The effect of herbivores and humans on the Sand Forest vegetation of Maputaland, northern KwaZulu-Natal, South Africa

Jerome Y. Gaugris[a] & Margaretha W. van Rooyen[b]

[a] Centre for Wildlife Management, University of Pretoria, 0002 Pretoria, South Africa. [b] Department of Plant Science, University of Pretoria, 0002 Pretoria, South Africa.

Abstract (194 words)

Sand Forest in the Maputaland region of KwaZulu-Natal in South Africa is deemed the most valuable, but also probably the most complex vegetation type of this part of the Maputaland-Pondoland-Albany hotspot of biodiversity. However, Sand Forest is under threat from the current human population growth in that region as well as uncontrolled increases in animal numbers in conservation areas. In this study the impacts of herbivores and humans on the state of woody resources at two sites under differing utilisation regimes were compared. Sand Forest was found to be a complex assemblage of tree communities defined by different canopy and subcanopy levels. Although marked differences in abundance we noted for selected species at the different sites, Sand Forest was still dominated by fine-grained species with an ideal population structure under both utilisation regimes. The fine-grained nature of Sand Forest implies that regeneration depends on the creation of small canopy gaps either by natural processes, humans or elephants, while the creation of large gaps could transform it into woodland. Management of conservation areas where Sand Forest occurs should therefore concentrate efforts on regulating animal populations to levels that provide gap properties that favour forest regeneration.

Keywords

Elephant; fine-grain forest; gaps; Sand Forest; size class distribution; succession; vegetation dynamics

MS: 6114 words (incl. references)

Introduction

African rural people utilise forests for a range of products that are essential to their survival, but thereby also save cash resources for other uses (Shackleton et al. 2007). The long-term sustainability of such resource use is, however, often questioned. In South Africa's Maputaland region of KwaZulu-Natal, demographic growth, society modernisation and tourism-related immigration (Peteers 2005; Jones 2006) are all increasing the demand on the environment. Therefore, valuing the wealth represented by the resource base is essential, but understanding the limits imposed by the dynamics of the resource base is critical to ensure its future (Boudreau et al. 2005; Pote et al. 2006; Shackleton et al. 2007).

These arguments are even more persuasive in an area that is classified as a global hotspot of biodiversity. Maputaland harbours a diverse and delicate mosaic of woodlands and forests interwoven with wetlands, and is recognised as a centre of plant endemism within the Maputaland-Pondoland-Albany biodiversity hotspot. The vegetation is well-represented within a network of conserved areas in the region (Mucina and Rutherford 2006). However, in a twist of fate, the vegetation within these conserved areas has come under threat from unregulated increases in herbivore numbers.

To date, information regarding the structure and dynamics of forests is most often gathered through a single survey, describing size class frequencies, which provide a static representation of plant populations at the time of study. Because once-off surveys often are the only source of information available, a range of techniques have been devised to derive as much knowledge as possible from size class distributions (Poorter et al. 1996; Condit et al. 1998; Lykke 1998; Obiri et al. 2002; Lawes and Obiri 2003; Niklas et al. 2003) to allow managers to make inferences on population dynamics.

In the present study, we focus on a rare vegetation type known as Sand Forest, which is endemic to the Maputaland Centre of Endemism. To avoid permanent biodiversity loss and long-term impairment of ecosystem functioning of the Sand Forest by over-utilisation, an evaluation of the natural resource base in Sand Forests was urgently called for. The objective of the study was to compare the state of woody resources within the Sand Forest on two sites under differing utilisation regimes to obtain a measure of the impacts of herbivores and humans on Sand Forest. We discuss how the presented data can improve our understanding of the forces driving the dynamics.

Study area

The study area encompasses two sites on the coastal plain of Maputaland in northern KwaZulu-Natal (-26.85º to -27.15º South and 32.35º to 32.60º East). Site one is located in the Tembe Elephant Park (Tembe), and site two in the neighbouring Manqakulane rural community, where the Tshanini Community Conservation Area (Tshanini) lies. The undulating landscape of sandy ancient littoral dunes is vegetated by open to closed woodlands, with patches of Sand Forest. The Muzi Swamp runs along the eastern side of the study area while the Pongola River runs along the western side. The region experiences hot, wet summers, while winters are cool to warm and dry. The mean annual rainfall for the period from 1959 to 2006 was 700 mm (Gaugris 2008) but large annual variations occur.

Tembe, a 30 000 ha reserve, was proclaimed with the dual mandate to conserve wildlife and protect the Sand Forest, and was fully fenced off in 1989 (Matthews et al. 2001). Tshanini was established in 2000 on the western 2 420 ha section of land of the Manqakulane Community. The community used this land until 1992 when they moved eastwards to the Muzi Swamp area where a clean water supply and better soils promised an easier life. Protected by tribal rules and a desire to turn it into a conservation area, harvesting of natural resources in Tshanini has been low since then (Gaugris et al. 2004).

These two sites allowed for an analysis of the effect of herbivores, especially the African elephant *Loxodonta africana*, on individual tree species. Because herbivore utilisation in Tshanini is negligible and current human utilisation very low Tshanini can be regarded as a control area for this study.

Methods

Five Sand Forest vegetation units, belonging to two subassociations of the Sand Forest Association, were sampled:

1. 1 *Afzelia quanzensis* Subassociation (AQ)

    1.1.1 *Afzelia quanzensis* Clumps (AQC)

    1.1.2 *Afzelia quanzensis* Forest (AQF)

1.2 Sand Forest Subassociation (SF)

    1.2.1 Short Sand Forest (SSF)

    1.2.2. Tall Sand Forest (TSF)

    1.2.3 Mature Sand Forest (MSF)

Three vegetation types, the *Afzelia quanzensis* Clumps, *Afzelia quanzensis* Forest and Mature Sand Forest were sampled for the first time (Gaugris 2008; Gaugris and Van Rooyen 2008). Rectangular transects of varying length (25 – 50 m) and width (4 – 10 m), depending on vegetation density, were used. A total of 59 transects were sampled in Tembe and 18 in Tshanini.

A classic species based size class distribution regression analysis on stem diameter values of woody plants (hereafter referred to as the SCD analysis) was conducted. Stem diameters of woody plants (for multi-stemmed individuals only the largest stem diameter was used) were classified into 12 size classes (>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 number of individuals per size class was divided by the class width to obtain a mean number of individuals per diameter unit (Condit et al. 1998) before calculating the density (Di) per size class per species per vegetation unit in each study site. The class midpoint (Mi) was set as the halfway measurement for each size class for each diameter size class (Condit et al. 1998). Logarithmic transformations (Condit et al. 1998) of the type ln(Di+1) and ln(Mi+1) were used to standardize the data (Lykke 1998; Niklas et al. 2003) before performing least square linear regressions. The slopes of these regressions were referred to as SCD slopes. Diameter size classes up to the largest size class with individuals present were included in the regressions; larger, empty size classes were omitted.

The minimum number of individuals sampled to perform a reliable regression analysis was set at 30 (hereafter referred to as the full analysis) (Lykke 1998; Niklas et al. 2003). Regressions were also calculated when the sampled number of individual ranged from 10 to 29 (hereafter referred to as the limited analysis) as some authors consider it a sufficient sample size (Condit et al. 1998; Lykke 1998). However, these species were treated separately.

There is a link between the position a species' mean stem diameter, termed "centroid", and the size class distribution midpoint (Niklas et al. 2003). A centroid skewed to the left of the midpoint indicates a young and growing population, whereas one skewed to the right indicates an older, relatively undisturbed population (Niklas et al. 2003). A centroid was also calculated at the vegetation type level, and is referred to as the mean centroid for the vegetation type.

Species were further classified into the following three types depending on the steepness of the size class regression slope:

- Type 1, species with slopes steeper or equal to half that of the vegetation unit in a utilisation regime (calculated on all individuals of all species). These species show good regeneration.
- Type 2, species with slopes shallower than half that of the vegetation unit in a utilisation regime, but steeper than a threshold slope coefficient of -0.15 (Lykke 1998).
- Type 3, species with slopes shallower than the above threshold or with positive slope coefficients.

The slopes and Y-axis intercepts of regressions were compared for species occurring within the same vegetation unit but under different utilisation regimes 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 at either slope or Y-axis intercept levels, the species was described through a pooled slope and Y-axis intercept.

Subcanopy and canopy densities were also calculated per species. Subcanopy density corresponded to the sum of densities per species for size classes 3 to 6, thereby removing all saplings from the analysis, and canopy density constituted size classes 7 to 12. The frequency of occurrence for each species in each vegetation unit was calculated.

The graphical model of Lawes and Obiri (2003) to determine species grain was applied to classify species as fine, coarse, or intermediate-grained (Figure 1). The critical lower bounds of 10 and 30 individuals/ha for the canopy and subcanopy levels respectively, and a minimum of 50% frequency of occurrence in the sampled transects (Lawes and Obiri 2003) were used as it allowed comparison at the regional level (KwaZulu-Natal forests). Grain was determined by the graphical position of species in the scatter plot within the above boundaries (Figure 1).

Results

Only 57 of the 105 inventoried woody species met the criterion for analysis with 33 of these in the Short Sand Forest (SSF), 55 within the Tall Sand Forest (TSF), 29 in the Mature Sand Forest (MSF) and 11 in the *Afzelia quanzensis* Subassociation.

Short Sand Forest

In general, species from the full analysis in Tshanini had steep slopes (Type 1 or 2) (Table 1). The most abundant species in the subcanopy were *Hymenocardia ulmoides*, and *Psydrax locuples*, while the canopy was dominated by *Dialium schlechteri, Ptaeroxylon obliquum* and *Pteleopsis myrtifolia*. Important species for household buildings, such as *Brachylaena huillensis* or *Ptaeroxylon obliquum* (Gaugris et al., 2007a) had steep slope coefficients. However, the former species was rare (33% frequency of occurrence, Table 1) and only found in the subcanopy. In the limited analysis, three shrub species showed shallow or positive slope coefficients (Type 3), denoting struggling populations. Mean centroid for the vegetation type was left-skewed relative to the midpoint and located within size class 3 in the full analysis and size class 4 in the limited one.

In Tembe's SSF *Croton pseudopulchellus* and *Cola greenwayi* had the highest subcanopy densities (Table 2), while the latter also had the highest canopy density. *Brachylaena huillensis* was present in most transects (80%), at a higher density than in Tshanini and also reached the canopy layer. However, *Dialium schlechteri, Psydrax locuples* and *Pteleopsis myrtifolia*, were present in greater abundance in Tshanini than in Tembe. The subcanopy density for *Dialium schlechteri* was lower than its canopy density. The species classified in the full analysis in Tembe all showed steep SCD curve coefficients (Type 1, Table 3), while 46% of species in the limited analysis fell within Type 3. Mean centroid was located in size classes 3 and 5 within the full and limited analyses respectively.

Comparisons between sites (Table 4) at the full analysis level revealed that out of five shared species, only *Drypetes arguta* was significantly different. No species were shared between the limited analyses, while all three species compared across analyses differed significantly between sites.

Tall Sand Forest

In the full analysis (Table 5) most species in Tshanini's TSF fell within Type 1 (Table 4), while the bulk of species in the limited analysis fell within Types 2 and 3. Mean centroid was located within size classes 4 and 5 for the full and limited analyses respectively. Most species in the full analysis had pyramidal population structures, except for *Cleistanthus schlechteri* and *Newtonia hildebrandtii* (Table 5). This was confirmed in the latter species by a positive curve slope coefficient. The canopy was dominated by these two species along with *Dialium schlechteri* and *Pteleopsis myrtifolia*, while the subcanopy was dominated by *Toddaliopsis bremekampii, Drypetes arguta* and *Cola greenwayi.* A range of species contained large (size classes 10 and 11) to very large (size class 12) individuals. In the limited analysis the population of *Balanites maughamii* showed an inverted pyramid structure, as did *Spirostachys africana*. Most species classified in this analysis had relatively low densities and were not prominent in the canopy.

Tembe's TSF subcanopy (full analysis, Table 6) was dominated by species such as *Croton pseudopulchellus, Drypetes arguta, Cola greenwayi* and *Hymenocardia ulmoides* and the canopy by *Cleistanthus schlechteri, Pteleopsis myrtifolia* and *Dialium schlechter*i. Large (size classes 10 and 11) to very large (size class 12) individuals were sampled in a range of species. The population structure of three large canopy trees (*Cleistanthus schlechteri, Dialium schlechteri, Newtonia hildebrandtii*) of this community showed an inverted pyramid shape as did some species in the limited analysis. The majority of species in the full analysis in Tembe (Table 6) fell into Type 1 (Table 4), while in the limited analysis the majority of species were of Type 3, followed by Type 1. Mean centroid was located within size classes 4 and 5 for the full and limited analyses respectively, which is similar to that found in Tshanini.

Comparisons of species between sites (Table 4) at full analysis level indicated that the SCD regressions differed significantly for five of the 16 species. *Brachylaena huillensis* had a higher Y-axis intercept and greater density values in Tembe than in Tshanini and occurred in nearly two thirds of all transects. Comparisons of three species at the limited analysis level indicated that population structure of only *Balanites maughamii* differed significantly and of the four comparisons across analyses only *Psydrax locuples* differed at the Y-axis intercept level.

Mature Sand Forest

Mature Sand Forest stands were only identified within Tembe and no comparisons between sites could be made. The most striking feature in the full analysis (Table 7) was the subcanopy density of species such as *Cola greenwayi, Drypetes arguta, Vepris lanceolata* and *Toddaliopsis bremekampii*, which exceeded 800 individuals/ha and appeared in >80% of transects. The canopy was dominated by *Cola greenwayi, Cleistanthus schlechteri* and *Dialium schlechteri*, but frequencies of the latter two species were lower.

All species within the full analysis were Type 1, while the majority of limited analysis species were Type 3 followed by Type 1 (Table 3). *Dialium schlechteri, Cleistanthus schlechteri* and *Newtonia hildebrandtii* had inverted pyramid structures, and the latter two species had positive slope coefficients (Table 7). Mean centroid was located within size classes 3 and 5 for the full and limited analyses respectively indicating that in general, populations of the common species were young and growing.

Afzelia quanzensis Subassociation

While *Afzelia quanzensis* was the characteristic species, usually forming the canopy of this vegetation unit, it was not the most abundant species. The subcanopy was dominated by a stand of *Vepris lanceolata* (Table 8) and the canopy by *Vepris lanceolata* and *Dialium schlechteri* with some emergents of *Cola greenwayi* and *Diospyros inhacaensis*. Prominent species in the subcanopy were *Diospyros inhacaensis, Drypetes arguta, Drypetes natalensis* and *Euclea natalensis*. In general, this community was of a fairly low stature, reaching heights of 8 to 10 m for the larger trees.

The two species in the full analysis belonged to Type 1, and so did most species in the limited analysis, although there were two species of Type 3. Mean centroid position indicated a young population and was located within size class 3 for both analyses. Saplings made a large contribution to the population structure.

Grain of species and communities

The grain of species was established for all species for which it was possible to identify grain by using the general model (Figure 1). Most species were fine-grained (Tables 1, 2, 5 – 8), and therefore all vegetation units sampled here, and the Sand Forest Association in general, were considered fine-grained (Table 9). Of note was that the large canopy species, regarded as defining Sand Forest, were those classified as coarse or intermediate-grained (*Newtonia hildebrandtii, Cleistanthus schlechteri, Balanites maughamii, Erythrophleum lasianthum* and *Dialium schlechteri*). However, they represented the minority in terms of the number of species classified. In the SSF and TSF, more species with a fine-grained character occurred in Tshanini than in Tembe. However, Tembe's Mature Sand Forest had a definitive fine-grain character and had the most species classified.

Discussion

At individual species level there was a high similarity between the two sites. In the SSF 50% of the compared species had similar SCD structures, while in the TSF 70% of species had similar SCD structures. However, on the whole relatively few of the analysed species could be compared across sites. Only eight (24%) of a total of 33 species for SSF and 23 (43%) out of 55 species for TSF could be compared. The similarity observed within species therefore does not reflect the fact that most species could not be compared between the two sites. This implies that there could in fact still be large differences between the sites at the vegetation unit level as was reported by Gaugris (2008).

Both sites had the majority of their common species (full analysis) classified within Type 1, representing self-sustaining populations. The less abundant species (limited analysis) were generally classified as Type 3, indicating potentially declining populations or mature long-lived early successional species (Condit et al. 1998). Moreover, in both analyses, centroids were generally skewed to the left, which confirmed populations with good regenerative potential. Pooling all species (combined analysis) it was clear that Type 1 dominated in Tembe, while Type 2 was equally important in Tshanini's TSF.

Marked differences in abundance between the sites were observed for several common species, e.g. *Dialium schlechteri, Hymenocardia ulmoides, Pteleopsis myrtifolia* and *Drypetes arguta* in the SSF. In all instances the subcanopy density was much higher in Tshanini, whereas canopy density was higher in Tembe. In most cases the Tembe populations also reached larger size classes. These differences indicate strong recruitment but also truncated populations in Tshanini. In the TSF, differences in abundance between the sites were less marked in the subcanopy, but in general canopy densities in Tembe far exceeded those in Tshanini. *Cola greenwayi* and *Croton pseudopulchellus* had steeper slopes and higher Y-axis intercepts in Tembe than in Tshanini, whereas the reverse was true for *Dialium schlechteri*. *Brachylaena huillensis* and *Ptaeroxylon obliquum* only differed regarding the intercepts, with *Brachylaena huillensis* having a healthier population in Tembe and *Ptaeroxylon obliquum* having a healthier population in Tshanini. In most instances, species in Tembe attained noticeably larger sizes than in Tshanini.

Various factors could be responsible for the differences in species' population structures. Differences at species level could be linked to natural patchiness in the forest (Burslem and Whitmore 1999; Chapman et al. 1999), or to either man or herbivores, or their absence altogether (Banda et al. 2006; Botes et al. 2006). Fire, although a noteworthy agent in Africa (Bond et al. 2003), is unlikely to have been the cause in recent years as no large tracts of Sand Forest have burned recently in both sites (Matthews 2006; Gaugris 2008). However, the presence of charcoal in soil underlying the Tall Sand Forest is testimony to the fact that fires do occur in the Sand Forest and that it is able to develop into Sand Forest again and the effect of fire in the past cannot be ruled out. The sites' close proximity in space rules out climatic factors as an explanation to these differences (Yeh et al. 2000). Additionally, no climatic or catastrophic disturbances appear on record since 1983 (Matthews 2006). The most likely reason for the differences therefore lies in the influence of herbivores and man.

For Tembe, the differences observed are most likely linked to herbivores, whereas the lack of any major disturbance agent in Tshanini in the past 15 years (see also (Maisels et al. 2001)), as well as the effects of man are evident in Tshanini. *Brachylaena huillensis* is a relatively abundant species at both canopy and subcanopy levels in Tembe's Short and Tall Sand Forest, but rare (frequency <10%) and only found in the subcanopy in Tshanini. Because this is the most sought after species for building construction (Gaugris et al. 2007a), its low abundance in Tshanini is believed to stem from selective extraction. The lack of individuals in the larger size classes for several species in Tshanini could likewise be the result of present selective harvesting or the lingering effects of higher levels of harvesting when the Manqakulane community were still living in the area.

Woody species in Tshanini are spread more evenly between Types 1 and 2 than in Tembe. Type 2 species have stagnant populations and could be the result of canopies closing and small tree abundance of light-requiring species decreases as light penetration in the subcanopy decreases. However, when gaps are opened, the abundance of such small classes usually increases (Babaasa et al. 2004). The size of gaps is influential, as the regeneration of Type 1 species occurs mainly under the canopy or in minor gaps such as branch breaks but Type 3 species need substantially larger gaps (Everard et al. 1995).

Type 3 species in Tembe and Tshanini show poor regeneration and their abundance is similar at both sites. These species are possibly long-lived early successional species persisting in the canopy and regenerating irregularly (Burslem and Whitmore 1999). Sampling in the present study did not include large gaps favouring recruitment of Type 3 species. Type 1 and 2 species occurrence therefore reflect the frequent occurrence of small gaps or absence of gaps. Indeed no gaps were encountered in Tshanini, whereas small gaps were noted during sampling in Tembe (Gaugris 2008). However, it is acknowledged that because of the transient nature of gaps, some gaps may not have been obvious during sampling.

Gaps created by elephants in Tembe's Sand Forest have been described as elephant refuges of two sizes (Shannon 2001). A grade 2 refuge represents a small canopy opening, but a grade 1 refuge represents clearings of 20 m diameter and larger. Both refuges are *de facto* gaps, and contribute to increased light penetration to the subcanopy (grade 1 refuge), or improved light conditions throughout the subcanopy (grade 2 refuge). Grade 2 refuges of elephants in Sand Forest may contribute to the greater proportion of tree species classified in Type 1 in Tembe, whereas grade 1 refuges are large enough for Type 3 species. However, while these refuges are still being actively used by elephants, trampling will prevent successful establishment of seedlings.

The results of the present study allow for an improved description and understanding of Sand Forest structure. Short Sand Forest is a dense thicket-like vegetation of short stature, rarely exceeding 8 m (Matthews et al. 2001) or 10 m in height (Gaugris 2008).

Subcanopy density often exceeds 800 individuals/ha for a range of medium to large sized woody species. The canopy is dominated by some of the same species, although at a much lower density than the subcanopy, while some woodland species, such as *Spirostachys africana,* are also present in the canopy. Apart from *Cleistanthus schlechteri* and *Dialium schlechteri,* which emerge above the uniformly low canopy, there are no really large trees. The centroid location skewed to the left of the midpoint, and approximately half of the species being classified as Type 1 indicate a young and dynamic community. Few trees have reached mature sizes because the maximum size class reached rarely exceeds size class 9 in SSF, but the same species grow to larger size classes in the TSF.

Tall Sand Forest forms a link between Short and Mature Sand Forest. Subcanopy density in TSF rarely exceeds 400 individuals/ha for any species, and the bulk of species have densities from 100 to 300 individuals/ha. This species rich unit reaches heights of 12 m with emergents around 15 m (Matthews et al. 2001; Gaugris and van Rooyen 2007). The full size class range occurs, and many species are represented by large mature trees, several of which are also the emergents or canopy species from SSF. However, additional species appear in the canopy of TSF. Because the centroid location is still strongly skewed to the left of the midpoint and 50% of all species are of Type 1 the Tall Sand Forest should also be regarded as a dynamic vegetation unit.

The Mature Sand Forest has a tall tree stratum of 12 to 15 m and a second lower canopy at 10 m (Gaugris 2008). This unit is characterised by subcanopy densities in excess of 1000 individuals/ha for some species, and large to very large individuals are commonplace in the canopy. The centroid position of common species shows a skew to the left, while the centroid position of less common species shows a centrally located centroid, indicating a mature population stage. Most species (61%) are classified as Type 1 indicating growing populations.

These three vegetation units describe what a successional pathway from Short to Mature Sand Forest: a suite of species appears in the SSF and is maintained in the TSF stage. The TSF stage leads to the establishment of a tall (12 – 15 m) canopy of large trees

(Mature Sand Forest), while the undergrowth goes through another change as light conditions are modified once this tall canopy has emerged.

The grain concept originates from forestry ecology in South Africa (Midgley et al. 1990), and represents a two-dimensional analysis comparing the number of individuals of a species at subcanopy and canopy levels (Everard et al. 1995; Lawes and Obiri 2003). The species grain indicates the regeneration scale of species. Coarse-grained species regenerate over large areas at low densities, and may not withstand intense utilisation. Fine-grained species have well-balanced subcanopy and canopy densities reflecting ideal population structures. The wealth of Type 1 species concurred with an abundance of fine-grained species in the Sand Forest and it is therefore fairly conclusive that Sand Forests are fine-grained forests.

Fine-grained forests are populated by shade-tolerant, fine-grained species, where the scale of patch-to-patch variation is small (Midgley et al. 1990; Everard et al. 1995). Scale of variation here refers to “the scale at which normal dynamic regeneration processes occur” (Everard et al. 1995), while patch is loosely used to define structures ranging from a few hectares to hundreds of hectares or more. Small patches of fine-grained forest can exist as sustainable entities (Everard et al. 1995) and small gaps are sufficient to ensure successful species regeneration. However, the grain concept does not include other reproductive processes, such as pollination and seed dispersal, which function at a different scale altogether (Everard et al. 1995; Maisels et al. 2001; O'Connor et al. 2007).

In terms of dynamics, the fine-grain nature indicates that at the patch level, Sand Forest is likely to sustain itself. However, the observations on avian species assemblages (Van Rensburg et al. 2000) and dung beetles (Botes et al. 2006) suggest that diversity between patches is such that many patches over a large area are required to conserve Sand Forest, and that these forests are susceptible to overutilisation by gap creating agents. Our study supports the notion that elephants are important agents affecting Sand Forest dynamics through the creation of small to intermediate gaps and associated changes in light regime. However, in a small, confined reserve where elephant density increases (Morley

2005), the risk that elephants will open more and larger gaps increases accordingly (O'Connor et al. 2007). Such gaps could change forest dynamics or even engender a retrogressive successional change to woodlands altogether as suggested by Van Rensburg et al. (2000). However, the absence of disturbance, observed in Tshanini, shows that species distribution curves possibly change from Type 1 to Type 2. In Sand Forest it therefore appears that no disturbance is equally problematic as over-disturbance.

Note on the methodology

The limitations of a size class analysis for obtaining information on population dynamics are acknowledged (Condit et al. 1998; Niklas et al. 2003). However, the incorporation of the grain concept contributed to an improved understanding of the structure and dynamics of Sand Forest.

The distinction between the full and limited analyses contributed to the value of the present study. The distinction proved particularly useful in separating different tree dynamics. For species in the limited analysis, the small number of individuals was information in itself and it allowed a better understanding of forest dynamics. Therefore, to overlook species where sampled individuals were low would have limited the ability to perceive patterns in the dynamics of this area. We therefore recommend that future studies in this field do not discard species with low abundance on the simple proviso that statistical significance would not be met.

Comparing two sites differing in utilisation regime and analysing as many parameters as possible has provided a much-improved understanding of the structure and dynamics of Sand Forest. Whenever long-term studies are not feasible we strongly recommend such practices. While the methodology is not new, the use of a variety of parameters in one study is novel. The use of species grain was extremely useful, it confirmed some observations with regards to dynamics and was easily adapted to our study’s purposes.

Sand Forest management implications

The fine-grain character is a positive sign for Sand Forest conservation as it simplifies management in conserved areas. We advise managers to control animal populations to promote the presence and regular creation of small canopy gaps. In a park like Tembe, this implies strict control of the elephant population, which is a delicate issue (O'Connor et al. 2007), although our study now lends credence to such a policy. Populations of other forest dwelling herbivores or temporary users should also be kept in check, to ensure that regeneration guilds of tree species are not over-utilised. However, culling of such species, or their natural removal by an increased carnivore population is easier to manage than elephant numbers.

Managing Sand Forest outside conserved areas, within the human dominated landscape, will prove more difficult. However, results from another study in KwaZulu-Natal showed that well-regulated human utilisation in a fine-grained forest did not adversely affect tree dynamics (Boudreau and Lawes 2005). Management will have to ensure that small gaps that simulate the natural dynamics are created. This could be achieved by the rotational harvest of small sectors of forest, where removal of smaller trees suitable for building construction in the region is controlled. From time to time the removal of large canopy individuals could be justified. The potential for sustainable harvesting within Tshanini's Sand Forest has been investigated (Gaugris and van Rooyen 2007; Gaugris et al. 2007b) and we recommend that a similar approach be followed at the regional level.

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Caption to figures

Table 1 Detail of species level size class distribution (SCD) regressions, including statistical significance, the maximum size classes (SC) reached, number of individuals sampled, centroid position, sapling, subcanopy and canopy density, frequency of occurrence in sample plots, and species grain for the Short Sand Forest in the Tshanini Community Conservation Area

Analysis	Species	Slope	Intercept	R^2	Signifi-cance	SC Max	Individuals sampled	Centroid in SC	Subcanopy density (ind/ha)	Canopy density (ind/ha)	Frequency (%)	Species grain
Community	**Community SCD**	**-2.37**	**11.24**	**0.97**	**	**12**	**2411**					
Full	*Acalypha glabrata*	-1.54	8.18	0.46	-	3	239	02	517	0	50	***NA***
Full	*Boscia filipes*	-0.13	2.93	0.00	-	8	48	05	733	33	83	Fine
Full	*Brachylaena huillensis*	-2.21	7.29	0.76	-	4	62	02	133	0	33	***NA***
Full	*Cleistanthus schlechteri*	-0.93	5.12	0.71	**	8	41	05	483	67	17	Fine (*NA*)
Full	*Dialium schlechteri*	-1.06	5.74	0.58	*	9	80	05	1050	150	83	Fine
Full	*Drypetes arguta*	-1.25	7.13	0.90	*	4	115	02	833	0	100	***NA***
Full	*Grewia microthyrsa*	-0.55	4.59	0.04	-	4	41	03	250	0	100	***NA***
Full	*Hymenocardia ulmoides*	-2.71	9.13	0.78	**	9	298	03	3467	17	100	Fine
Full	*Hyperacanthus microphyllus*	-0.95	3.87	0.11	-	7	57	03	767	17	100	Fine
Full	*Monodora junodii*	1.46	1.31	0.27	-	5	33	04	483	0	100	***NA***
Full	*Psydrax locuples*	-1.91	8.11	0.87	**	9	205	03	2150	100	83	Fine
Full	*Ptaeroxylon obliquum*	-2.17	8.30	0.85	**	9	508	02	483	133	100	Fine
Full	*Pteleopsis myrtifolia*	-1.63	7.08	0.75	**	9	126	04	1567	100	100	***NA***
Full	*Salacia leptoclada*	-2.88	8.11	0.85	-	4	77	02	300	0	100	***NA***
Full	*Toddaliopsis bremekampii*	-0.88	6.47	0.27	-	5	153	03	1917	0	83	***NA***
Full	*Uvaria caffra*	-0.55	3.47	0.03	-	6	44	03	500	0	100	***NA***
	Mean SCD centroid location for common species:							03				
Limited	*Coddia rudis*	-1.50	5.75	0.97	-	3	20	02	83	0	67	***NA***
Limited	*Croton steenkampianus*	4.10	-0.65	0.55	-	3	17	03	100	0	100	***NA***
Limited	*Euclea natalensis*	-1.46	5.33	0.76	*	7	29	03	117	17	50	Fine
Limited	*Margaritaria discoidea*	0.89	1.66	0.13	-	5	23	04	367	0	50	***NA***
Limited	*Ochna arborea*	0.57	1.99	0.04	-	5	18	03	200	0	83	***NA***
Limited	*Spirostachys africana*	-0.88	3.95	0.44	*	12	22	06	100	117	50	Intermediate
	Mean SCD centroid location for common species:							04				

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

NA Not applicable, following the species grain, it indicates that while grain could be determined, the frequency of occurrence is too low to warrant inclusion in the model

Table 2 Detail of species level size class distribution (SCD) regressions, including statistical significance, the maximum size classes (SC) reached, number of individuals sampled, centroid position, sapling, subcanopy and canopy density, frequency of occurrence in sample plots, and species grain for the Short Sand Forest in the Tembe Elephant Park

Analysis	Species	Slope	Intercept	R^2	Signi-ficance	SC Max	Individuals sampled	Centroid in SC	Subcanopy density (ind/ha)	Canopy density (ind/ha)	Frequency (%)	Species grain
Community	**Community SCD**	**-1.92**	**9.91**	**0.98**	**	**10**	**850**					
Full	*Brachylaena huillensis*	-1.81	6.53	0.83	**	6	31	03	245	19	80	Fine
Full	*Cola greenwayi*	-1.35	6.59	0.87	**	6	63	04	660	151	60	Fine
Full	*Croton pseudopulchellus*	-2.96	9.90	0.89	*	3	247	02	1264	0	80	***NA***
Full	*Drypetes arguta*	-1.66	7.04	0.95	**	6	59	04	698	57	70	Fine
Full	*Hymenocardia ulmoides*	-1.54	5.99	0.71	**	6	31	04	453	19	80	Fine
Full	*Salacia leptoclada*	-3.11	8.63	0.90	*	3	65	02	321	0	60	***NA***
Full	*Toddaliopsis bremekampii*	-1.50	6.31	0.74	*	5	41	03	566	19	60	Fine
	Mean SCD centroid location for common species:							03				
Limited	*Dialium schlechteri*	0.26	0.73	0.12	-	10	14	09	75	189	80	Intermediate
Limited	*Drypetes natalensis*	-1.18	5.28	0.87	**	7	24	05	245	94	80	Fine
Limited	*Erythrophleum lasianthum*	0.02	0.99	0.00	-	10	10	09	19	151	80	Coarse
Limited	*Ochna natalitia*	-0.45	3.92	0.32	-	3	12	03	189	0	50	***NA***
Limited	*Pavetta lanceolata*	2.68	0.34	0.50	-	2	20	03	302	0	40	***NA***
Limited	*Psydrax locuples*	-0.07	2.47	0.00	-	4	10	04	170	0	60	***NA***
Limited	*Psydrax obovata*	-0.34	3.06	0.04	-	6	28	05	472	38	40	Fine (NA)
Limited	*Pteleopsis myrtifolia*	-0.57	3.96	0.65	**	7	23	06	226	170	90	Fine
Limited	*Tricalysia junodii*	-2.98	7.80	1.00	-	0	28	01	0	0	60	***NA***
Limited	*Tricalysia lanceolata*	0.15	2.95	0.00	-	2	16	03	245	0	50	***NA***
Limited	*Vepris lanceolata*	-1.11	3.81	0.23	-	5	13	03	94	38	30	Fine (NA)
	Mean SCD centroid location for common species:							05				

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

NA Not applicable, following the species grain, it indicates that while grain could be determined, the frequency of occurrence is too low to warrant inclusion in the model

Table 3 The percentage of species with Type 1 to 3 slopes for the Sand Forest vegetation of Tembe Elephant Park (TEP) and Tshanini Community Conservation Area (TCCA), for the full (≥30 individuals sampled) and limited (10 - 29 individuals sampled) analyses. The total number of species (No spp) for analyses by vegetation unit or subunit is indicated in the top line of each analysis

Analysis	Type	Percentage of species per Type by vegetation units and sites					
		Short Sand Forest		Tall Sand Forest		Mature Sand Forest	*Afzelia quanzensis* Subassociation
		TCCA	TEP	TCCA	TEP	TEP	TEP
	No spp→	16	7	22	21	12	2
Full		(%)	(%)	(%)	(%)	(%)	(%)
	Type 1	50	100	59	80	100	100
	Type 2	38	0	27	10	0	0
	Type 3	13	0	14	10	0	0
	No spp→	6	11	14	14	16	8
Limited		(%)	(%)	(%)	(%)	(%)	(%)
	Type 1	33	27	7	36	31	63
	Type 2	17	27	50	21	25	13
	Type 3	50	46	43	43	44	25
	No spp→	22	18	36	35	28	10
Combined		(%)	(%)	(%)	(%)	(%)	(%)
	Type 1	45	55	39	63	61	70
	Type 2	32	17	36	14	14	10
	Type 3	23	28	25	23	25	20

Type 1 Slopes steeper or equal to half that of the vegetation unit evaluated

Type 2 Slopes shallower than half that of the vegetation unit evaluated but steeper than - 0.15

Type 3 Slopes shallower than - 0.15 coefficient or with positive slope coefficients

Table 4 A comparison of size class distribution (SCD) parameters between Tembe Elephant Park (TEP) and Tshanini Community Conservation Area (TCCA) within a species (F = Full analysis, ≥30 individuals sampled; L = Limited analysis, 10 – 29 individuals sampled)

Vegetation unit	Species	Comparison levels Analysis	Slope comparison			Intercept comparison			Outcome	Note*
			P-value	Signifi-cance	Pooled slope	P-value	Signifi-cance	Pooled intercept		
Short Sand Forest	*Brachylaena huillensis*	F / F	0.67	-	-1.87	0.66	-	6.74	Similar	-
	Drypetes arguta	F / F	0.33	-	-1.60	0.05	*	-	Different	-
	Hymenocardia ulmoides	F / F	0.12	-	-2.20	0.26	-	7.69	Similar	-
	Salacia leptoclada	F / F	0.83	-	-3.03	0.67	-	8.41	Similar	-
	Toddaliopsis bremekampii	F / F	0.48	-	-1.32	0.10	-	6.44	Similar	-
	Dialium schlechteri	L / F	<0.01	**	-	-		-	Different	X
	Psydrax locuples	L / F	0.03	*	-	-		-	Different	X
	Pteleopsis myrtifolia	L / F	0.02	*	-	-		-	Different	-
Tall Sand Forest	*Brachylaena huillensis*	F / F	0.46	-	-1.55	<0.01	**	-	Different	-
	Cleistanthus schlechteri	F / F	0.82	-	-0.44	0.66	-	3.13	Similar	-
	Cola greenwayi	F / F	0.01	*	-	-		-	Different	-
	Croton pseudopulchellus	F / F	0.04	*	-	-		-	Different	-
	Dialium schlechteri	F / F	<0.01	**	-	-		-	Different	-
	Drypetes arguta	F / F	0.32	-	-1.90	0.30	-	7.37	Similar	-
	Haplocoelum foliolosum	F / F	0.47	-	-1.02	0.45	-	4.04	Similar	-
	Hymenocardia ulmoides	F / F	0.29	-	-1.61	0.22	-	6.25	Similar	-
	Hyperacanthus microphyllus	F / F	0.35	-	-0.82	0.07	-	3.62	Similar	-
	Monodora junodii	F / F	0.88	-	0.30	0.72	-	1.34	Similar	-
	Newtonia hildebrandtii	F / F	0.15	-	-0.06	0.64	-	1.02	Similar	-
	Ptaeroxylon obliquum	F / F	0.11	-	-1.18	0.04	*	-	Different	-
	Pteleopsis myrtifolia	F / F	0.98	-	-0.63	0.62	-	3.62	Similar	-
	Salacia leptoclada	F / F	0.26	-	-2.84	0.80	-	7.32	Similar	-
	Toddaliopsis bremekampii	F / F	0.81	-	-2.04	0.55	-	7.07	Similar	-
	Uvaria caffra	F / F	0.40	-	-1.23	0.91	-	4.21	Similar	-
	Balanites maughamii	L / L	0.01	*	-	-		-	Different	-
	Grewia microthyrsa	L / L	0.87	-	-0.33	0.99	-	2.28	Similar	-
	Zanthoxylum leprieuri	L / L	0.22	-	-0.43	0.32	-	1.97	Similar	-
	Boscia filipes	F / L	0.35	-	-0.18	0.24	-	1.60	Similar	X
	Psydrax locuples	F / L	0.08	-	-1.61	0.01	*	-	Different	-
	Strychnos henningsii	F / L	0.16	-	-0.12	0.33	-	1.78	Similar	-
	Suregada zanzibariensis	L / F	0.61	-	-0.58	0.89	-	2.58	Similar	X

** Highly significant (p ≤ 0.01); * Significant (p ≤ 0.05); - Not significant (p > 0.05)
Note* Analyses marked with an X were conducted on regression slopes where F was not significant in at least one site.

Table 5 Detail of species level size class distribution (SCD) regressions, including statistical significance, the maximum size classes (SC) reached, number of individuals sampled, centroid position, sapling, subcanopy and canopy density, frequency of occurrence in sample plots, and species grain for the Tall Sand Forest in the Tshanini Community Conservation Area

Analysis	Species	Slope	Intercept	R^2	Signifi-cance	SC Max	Individuals sampled	Centroid in SC	Subcanopy density (ind/ha)	Canopy density (ind/ha)	Frequency (%)	Species grain
Community	**Community SCD**	**-1.86**	**9.21**	**0.97**	**	**12**	**2883**					
Full	*Acalypha glabrata*	-1.48	5.45	0.52	-	4	97	02	130	0	92	***NA***
Full	*Boscia filipes*	-0.44	2.47	0.13	-	9	50	05	140	13	58	Fine
Full	*Brachylaena huillensis*	-1.39	4.18	0.87	**	6	33	03	37	0	8	***NA***
Full	*Cleistanthus schlechteri*	-0.47	3.14	0.49	*	11	90	07	113	143	75	Intermediate
Full	*Cola greenwayi*	-0.30	3.18	0.03	-	8	172	05	490	30	75	Fine
Full	*Croton pseudopulchellus*	-1.22	4.05	0.29	-	6	68	03	127	0	58	***NA***
Full	*Dialium schlechteri*	-1.01	4.44	0.84	**	11	96	05	160	70	100	Fine
Full	*Drypetes arguta*	-2.13	7.57	0.91	**	7	392	03	560	3	83	***NA***
Full	*Euclea natalensis*	-1.63	4.53	0.75	*	7	44	03	13	7	75	***NA***
Full	*Haplocoelum foliolosum*	-1.13	4.37	0.89	**	9	62	05	87	30	75	Fine
Full	*Hymenocardia ulmoides*	-1.72	6.36	0.93	**	10	197	04	393	17	92	Fine
Full	*Hyperacanthus microphyllus*	-1.38	5.26	0.68	*	6	107	03	203	0	100	***NA***
Full	*Manilkara concolor*	0.35	1.06	0.11	-	7	35	05	103	10	17	Fine
Full	*Monodora junodii*	0.24	1.32	0.04	-	7	48	05	150	3	67	***NA***
Full	*Newtonia hildebrandtii*	0.16	0.40	0.08	-	12	34	09	33	80	58	Intermediate
Full	*Psydrax locuples*	-1.94	6.08	0.94	**	8	113	03	127	3	58	***NA***
Full	*Ptaeroxylon obliquum*	-1.40	5.36	0.99	**	10	108	04	140	33	83	Fine
Full	*Pteleopsis myrtifolia*	-0.64	3.56	0.49	*	10	90	06	190	80	100	Fine
Full	*Salacia leptoclada*	-2.52	6.76	0.87	**	6	150	02	163	0	83	***NA***
Full	*Suregada zanzibariensis*	-0.42	2.27	0.08	-	7	31	04	80	3	58	***NA***
Full	*Toddaliopsis bremekampii*	-2.07	7.25	0.89	**	11	397	03	717	3	100	***NA***
Full	*Uvaria caffra*	-0.86	3.67	0.21	-	6	63	03	153	0	100	***NA***
		Mean SCD centroid location for common species:						04				
Limited	*Balanites maughamii*	0.08	0.28	0.06	-	12	14	10	10	37	42	Coarse
Limited	*Mystroxylon aethiopicum*	-0.24	1.67	0.07	-	8	20	05	50	10	67	Fine
Limited	*Coddia rudis*	-1.79	4.80	0.98	-	3	29	02	17	0	50	***NA***
Limited	*Grewia microthyrsa*	-0.50	2.48	0.10	-	4	13	03	17	0	42	***NA***

Limited	*Hippocratea delagoensis*	1.08	0.36	0.36	-	5	29	04	93	0	58	***NA***
Limited	*Margaritaria discoidea*	-0.68	2.48	0.57	-	5	11	04	20	0	33	***NA***
Limited	*Ochna arborea*	-0.11	1.14	0.02	-	7	10	05	27	3	50	***NA***
Limited	*Rhus gueinzii*	-0.87	2.87	0.81	**	7	14	04	20	3	58	***NA***
Limited	*Rothmannia fischeri*	-0.07	1.27	0.01	-	9	24	06	50	27	58	Fine
Limited	*Spirostachys africana*	0.19	-0.09	0.26	-	11	12	08	7	33	33	Coarse (*NA*)
Limited	*Strychnos henningsii*	0.54	0.61	0.20	-	5	12	04	33	0	25	***NA***
Limited	*Tarenna litoralis*	-0.31	2.20	0.15	-	5	14	03	33	0	25	***NA***
Limited	*Vitex ferruginea*	-0.32	1.81	0.19	-	7	15	05	37	7	33	***NA***
Limited	*Zanthoxylum leprieuri*	-0.18	1.32	0.04	-	7	11	04	27	3	58	***NA***
		Mean SCD centroid location for common species:						05				

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

NA Not applicable, following the species grain, it indicates that while grain could be determined, the frequency of occurrence is too low to warrant inclusion in the model

Table 6 Detail of species level size class distribution (SCD) regressions, including statistical significance, the maximum size classes (SC) reached, number of individuals sampled, centroid position, sapling, subcanopy and canopy density, frequency of occurrence in sample plots, and species grain for the Tall Sand Forest in the Tembe Elephant Park

Analysis	Species	Slope	Intercept	R^2	Signifi-cance	SC Max	Individuals sampled	Centroid in SC	Subcanopy density (ind/ha)	Canopy density (ind/ha)	Frequency (%)	Species grain
Community	**Community SCD**	**-1.87**	**9.77**	**0.98**	**	**12**	**4632**					
Full	*Brachylaena huillensis*	-1.59	5.79	0.96	**	11	123	03	125	21	65	Fine
Full	*Cassipourea mossambicensis*	-1.27	4.38	0.88	**	8	40	04	58	9	46	***NA***
Full	*Cleistanthus schlechteri*	-0.42	3.12	0.54	**	12	119	07	125	222	81	Intermediate
Full	*Cola greenwayi*	-1.84	7.50	0.96	**	12	461	04	703	140	84	Fine
Full	*Croton pseudopulchellus*	-3.33	9.84	0.93	**	8	1241	02	971	3	100	***NA***
Full	*Croton steenkampianus*	-2.83	6.74	0.85	-	3	76	02	21	0	35	***NA***
Full	*Dialium schlechteri*	0.15	0.78	0.08	-	12	59	09	24	152	76	Coarse
Full	*Drypetes arguta*	-1.73	7.22	0.90	**	8	440	04	898	46	97	Fine
Full	*Drypetes natalensis*	-1.22	4.75	0.95	**	8	69	04	104	24	54	Fine
Full	*Haplocoelum foliolosum*	-0.97	3.82	0.82	**	12	47	05	46	43	49	Fine (*NA*)
Full	*Hymenocardia ulmoides*	-1.50	6.13	0.95	**	10	197	04	332	79	81	Fine
Full	*Hyperacanthus microphyllus*	-0.55	2.50	0.14	-	8	41	04	107	6	54	***NA***
Full	*Leptactinia delagoensis*	-1.42	4.61	0.53	-	5	47	03	88	0	41	***NA***
Full	*Monodora junodii*	0.38	1.34	0.07	-	6	36	04	100	0	41	***NA***
Full	*Newtonia hildebrandtii*	-0.27	1.65	0.12	-	12	41	10	6	100	57	Coarse
Full	*Psydrax obovata*	-0.60	3.52	0.48	-	8	73	05	137	43	49	Fine (*NA*)
Full	*Ptaeroxylon obliquum*	-0.96	3.75	0.65	**	10	57	04	64	30	73	Fine
Full	*Pteleopsis myrtifolia*	-0.63	3.69	0.60	**	10	100	06	88	164	70	Intermediate
Full	*Salacia leptoclada*	-3.37	8.10	0.96	**	5	200	02	100	0	78	***NA***
Full	*Strychnos henningsii*	-0.32	2.34	0.25	-	8	37	05	76	30	51	Fine
Full	*Toddaliopsis bremekampii*	-0.833	6.691748	0.86494	**	7	223	02	208	1	76	***NA***
Full	*Tricalysia delagoensis*	-0.70	2.74	0.20	-	8	34	04	73	3	35	***NA***
Full	*Tricalysia junodii*	-4.00	7.64	0.87	-	4	159	01	9	0	62	***NA***
Full	*Uvaria caffra*	-1.61	4.75	0.97	**	6	35	03	43	0	32	***NA***
Full	*Uvaria lucida*	-2.45	6.91	0.95	**	7	197	02	94	3	68	***NA***
Full	*Vepris lanceolata*	-1.46	4.33	0.90	**	8	30	03	24	3	32	***NA***
		Mean SCD centroid location for common species:						04				

Limited	*Balanites maughamii*	-0.43	1.69	0.44	*	12	12	07	18	12	14	Intermediate (*NA*)
Limited	*Boscia filipes*	0.03	0.85	0.00	-	10	28	06	52	33	49	Fine (*NA*)
Limited	*Brachylaena discolor*	-2.55	5.50	0.96	*	4	27	02	12	0	19	***NA***
Limited	*Burchellia bubalina*	-0.10	1.80	0.03	-	5	13	04	33	0	16	***NA***
Limited	*Combretum celastroides*	-0.07	1.44	0.01	-	8	28	05	67	15	43	Fine (*NA*)
Limited	*Erythrophleum lasianthum*	-0.31	1.39	0.32	-	12	14	08	3	33	30	Coarse (*NA*)
Limited	*Grewia microthyrsa*	-0.27	2.19	0.04	-	6	28	04	73	0	49	***NA***
Limited	*Manilkara discolor*	0.13	0.43	0.11	-	12	28	09	18	67	43	Coarse (*NA*)
Limited	*Pavetta lanceolata*	-1.12	3.67	0.44	-	5	29	03	67	0	35	***NA***
Limited	*Psydrax locuples*	-1.29	3.78	0.79	**	8	23	03	18	3	41	***NA***
Limited	*Strychnos decussata*	0.41	-0.05	0.31	-	8	16	06	37	12	8	Fine (*NA*)
Limited	*Strychnos gerrardii*	-0.28	1.67	0.06	-	7	16	04	37	6	19	***NA***
Limited	*Suregada zanzibariensis*	-0.95	3.13	0.61	-	5	16	03	37	0	27	***NA***
Limited	*Tricalysia lanceolata*	-0.42	2.54	0.11	-	4	12	03	18	0	19	***NA***
Limited	*Wrightia natalensis*	0.31	-0.29	0.45	*	11	19	09	3	55	41	Coarse (*NA*)
Limited	*Zanthoxylum leprieuri*	-1.04	3.09	0.64	-	5	12	03	18	0	19	***NA***
		Mean SCD centroid location for common species:						05				

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

NA Not applicable, following the species grain, it indicates that while grain could be determined, the frequency of occurrence is too low to warrant inclusion in the model

Table 7 Detail of species level size class distribution (SCD) regressions, including statistical significance, the maximum size classes (SC) reached, number of individuals sampled, centroid position, sapling, subcanopy and canopy density, frequency of occurrence in sample plots, and species grain for the Mature Sand Forest in the Tembe Elephant Park

Analysis	Species	Slope	Intercept	R^2	Significance	SC Max	Individuals sampled	Centroid in SC	Subcanopy density (ind/ha)	Canopy density (ind/ha)	Frequency (%)	Species grain
Community	**Community SCD**	**-1.54**	**10.30**	**0.96**	**	**12**	**1038**					
Full	*Acalypha glabrata*	-2.80	8.14	0.96	**	5	88	02	340	0	73	***NA***
Full	*Cola greenwayi*	-1.65	7.90	0.91	**	9	193	04	1811	321	87	Fine
Full	*Croton pseudopulchellus*	-2.46	7.01	0.70	*	8	75	02	151	19	47	Fine
Full	*Drypetes arguta*	-1.52	6.96	0.74	*	7	97	03	1208	38	100	Fine
Full	*Drypetes natalensis*	-1.20	5.58	0.87	**	9	38	05	415	94	67	Fine
Full	*Haplocoelum foliolosum*	-0.98	4.63	0.38	*	11	47	05	358	132	80	Fine
Full	*Ptaeroxylon obliquum*	-1.01	5.34	0.83	**	10	45	05	245	226	67	Fine
Full	*Salacia leptoclada*	-2.22	7.21	0.92	*	4	51	02	170	0	100	***NA***
Full	*Toddaliopsis bremekampii*	-1.40	6.53	0.71	*	6	67	03	811	0	93	***NA***
Full	*Tricalysia junodii*	-3.19	6.75	0.63	-	5	46	01	19	0	67	***NA***
Full	*Uvaria lucida*	-3.75	8.97	0.98	**	4	152	01	113	0	67	***NA***
Full	*Vepris lanceolata*	-1.63	7.06	0.86	**	8	96	03	1038	57	93	Fine
		Mean SCD centroid location for common species:						03				
Limited	*Balanites maughamii*	-0.47	2.39	0.16	-	12	12	08	94	75	53	Fine
Limited	*Boscia filipes*	0.00	1.78	0.00	-	8	10	05	113	57	53	Fine
Limited	*Cavacoa aurea*	-1.50	5.65	0.77	**	8	26	04	226	38	20	Fine (*NA*)
Limited	*Cleistanthus schlechteri*	0.45	0.38	0.25	-	12	21	08	113	283	40	Intermediate (*NA*)
Limited	*Dalbergia obovata*	***NA***	***NA***	***NA***	-	1	13	01	0	0	20	***NA***
Limited	*Dialium schlechteri*	-0.42	3.20	0.29	-	12	24	08	151	264	80	Intermediate
Limited	*Diospyros inhacaensis*	-0.92	4.30	0.46	-	8	19	05	264	19	60	Fine
Limited	*Dovyalis longispina*	-1.58	5.28	0.75	-	5	18	02	94	0	53	***NA***
Limited	*Euclea natalensis*	-2.17	5.51	0.34	-	4	18	02	57	0	60	***NA***
Limited	*Hymenocardia ulmoides*	-1.22	5.20	0.74	**	10	28	05	283	113	67	Fine
Limited	*Monodora junodii*	0.21	1.72	0.02	-	8	19	06	245	94	40	Fine (*NA*)
Limited	*Newtonia hildebrandtii*	0.86	-1.15	0.64	**	12	25	10	0	58	53	***NA***
Limited	*Pteleopsis myrtifolia*	-0.49	3.01	0.27	-	10	14	07	113	94	73	Fine
Limited	*Rothmannia fischerii*	1.17	-0.20	0.63	*	7	13	06	208	38	33	Fine (*NA*)
Limited	*Strychnos decussata*	0.23	1.15	0.03	-	10	18	06	189	151	80	Fine
Limited	*Strychnos henningsii*	-0.31	3.64	0.16	-	8	29	05	434	75	100	Fine
Limited	*Tricalysia delagoensis*	0.65	1.63	0.07	-	5	11	03	113	0	27	***NA***
		Mean SCD centroid location for common species:						05				

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

NA Not applicable, following the species grain, it indicates that while grain could be determined, the frequency of occurrence is too low to warrant inclusion in the model

Table 8 Detail of species level size class distribution (SCD) regressions, including statistical significance, the maximum size classes (SC) reached, number of individuals sampled, centroid position, sapling, subcanopy and canopy density, frequency of occurrence in sample plots, and species grain for the *Afzelia quanzensis* Subassociation in the Tembe Elephant Park

Analysis	Species	Slope	Intercept	R^2	Significance	SC Max	Individuals sampled	Centroid in SC	Subcanopy density (ind/ha)	Canopy density (ind/ha)	Frequency (%)	Species grain
Community	Community SCD	-1.64	8.54	0.88	**	12	297					
Full	*Haplocoelum foliolosum*	-1.34	4.33	0.32	-	10	31	02	50	50	67	Fine
Full	*Vepris lanceolata*	-1.50	7.49	0.87	**	8	31	04	1100	250	100	Fine
		Mean SCD centroid location for common species:						03				
Limited	*Cola greenwayi*	-0.92	3.38	0.12	-	8	12	03	100	50	67	Fine
Limited	*Dialium schlechteri*	0.03	2.07	0.00	-	11	10	07	167	333	67	Intermediate
Limited	*Diospyros inhacaensis*	-1.92	7.13	0.76	**	8	19	03	450	50	67	Fine
Limited	*Drypetes arguta*	-2.07	7.54	0.77	*	5	28	02	450	0	67	***NA***
Limited	*Drypetes natalensis*	-0.72	4.34	0.10	-	7	15	03	350	0	33	***NA***
Limited	*Euclea natalensis*	-2.03	7.65	0.90	**	7	26	02	350	0	67	***NA***
Limited	*Monanthotaxis caffra*	***NA***	***NA***	***NA***		1	11	01	0	0	33	***NA***
Limited	*Ochna barbosae*	4.95	-0.48	0.44	-	3	11	02	222	0	67	***NA***
Limited	*Toddaliopsis bremekampii*	-1.47	6.77	0.72	-	4	14	02	300	0	67	***NA***
		Mean SCD centroid location for common species:						03				

** Highly significant ($p \leq 0.01$); * Significant ($p \leq 0.05$); - Not significant ($p > 0.05$)
NA Not applicable, following the species grain, it indicates that while grain could be determined, the frequency of occurrence is too low to warrant inclusion in the model

Table 9 The number of species by grain category and the derived community grain for the various vegetation units of Tshanini Community Conservation Area (TCCA) and Tembe Elephant Park (TEP), Maputaland, northern KwaZulu-Natal, South Africa

Grain	Short Sand Forest		Tall Sand Forest		Mature Sand Forest	*Afzelia quanzensis* Subassociation
	TCCA	TEP	TCCA	TEP	TEP	TEP
Fine	7	6	9	7	14	4
Intermediate	1	1	2	2	1	1
Coarse	0	1	1	2	0	0
Fine	**X**	**X**	**X**	**X**	**X**	**X**
Intermediate	-	-	-	-	-	-
Coarse	-	-	-	-	-	-

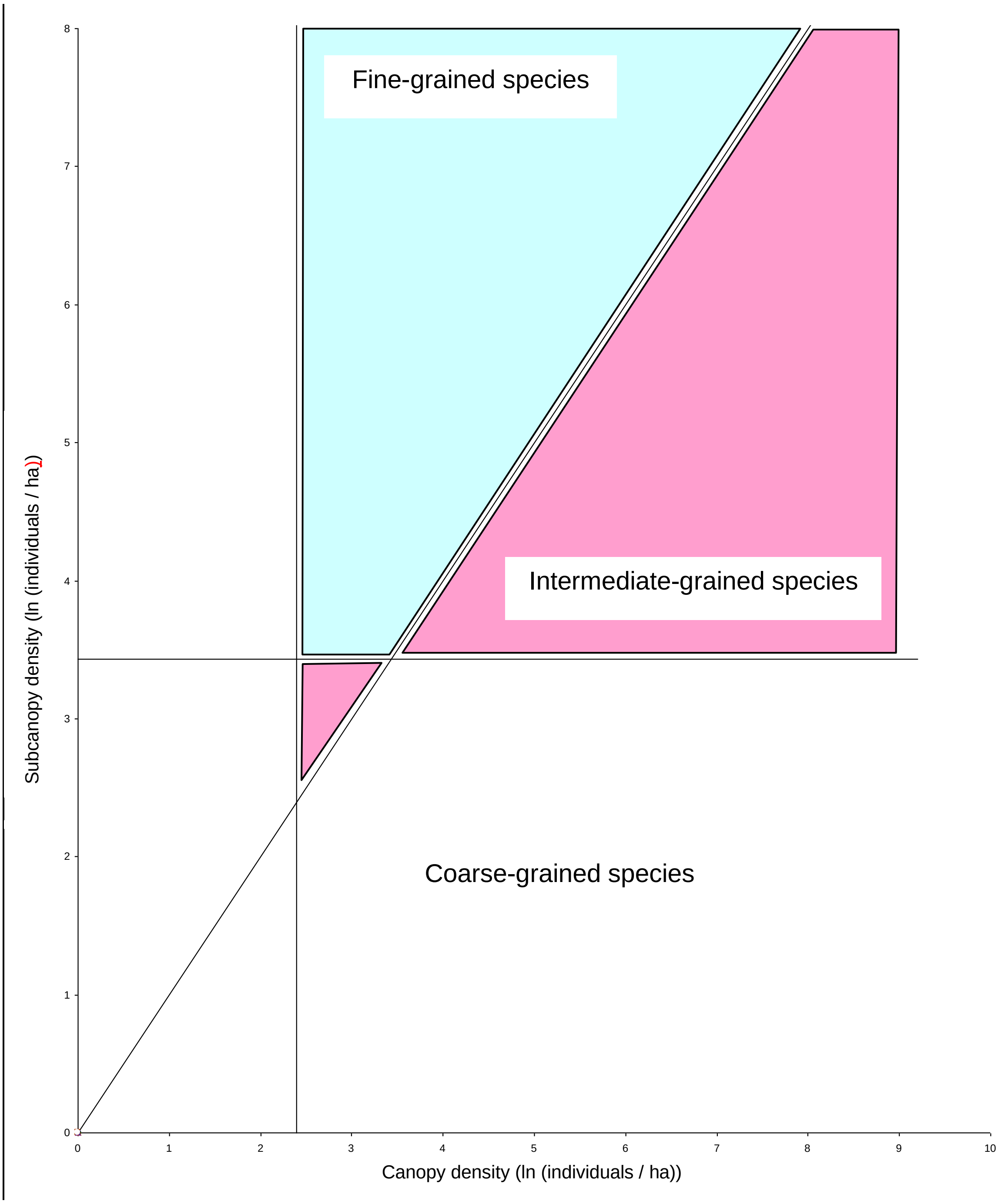

Figure 1 The graphical grain determination model based on canopy density (X-axis) and subcanopy density (Y-axis) used to evaluate tree species' grain in the two study sites in KwaZulu-Natal, South Africa. Values are ln-transformed to improve readability. The model is adapted from Lawes and Obiri (2003).