservation of sections of land without agricultural value and this represents the most easily accessible solution to preserving the natural landscapes of Maputaland. Conservation of botanical reserves where increased tree density and associated increased carbon storage could happen may be considered under the Reduced Emissions from Deforestation and forest Degradation (REDD+) mechanism's following activities: conservation, sustainable management of forests and increased carbon stocks. The financial incentives that could be derived from registering such projects within this mechanism may be a workable solution to conserve natural landscapes in human driven areas of Maputaland.

In general, the grain model worked successfully in the Maputaland woodland environment. The classification outcomes were borne out by theory, and it appears a useful tool to determine the drivers of woodland dynamics. For the Closed Woodland units, the success may be inherent to these units' close relationship to forests. However, the concept seems to work in Open and Sparse Woodland units as well. But in those instances, we feel that grain reflects the frequency at which recruitment occurs in response to typical woodland disturbance (fire and herbivory) rather than gap-formation principles. Fine-grained species seem to find suitable conditions for recruitment continuously whereas coarse-grained species have limited opportunities and pulsed recruitment. The nature of these limited opportunities is difficult to determine here but options such as a temporary and simultaneous release from fire and grazing or favourable climatic conditions appear possible.

From the present study it is clear that man and herbivores significantly alter woodland tree species population structure in Maputaland. However, it is equally encouraging that Maputaland's woodlands are dynamic vegetation units showing an ability to recover rapidly when released from pressure. Management strategies could use the information gathered in this study to set thresholds of potential concern regarding both herbivore and human utilisation.

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