

## Vegetation of the Tembe Elephant Park, Maputaland, South Africa

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A hierarchical classification, vegetation map, description and ecological interpretation of the plant communities of the Tembe Elephant Park and surrounding areas are presented. The study area falls within the Maputaland Centre of Endemism, which is part of the Maputaland-Pondoland Region, a centre of plant diversity rich in endemic plants and animals. Sixty-four sample plots were distributed in a stratified manner throughout the study area. A TWINSPAN classification, refined by Braun-Blanquet procedures, revealed eight distinct, mainly woodland plant communities. Much of the vegetation distribution can be ascribed to vegetation dynamics and the geomorphological evolution of the region. Dynamics of water in the landscape either directly or indirectly, through its role in moisture levels and soil formation, plays a role in the determination of plant communities at the higher levels. The proposed classification and general descriptions can be used for

nature reserve management, land-use planning and further research. Ordinations based on floristic data give an indication of floristic and associated habitat and environmental relationships. Soil character and moisture differences are usually slight, hence the sand-based communities do not have distinct boundaries, except for Sand Forest. Indications are that in the case of Sand Forest the distinct boundary zone of nearly bare soil may well be the result of allelopathy. Eighty-four Maputaland Centre plant endemics/near-endemics were recorded for the study area, with Sand Forest being the most prolific habitat for such taxa, many which appear to be neoendemics. Because of its hypothesised origin (especially lack of specific historic events) and vegetation dynamics, the inclusion of Sand Forest in conservation areas is no guarantee of the future persistence of this rare vegetation type.

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### Introduction

Maputaland, a region of great scenic beauty and rich biodiversity, shows considerable ecotourism potential. Several conservation areas have been proclaimed in the region, including the Greater St Lucia Wetland Park (a World Heritage site), Tembe Elephant Park, Maputo Elephant Reserve, Ndumo Game Reserve, Mkuzi Game Reserve and Kosi Bay Coastal Forest Reserve. Recently, Mozambique granted a concession comprising approximately 230 000ha for ecotourism development in southern Mozambique. Currently initiatives for establishing a trans-frontier conservation area ('peace park') between northern KwaZulu-Natal and southern Mozambique are underway, effectively linking Tembe Elephant Park with some of the Mozambican parks and conservation areas.

An area comprising southern Mozambique and the northern part of KwaZulu-Natal is recognised as a Centre of Plant Endemism, namely the Maputaland Centre [MC] (Van Wyk 1994, 1996). High levels of endemism are spread across virtually the whole taxonomic spectrum, involving both plants and animals. The Maputaland region is also of exceptional

biogeographical interest because of the sharp biogeographical transformation of both plants and animals in the region (Poynton 1961, Bruton and Cooper 1980). Maputaland is at the southern end of the tropics in Africa and many organisms reach the southernmost limit of their range here.

Tembe Elephant Park [TEP] was proclaimed in 1983. It lies within the core area of the MC and contains many rare plant and animal species. Noteworthy is the presence in the park of a rare forest type, locally referred to as Sand Forest and in Mozambique as Licuati Forest. Sand Forest is very distinctive, with a unique combination of plant and animal species. As far as is known, this vegetation type is more or less restricted to ancient coastal dunes in northern KwaZulu-Natal and the extreme southern portion of Mozambique (Maputaland). Good examples of Sand Forest can be seen in the Greater St Lucia Wetland Park, Ndumo and Mkuze Game Reserves, and particularly the TEP. Sand Forest harbours many rare and unusual plant and animal species, including several MC endemics. Because of its restricted occurrence and unusual species complement, Sand Forest

is one of the most important plant communities in the MC.

The vegetation of Maputaland is very diverse, with at least fifteen broad vegetation types described for the KwaZulu-Natal portion of the region (Moll 1977, 1980); one of these is Sand Forest. However, with the exception of the pioneering work of Myre (1964, 1971) on the vegetation of southern Mozambique, very little detailed work has been done on the phytosociology of the region's sand-associated vegetation types. Myre's vegetation classification concentrated on the grasslands, with only superficial descriptions being given for woodland and associated communities. Detailed vegetation descriptions have, however, been published for Ndumo Game Reserve (De Moor *et al.* 1977) and Mkuzi Game Reserve (Goodman 1990), but these areas are not chiefly on sand. Klingelhoeffer (1987) did some work on the vegetation of TEP, but this was a broad scale study related to elephant in the area. Data on floristic diversity and detailed habitat relations are still lacking for TEP and neighbouring areas.

Management of conservation areas in Maputaland requires more knowledge of the phytodiversity and biological intricacies of the region. In this paper we aim to provide ecological and floristic data for the Sand Forest and associated woodland habitat of a part of Maputaland by identifying, characterising, interpreting and mapping the major vegetation units and their variations that occur in the TEP and surrounding areas. An assessment of the floristic richness and level of endemism in the study area is also supplied.

### Study area

Tembe Elephant Park is situated in northern KwaZulu-Natal (Figure 1). The park is 30 013ha in extent and its northern limit is the international boundary between South Africa and Mozambique. The central part of Maputaland is mainly an extensive level plain of sandy soils, covered by open and closed woodland with patches of short and tall Sand Forest usually bordered by grassland. Moll and White (1978) classified the vegetation of this central portion into Pallid Sand Bushveld, Sand Forest, the Muzi Swamp, Palmveld and Grassland. Wild and Barbosa (1967) mapped the vegetation of this region as Dry Semi-deciduous (lowland-sublittoral) Forest as well as Woodland and Savanna Woodland (southeastern sublittoral) with extra-tropical species. Granger (1996) referred to a large portion of these areas as Subhumid Lowveld Bushveld.

The area now known as TEP was, until recently, still relatively undeveloped, with very little human influence. No major fences occurred south, east or west, with only the international border fence to the north. The international border fence was not an obstacle for game and allowed free movement, even for elephants. Very few people lived in this area because of the scarcity and seasonality of surface water; most lived along the Muzi Swamp. Soils in the region are generally too nutrient-poor for cultivation, except along the Muzi Swamp. In the past, the density of people along the Muzi Swamp was nevertheless low, as sections of the swamp can be dry for some months of the year. The more permanent waters of the northern sections of the Muzi Swamp are saline (salinity gradients of 0.5–5%) and there-

fore not suitable for irrigation (Klingelhoeffer 1987).

### Topography

TEP lies in the southernmost portion of the broad Mozambican Coastal Plain. This flattish, undulating area of sand ridges is bordered by the Lebombo Mountains to the west and by the Indian Ocean to the east. Locally, in TEP linear north-south trending dunes interspersed with depressions are found. If soil clay content is high, there may form perennial pans. The highest dunes (Nhlela and Beacon Ridges) in the study area, reach a height of 129m a.s.l. and the lowest lying areas (e.g. Muzi Swamp) are at approximately 50m a.s.l. These two dune ridges are the highest areas on the Mozambican Coastal Plain.

### Climate

Rainfall and temperature data for weather stations relevant to the study area are given in Table 1. Sihangwana, the station representing the study area, is amongst others, compared to stations at Ndumo and Makatini (both drier areas) as well as the one at Kosi Bay (wetter coastal area). Maputaland lies within a transitional zone between the tropics to the north and sub-tropical coastal conditions to the south, with hot summers and cool to warm winters. The climate of the region can be described as warm to hot, humid and sub-tropical (Schultze 1982). Average humidity is relatively high, even in the drier inland parts of the region. Winters are drier than summers, although rain is received throughout the year. During the dry season, morning mist is not uncommon, but during the day from April to July, percentage relative humidity is comparatively low (Table 2).

### Geology

TEP is underlain by Mesozoic and Cainozoic (<64Ma) geological units that can be traced southwards and northwards along the Mozambican Coastal Plain. The basal lithological unit are marine siltstone of the St Lucia Formation; these Late Cretaceous deposits are not exposed in the study area. Unconformably overlying these rocks are the basal units of the Maputaland Group (Cainozoic), namely the Uloa and Umkwelane Formations (Neogene), which underlie the dune sand deposits currently defining the surface relief in this area (Botha 1997, Maud and Botha 2000). The shallow marine, littoral and coastal dune deposits of the Maputaland Group represent a succession of regressive events following marine transgressions. High dune cordons, which can be traced for long distances along the inland margin of the coastal zone, mark stillstands during the Mio-Pliocene marine regression that deposited the Uloa/Umkwelane Formation sediments. The oldest ridges are probably Early Pleistocene (3 million – 30 000 years old) (Davis 1976, Hobday 1976, Maud and Botha 2000) whereas the youngest are probably Late Pleistocene (30 000 – 10 000 years old). These are some of the youngest formations in southern Africa.

The calcareous conglomerate and sandstone comprising the Uloa Formation is an important aquifer overlying the impervious Cretaceous siltstones; it lies at depths of more

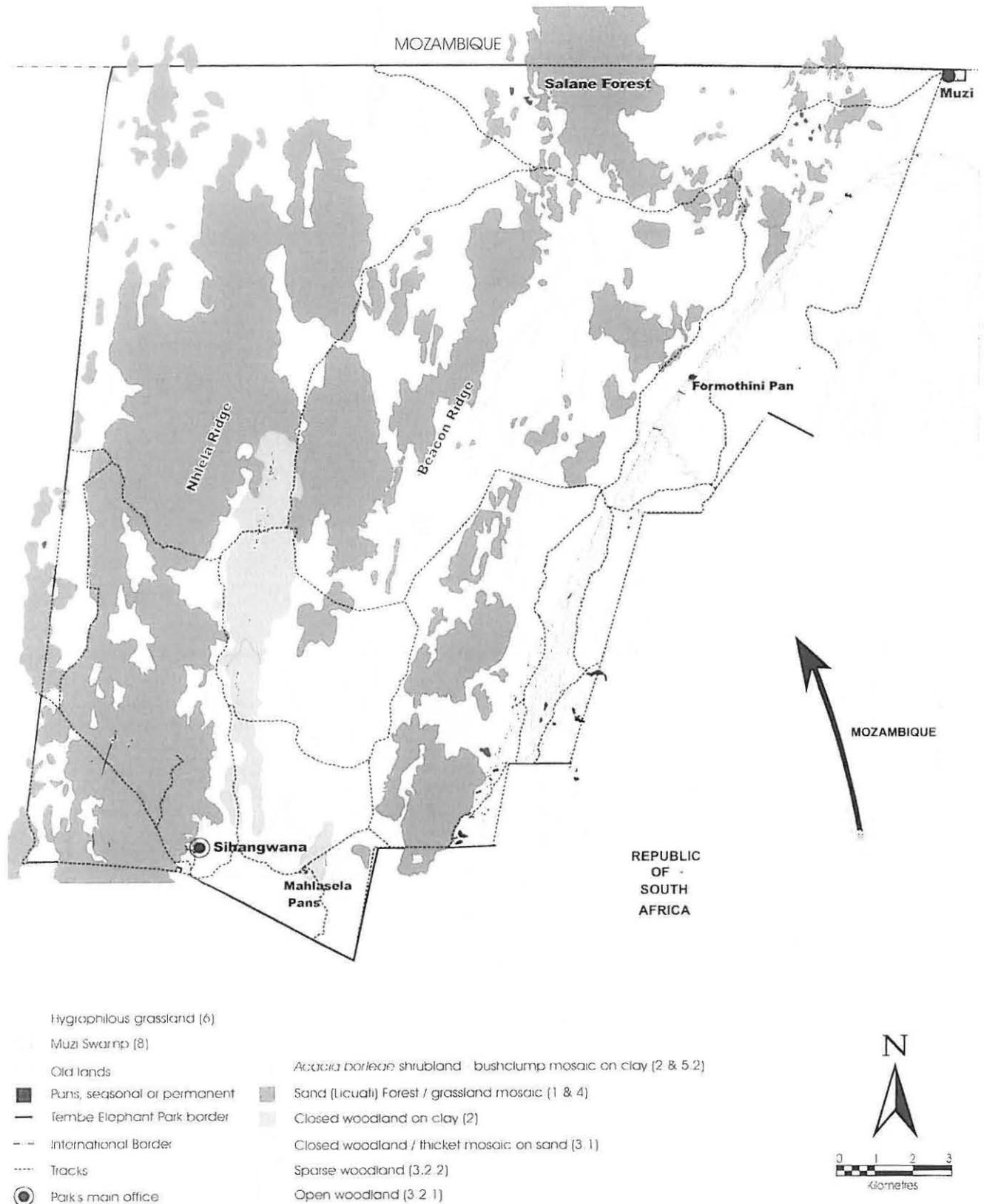


Figure 1: Map showing the location of the Tembe Elephant Park and its broad vegetation types. Numbers in brackets refer to the specific plant communities (see text) combined under that mapping unit

**Table 1:** Mean annual and absolute maximum and minimum rainfall for six weather stations in the region (based on local weather stations and Weather Bureau records)

Station	Period (yrs)	Annual rainfall (mm)		
		Mean	Absolute max. (year)	Absolute min. (year)
Kosi Bay	42	944	1 552 (1985)	506 (1959)
Sihangwana	32	707	2 105 (1975)	245 (1960)
Ndumo	71	614	1 160 (1938)	276 (1931)
Makatini	18	633	1 144 (1984)	433 (1968)
Pongola	13	638	871 (1955)	488 (1953)
Richards Bay	13	1 127	1 807 (1971)	558 (1982)

**Table 2:** Mean annual and absolute maximum and minimum temperature for six weather stations of the region (based on local weather stations and Weather Bureau records)

Station	Period (yrs)	Mean	Annual temperature (°C)		Average relative humidity (%) (min, max)
			Average max (absolute, year)	Average min. (absolute, year)	
Makatini	28	22.4	34.9 (44.2, 1976)	5.7 (0.1, 1975)	51 (32, 98)
Sihangwana	8	23.6	35.4 (45, 1995)	7.3 (4, 1995)	60 (43, 100)
Ndumo	11	23.1	35.2 (44.5, 1977)	12 (6.4, 1977)	56 (30, 97)
Ngutshana	4	21.3	22 (40.6, 1995)	- (4, 1994)	65 (44, 93)
Pongola	31	21.8	35 (43.4, 1954)	12 (2.5, 1954)	45 (28, 90)
Richards Bay	13	21.8	26.7 (42.5, 1976)	16.9 (5.1, 1972)	68 (49, 97)

than 30m beneath the surface dune sands. The topography in the study area is defined by high, linear, north-south oriented dune cordons with poorly preserved parabolic dunes superimposed on the surface. Sand comprising these dunes represents the Plio-Pleistocene weathering products of the underlying Uloa/Umkwelane Formation rocks with localised aeolian as well as sheetwash and reworking of sand off high-lying areas.

The colour and textural characteristics of surface geological units in the study area are dominated by post-depositional, pedogenic weathering of the sands. Distribution of the sands, which represents a broad soil chronosequence, is characteristic of the entire coastal plain. The oldest Plio-Pleistocene weathering profiles are red and dominant in the western areas or in localised places where old sands rise above the surrounding deposits. Lesser-developed, yellowish and grey profiles formed in younger redistributed sands during the Pleistocene and Holocene, occur in degraded dune fields or areas dominated by a high water table. Calcrete deposits have formed adjacent to the Muzi Swamp and thick peat deposits have accumulated in the permanent swamps.

### Soils

Surface geological units are dominated by pedogenic features and the soils formed in the fine-grained dune sands are typically red, yellowish or grey, apedal soils with incipient horizon development. Typically, the soils comprise a thin,

organic-enriched A-horizon underlain by sandy subsoil with illuviated lines forming sparse ferruginous mottles or clay-enriched mottles and lamellae at depths of 3–4m below the surface. Higher clay content in the red profiles is attributed to more intense weathering of labile minerals over a long period. Broad soil patterns mapped in the study area have differentiated the high dunes comprising red/yellow, high base status soils from the surrounding lower relief areas where regic sands are dominant.

The high Nhlela and Beacon Ridges probably represent the weathered remnants of the oldest dune systems in the study area. Well-drained profiles characterised by very deep, red or yellowish, high base status soils with <5% clay are common on these high topographical features which have the steepest gradients and short hillslopes. These soils are classified according to the South African system as the Hutton or Clovelly Forms (Soil Classification Working Group 1991) and can be grouped as entisols or inceptisols (Soil Survey Staff 1996) or arenosols (FAO–UNESCO 1974).

The low gradient areas with long slope lengths comprise degraded, low dunes that are characterised by sandy profiles with yellowish brown or light grey subsoil horizons. These profiles are moderately well-drained, although high water tables within low-lying interdune depressions result in bleached, grey soil profiles. These yellowish Clovelly or grey Fernwood Form soils (Soils Classification Working Group 1991) show a sharp reduction of organic carbon to levels of less than 0.5% within 30cm of the surface. Most subsoils

classify as regosols (FAO–UNESCO 1974) or entisols (Soil Survey Staff 1996).

Lateral ground water migration towards interdune depressions or the Muzi Swamp base level has resulted in formation of clay-rich, slightly saline or calcareous duplex soils in low-lying sites. Where the dune sands border on the Muzi Swamp, narrow areas of sodic Estcourt Form soils (Soil Classification Working Group 1991) with prismatic subsoil structure are common. These natric soils can be classified broadly as planosols (FAO–UNESCO 1974).

Permanent swamps in the Muzi system are characterised by gleying conditions with peat formation and development of organic-rich histosols (FAO–UNESCO 1974, Soil Survey Staff 1996) or soils of the Champagne Form (Soil Classification Working Group 1991).

### Hydrology

Water table and ground water movements play an important role in relation to vegetation patterns in most parts of Maputaland, including the TEP, as the area is covered by deep sand. From borehole data, water table depths are on average approximately 35m, but depths of 60m below surface have been recorded. In some places, water table depths can exceed 90m (borehole of 90m without reaching water). An elevated water table is present in a few places such as the seasonal pans that occur on the duplex soils. Ground water is almost exclusively replenished by rainwater. After rains, quick fluctuations in local water levels can be experienced for a period. From work done by Kruger (1986) in the neighbouring areas to Sileza Nature Reserve, which have very similar soils as TEP, it is estimated that vertical seepage rates are in the order of 0.1m/day. Water movements through the sands are at an average transmissivity of 20m<sup>2</sup>/day and co-efficient of storativity of 1<sup>-10</sup><sup>-3</sup>. Permeabilities are highly variable, because the Pleistocene sediments underlying the coversands show extreme east-west lateral variability (Hattingh 1998). In general, the swamps and marshes are surface expressions of the groundwater table, with little or no evidence of perched groundwater horizons occurring in the area. The only permanent water in the TEP (most years) is the Muzi Swamp, in the east of the reserve. The flow direction of the Muzi Swamp in this area is north, into Mozambique. The only other sources of surface water in the reserve, are the seasonal pans that occur on the duplex soils. These pans are usually dry during the winter period from April to September.

### Methods

Sixty-four sample plots (10 x 10m; in accordance with the plot size used by Matthews *et al.* 1999) were distributed in a stratified random manner throughout the study area. As far as possible, the plots were equally distributed in the different physiographical-physiognomically homogeneous units, distinguished on the basis of physical environment, physiognomy, dominant plant species composition and abundance. Sampling was carried out from January to May 1996. Scientific names of taxa follow Arnold and De Wet (1993). Terminology to describe vegetation structure follow Edwards

(1983). The following information was recorded for each sample plot: 1, total floristic composition and cover-abundance value for each plant species, according to the Braun-Blanquet cover-abundance scale as described by Mueller-Dombois and Ellenberg (1974); 2, water table depth at the time of sampling, using a 2m soil auger; 3, soil type/form (FAO–UNESCO 1974, Soil Classification Working Group 1991) and basic colour; 4, amount of organic material ranked as distinct or indistinct and its depth of occurrence; 5, topographical position based on terrain types (Land Type Survey Staff 1986), namely (1) crest, (2) scarp, (3) midslope, (4) footslope and (5) valley bottom or floodplain; 6, geology, according to 1:250 000 geological survey maps and relevant literature (Geological Survey 1986, South African Committee for Stratigraphy 1980, Botha 1997) and locally at a larger scale, based on personal observations in the field; 7, land type according to 1:250 000 land type map (Land Type Survey Staff 1986); 8, a 50 point herbaceous species survey using the step-point method (Mentis 1981)

Largely unpublished soil analysis data were used in the description of the soils. These were based on soil samples taken from what was considered a representative example of the different plant community types as distinguished in this study. Not all sub-communities were sampled due to the cost involved in detailed soil analyses. Chemical analysis (pH, macro and micro nutrients) of the soil was done at the surface and at 1m, 2m, 3m and 4m depths. The pooled results of these different level samples were used in the discussions that follow.

Two-way indicator species analysis (TWINSPAN) was applied to the basic floristic data set to derive a first approximation of the possible plant communities (Hill 1979a). Refinement of this classification was done by the application of Braun-Blanquet procedures (Behr and Bredenkamp 1988, Bredenkamp *et al.* 1989).

Major vegetation and associated habitat gradients, as well as the floristic relationships among the plant communities were explained by subjecting the floristic data set to Detrended Correspondence Analysis [DECORANA] (Hill 1979b).

Maputaland Centre [MC] endemic and near-endemic plant taxa mentioned in the text are based mainly on the work of Van Wyk (1996). The term 'endemic' is used to refer to a taxon limited in its range to a restricted geographical area, or a particular substrate. When a taxon is predominantly confined to a particular area or substrate, but is also marginally present elsewhere (sometimes in the form of distant satellite populations), it is called a 'near-endemic' (Matthews *et al.* 1993).

### Results

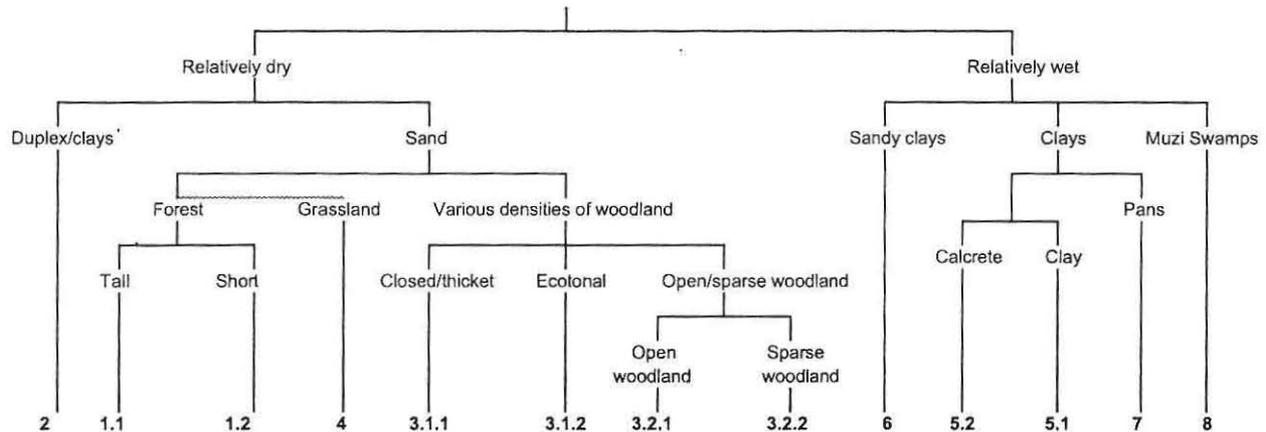
#### Classification

Eight major plant communities were identified (Table 3). These are mapped for TEP in Figure 1. Since the whole study area contains regic sand, no major geological feature plays a role in differentiating the plant communities. These major communities relate to the presence of clay and varying degrees of soil moisture in the regic sands. Soil character and moisture differences are usually slight, hence the sand-based communities do not have distinct boundaries









**Figure 2:** Dendrogram illustrating the habitat relationships of the different plant communities. Community numbers correspond with descriptions in the text. Grassland community 4 is always associated with the margin of Sand Forest. It is hypothesised that these grassland zones around Sand Forest are the result of an inhibitory effect induced by allelochemicals originating from the forest, hence the dotted line

(except Sand Forest) but grade into each other, although each community is quite distinct in the field. It is proposed that much of the vegetation distribution can be attributed to the vegetation dynamics (succession) and historic evolution of the geomorphology of the region. The number of plant species per plot (species richness) ranges from a minimum of 11 to a maximum of 55, with an average of 34.

The hierarchical classification of the vegetation reinforces the correlation between habitat and plant communities (Figures 2 and 3). The distribution among various plant communities of MC endemic/near-endemic plant taxa, is listed in Table 4. A summary of selected community attributes is supplied in Table 5.

Plant communities recognised in the study area are classified as follows:

1. *Drypetes arguta-Uvaria lucida* subsp. *virens* Sand Forest of deep sandy areas (dry sands).
  - 1.1 *Cola greenwayi-Balanites maughamii* tall Sand Forest.
  - 1.2 *Psydrax fragrantissima-Hyperacanthus microphyllus* short Sand Forest.
2. *Spirostachys africana-Berchemia zeyheri* closed woodland on duplex soils (clays).
3. *Strychnos madagascariensis-Combretum molle* woodland of deep sandy areas.
  - 3.1 *Acacia burkei-Euclea natalensis* closed woodland and thicket.
    - 3.1.1 *Zanthoxylum capense-Clausena anisata* closed woodland and thicket on sand.
    - 3.1.2. *Panicum maximum-Acacia burkei* ecotonal closed woodland.
  - 3.2 *Salacia kraussii-Themedra triandra* open woodland on sand.
    - 3.2.1 *Andropogon gayanus-Albizia versicolor* open woodland on sand.
    - 3.2.2 *Helichrysum kraussii-Dichapetalum cymosum* sparse woodland.
4. *Andropogon schirensis-Tephrosia longipes* subsp. *longipes* grassland associated with Sand Forest.

5. *Nidorella auriculata-Justicia flava* hygrophilous grassland on clay-rich soils.

5.1 *Waltheria indica-Sporobolus pyramidalis* grassland on clay between thicket and pan marsh edges.

5.2 *Acacia borleae-Kohautia virgata* shrubland on clay soils often associated with calcrete.

6. *Imperata cylindrica-Eragrostis lappula* grassland on sandy clay soils associated with the Muzi Swamp and other marsh/pan areas.

7. *Oxalis* cf. *semiloba-Nymphaea nouchali* aquatic vegetation of standing water in marshes and pans.

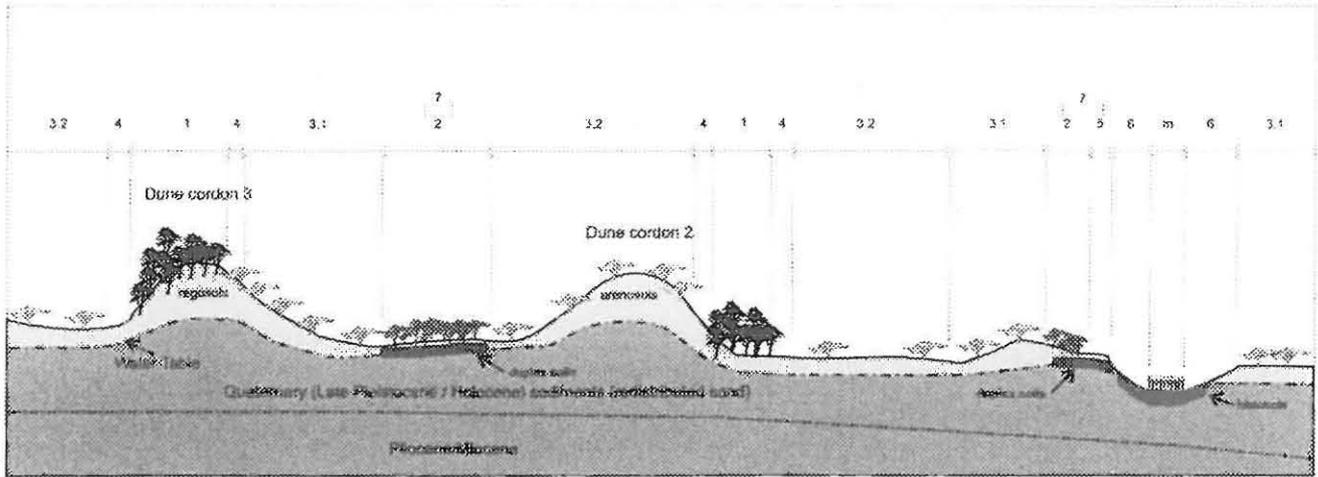
8. *Phragmites australis* reed beds of the Muzi Swamp.

## Description of plant communities

### 1. *Drypetes arguta-Uvaria lucida* subsp. *virens* Sand Forest of deep sandy areas (dry sands)

A major community which is mostly associated with dunes (crests, slopes but also in some interdune depressions), on the orange-brown arenosols and dystric regosols. Soils are sand with very little clay and low pH values (pH 5.6). Results of a separate soil analysis showed Sand Forest soils to be more acidic than those of the other regic sand communities.

This plant community is characterised by species group C (Table 3). Diagnostic consistent species include the tree *Pteleopsis myrtifolia*, the understory shrubs *Drypetes arguta*, *Croton pseudopulchellus* and the liana *Uvaria lucida* subsp. *virens*. Prominent species (>50% constancy) include the trees *Hymenocardia ulmoides*, *Dialium schlechteri*, *Cleistanthus schlechteri*, *Brachylaena huilensis*, *Manilkara discolor*, the understory shrubs *Todallipopsis bremekampii*, *Salacia leptoclada*, *Drypetes natalensis*, *Monodora junodii*, *Leptactinia delagoensis* subsp. *delagoensis*, *Vitex amboniensis* and the liana *Secamone delagoensis*. In places *Newtonia hildebrandtii* can be quite prominent but is not always consistent. The understory shrub *Synaptolepis kirkii*, the grass *Panicum deustum* and the liana *Monanthotaxis caffra* have a high constancy in this commu-



**Figure 3:** Schematic representation of the distribution of the different plant communities in the Tembe Elephant Park and surrounding areas. Dotted lines indicate overlapping distributions. Community numbers correspond with descriptions in the text. m = Muzi Swamp

nity. Species group E links the forest community with the thicket communities, indicating a floristic relationship. These more shade-tolerant species are common to such closed habitats; none are trees, most being herbaceous shrubs and creepers. On average 35 species were recorded per sample plot. Forty-two MC endemic/near-endemic species were recorded of which 27 are restricted to these forests, thus making this one of the richest communities for MC endemic/near-endemic plant species (Table 4).

Structurally, this plant community is a forest, in some instances having a low canopy of approximately 5m and in other places extending up to approximately 15m. The species composition is typical of what has been called Licuati or Sand Forest (Myre 1964, Moll and White 1978, Ward 1981, Matthews *et al.* 1999), with species present such as *Dialium schlechteri*, *Pteleopsis myrtifolia*, *Ptaeroxylon obliquum*, *Croton pseudopulchellus* and *Newtonia hildebrandtii*. Protruding crowns of some of the larger tree species in Sand Forest are covered by many epiphytes, such as *Microcoelia exilis* and various lichens including *Usnea* spp.

This major community is subdivided into two sub-communities based on structure and floristic composition.

### 1.1 *Cola greenwayi*-*Balanites maughamii* tall Sand Forest

A sub-community which is mostly associated with dunes (slopes but also in some interdune depressions), on the orange brown arenosols and dystric regosols. Soils are sand with very little clay and acidic (pH 5.6).

This sub-community is characterised by species group A (Table 3). Diagnostic consistent species include the tall tree *Balanites maughamii* and understory shrub *Cola greenwayi*. Prominent species (>50% constancy) include the trees *Ptaeroxylon obliquum*, *Haplocoelum gallense*, *Wrightia natalensis*, the understory shrubs *Suregada zanzibariensis*, *Strychnos henningsii*, the creepers *Acacia kraussiana*,

*Strophanthus luteolus* and the grass *Panicum laticomum*. On average, 35 species were recorded per sample plot. Thirty-one MC endemic/near-endemic species were recorded, of which five are restricted to this community (Table 4).

### 1.2 *Psydrax fragrantissima*-*Hyperacanthus microphyllus* short Sand Forest

A sub-community which is mostly associated with dunes (crests, slopes, but also in some interdune depressions), on the orange brown arenosols and dystric regosols. Soils are sand with very little clay and acidic (pH 5.6). Reasons for the floristic differences between this community and the previous one are not clear, but may well be due to vegetation dynamics.

This sub-community is characterised by species group B (Table 3). Diagnostic consistent species include the shrubs *Psydrax fragrantissima* and *Hyperacanthus microphyllus*. Prominent species (>50% constancy) include the short trees *Cassipourea mossambicensis*, *Combretum mkuzense*, *Zanthoxylum leprieurii*, the shrubs *Tricalysia junodii*, *Grewia microthyrsa*, *Phyllanthus* sp. nov., *Oxyanthus latifolius*, *Tarenna littoralis* and the sedge *Cyperus albostrigatus*. On average, 35 species were recorded per sample plot. Thirty-four MC endemic/near-endemic species were recorded of which six are restricted to this community (Table 4).

### 2. *Spirostachys africana*-*Berchemia zeyheri* closed woodland on duplex soils (clays)

A major community which is found on the clay-rich duplex soils normally associated with bottomlands of dunes as well as the borders of the Muzi Swamp. Perennial pans are to be found interspersed throughout these clay areas. Many of these pans have developed from mud wallows use by game species, especially elephant. This community is found on the grey-brown planosols.

This plant community is characterised by species group D



Table 4 cont.

Endemic/near-endemic taxon	Family	Plant community number								
		1.1	1.2	2	3.1	3.2	4	5	6	7
<i>Plectroniella armata</i>	Rubiaceae	x		x	x					
<i>Psydrax fragrantissima</i>	Rubiaceae	x	xxx							
<i>Psydrax locuples</i>	Rubiaceae	x	xx	x	xx					
<i>Pyrostria hystrix</i>	Rubiaceae			xx						
<b><i>Rhus kwazuluana</i></b>	Anacardiaceae				x					
<i>Salacia kraussii</i>	Celastraceae					xxx	x			
<i>Sanseveria coccinia</i>	Liliaceae				x					
<i>Schotia capitata</i>	Fabaceae			xxx						
<i>Sclerochiton apiculatus</i>	Acanthaceae		x							
<i>Secamone delagoensis</i>	Asclepiadaceae	xxx	xxx	xxx	x					
<b><i>Striga junodii</i></b>	Scrophulariaceae								x	
<i>Strophanthus gerrardii</i>	Apocynaceae	x								
<i>Strophanthus luteolus</i>	Apocynaceae	xx	x							
<i>Tarenna junodii</i>	Rubiaceae		x		x					
<i>Thespesia acutiloba</i>	Malvaceae			x						
<i>Todallipsis bremekampii</i>	Rutaceae	xxx	xxx							
<b><i>Tricalysia delagoensis</i></b>	Rubiaceae	x	x	x						
<i>Tricalysia junodii</i> var. <i>junodii</i>	Rubiaceae		xx							
<i>Triliceras mossambicense</i>	Turneraceae						xx			
<i>Vahlia capensis</i> subsp. <i>vulgaris</i> var. <i>latifolia</i>	Vahliaceae								xx	
<i>Vernonia centaureoides</i>	Asteraceae				x	xx		x		
<b><i>Warburgia salutaris</i></b>	Canellaceae			x						
<i>Wrightia natalensis</i>	Apocynaceae	xx	x							
Restricted to sub-community		5	6		1	6				
Restricted to community			27	10		13	2	1	6	0
Sub-community total		31	34		29	23				
<b>TOTAL</b>										
84 Species (11% of flora of study area)	41 Families		42	20	37	10	1	7	0	

XXX = Abundant

XX = Average

X = Rare

Species in bold have been recorded from TEP, although not recorded in sample plots

Bold blocks represent species restricted to a particular plant community

(Table 3); diagnostic consistent species include the trees *Spirostachys africana*, *Berchemia zeyheri* and *Cassine aethiopica*. Prominent species (>50% constancy) include the trees *Ziziphus mucronata*, *Sideroxylon inerme*, *Euphorbia ingens*, *Acacia senegal*, *Pappea capensis*, *Schotia brachypetala*, the shrubs *Euclea divinorum*, *Dovyalis longispina*, *Schotia capitata*, *Carissa bispinosa*, *Pavetta catophylla*, the forbs *Justicia protracta*, *Protasparagus suaveolens*, the creepers *Senecio viminalis*, *Capparis brassii* and *Capparis tomentosa*. The understory shrubs *Rhus gueinzii*, *Coddia rudis* and the forb *Protasparagus natalensis* have a high constancy in this community and are character species of species group G; *Coddia rudis* having its highest cover values in this community. This community has many species associated with the more sandy areas. This can be ascribed to the duplex nature of this community's soil. It would be expected that sand-associated species should be found in the more sandy areas on the clay. These species would occur in the form of shrubs and forbs as reflected in the species groups G and H, but very few tree species are represented. Other taxa showing a strong affinity to this community are *Euclea natalensis*, *Grewia caffra* and *Catunaregam spinosa* subsp. *spinosa*

(species group H, Table 3). This reaffirms the association with sandy soils thicket vegetation although all of these species are shrubs and not trees; *Euclea natalensis* can be over 2m in height. On average, 45 species were recorded per sample plot, the richest of all the plant communities in the TEP. Twenty endemic/near-endemic MC species were recorded, of which ten are restricted to this community (Table 4).

In structure this plant community varies from areas of dense vegetation to thickets associated with termitaria, which are on clay (duplex soils). Species composition of these thickets on termitaria is similar to that found in other areas in South Africa, such as Roodeplaat Dam Nature Reserve, and are sometimes referred to as bush clumps (Van Rooyen 1984).

### 3. *Strychnos madagascariensis*-*Combretum molle* woodland of deep sandy areas

A community which is found on dune crests, slopes, and interdune depressions, on the grey dystic regosols. This community is the most dominant and widespread community in the study area.

**Table 5:** Environmental factors associated with the different plant communities. Other selected attributes are also presented

Plant community number	Predominant soil type	Average number of plant species per relevé	Number of MC endemics	Number of suffrutex species	Percentage clay**	Predominant soil colour	pH**	Size*** (ha)
1	arenosols/dystric regosols	35	33	0	4.26	orange-brown	5.6	4 500
2	planosols/duplex	45	14	1	NA	brown	NA	3 000
3.1	dystric regosols	41	25	4	1.95	grey-brown	5.5	15 000*
3.2.1	dystric regosols	37	15*	8	4.76	orange-grey	5.34	
3.2.2	dystric regosols	37	15*	9	0.62	grey-brown	5.8	3 000
4	arenosols/dystric regosols	23	9	4	6	grey-orange	5.47	1 200
5.1	planosols	29	1*	1	NA	grey-brown	NA	
5.2	planosols	23	1*	0	22.68	orange-brown	9	
6	planosols/humic gleysols	21	5	0	NA	brown-grey	NA	3 000*
7	planosols	13	0	0	NA	brown-grey	NA	

\* = Figure is for community combined

\*\* = Figure is for the representative soil samples

\*\*\* = Estimate

NA = Not Available

This plant community is characterised by species group L (Table 3). Diagnostic consistent species include the tall to short shrub *Strychnos madagascariensis*, and the trees *Combretum molle* and *Acacia burkei*. Prominent species (>50% constancy) include the tree *Sclerocarya birrea*, the shrubs *Strychnos spinosa*, *Dichrostachys cinerea* and the creeper *Rhoicissus revouillii*. On average, 39 species were recorded per sample plot. Thirty-seven MC endemic/near-endemic species were recorded of which thirteen are restricted to this community, making this the second richest community in the TEP for MC endemic/near-endemic species (Table 4).

This community is the dominant vegetation type of TEP, thus the diagnostic species represent the general species for this area and as such would not be very consistent. Structurally this plant community is a woodland of varying density, from closed to open. Canopy height varies from approximately 5m, extending up to 10m in places. This major community is what Granger (1996) called Subhumid Lowveld Bushveld, although his species composition described for this unit is not very typical.

This major community is subdivided into two sub-communities based on vegetation density, structure and floristic composition.

### 3.1 *Acacia burkei*-*Euclea natalensis* closed woodland and thicket

A sub-community which is found on dune crests, slopes and interdune depressions, on the grey dystric regosol. Soils are acidic (pH 5.5) sands with very little clay, although sometimes may have very narrow bands of clay present. This is one of the most widespread sub-communities in the study area.

This sub-community has no diagnostic species. It is characterised by the absence of species group K and the presence of species group H. Although species group H is also associated with thicket on clay, these species are linked to the

presence of narrow clay bands (Table 3). Prominent species (>50% constancy) include the shrubs *Euclea natalensis*, *Grewia caffra*, *Catunaregam spinosa* and *Bridelia cathcartica* (species group H). Another species showing a strong affinity to this community is the tree *Acacia burkei*, which has its highest constancy in this community (species group L). On average 41 species per plot were recorded, this community having the second highest number of species among the studied plant communities. Twenty-eight MC endemic/near-endemic species were recorded, of which one was restricted to this community (Table 4).

This plant community can be distinguished based on density, which in most cases varies from continuous to sub-continuous crown gaps, with a canopy from 8m to approximately 12m high.

This sub-community is subdivided into two variations, one being a generally dense plant community and the other an ecotonal form which is less dense and having affinities with the more open woodlands.

#### 3.1.1 *Zanthoxylum capense*-*Clausena anisata* closed woodland and thicket on sand

A community which is found on dune crests, slopes and interdune depressions throughout the TEP, on the grey brown dystric regosols, which sometimes may have very narrow clay bands present.

This plant community is characterised by species group F (Table 3). Diagnostic consistent species include the tree *Zanthoxylum capense* and the shrub *Clausena anisata*. Prominent species (>50% constancy) include the trees *Vepris lanceolata* and the forb *Achyranthes aspera*. Other species showing a strong affinity to this community are the shrubs *Phyllanthus reticulatus*, *Grewia caffra* and the tree *Acacia burkei* (species group L). The shrubs are from species groups G and H, showing an association with thicket vegetation. *Acacia burkei* has its highest constancy in this

community. On average 42 species per plot were recorded, making this the second richest plant community.

### 3.1.2 *Panicum maximum-Acacia burkei* ecotonal closed woodland

A community which is found on dune crests, slopes and interdune depressions throughout TEP, on the grey brown dystric regosols, which may sometimes have very narrow clay bands present.

This plant community is characterised by the absence of species groups F and G (Table 3) and the presence of H and L. This community has no diagnostic or prominent species as it is an ecotonal community associated with less dense areas with essentially no clay in the soil. Species showing a strong affinity to this community are the shrub/tree *Combretum molle* and the grass *Panicum maximum*. The tree *Acacia burkei* attains its highest cover-abundance in this community. Other species showing an affinity to this community is the tree *Terminalia sericea* and the grass *Digitaria eriantha*, both belonging to species group O (species associated with open to sparse vegetation). All the above species belong to more generally distributed species groups and species more strongly associated with less dense vegetation. On average 35 species were recorded per sample plot.

### 3.2 *Salacia kraussii-Themedra triandra* open woodland on sand

A community which is found on dune crests, slopes and interdune depressions throughout TEP, on the grey brown to orange grey dystric regosols. This is also one of the more widespread communities of the study area.

This plant community is characterised by the presence of species group K (Table 3). Diagnostic consistent species include the geoxylic-suffrutex *Salacia kraussii*, the grasses *Themeda triandra*, *Pogonarthria squarrosa* and *Eustachys paspaloides*. Not all these species have high constancy. The tree *Terminalia sericea* attains its highest cover values in this community and is also the most consistent species (100% present) (species group O, Table 3). Species group O is associated with open to sparse vegetation cover. Prominent species (>50% constancy) include the shrubs *Vangueria infausta*, *Brachylaena discolor* and the grass *Cymbopogon validus*. Another species that shows a strong affinity to this community is *Strychnos madagascariensis*, which has its highest cover-abundance values in this community. On average 37 species per sample plot were recorded. Twenty-two MC endemic/near-endemic species were recorded, of which six are restricted to this community (Table 4).

This community can be distinguished based on density, which in most cases varies from open to sparse woodland, with few tall trees from approximately 8m to 10m.

This community is subdivided into two sub-communities based on vegetation density and floristics.

### 3.2.1 *Andropogon gayanus-Albizia versicolor* open woodland on sand

A sub-community which is found on dune crests, slopes, and interdune depressions throughout TEP, on the orange grey dystric regosols. Soils are acidic (pH 5.34) and sandy with very little clay. This is also one of the more widespread sub-communities of the study area.

This plant community is characterised by the presence of species group I (Table 3). Diagnostic consistent species include the grass *Andropogon gayanus* and the tree *Albizia versicolor*. Prominent species (>50% constancy) include the shrubs *Sapium integerrimum*, *Garcinia livingstonei* and the forb *Hoslundia opposita*. Another species that shows a strong affinity to this community is *Strychnos madagascariensis*, which has its highest abundance values in this sub-community. The grass *Panicum maximum* also attains very high abundances in this sub-community. Other species are the trees *Combretum molle*, *Terminalia sericea*, the geoxylic-suffrutex *Eugenia mossambicensis* and the grasses *Digitaria eriantha*, *Diheteropogon amplexans* and *Perotis patens*. The last two species come from species group N, this group representing grassland areas associated with Sand Forest edges. On average 37 species per sample plot were recorded.

This community has few tall trees from approximately 8m to 10m.

### 3.2.2 *Helichrysum kraussii-Dichapetalum cymosum* sparse woodland

A sub-community which is found mainly on the flat areas between dunes, but also occurring to a lesser degree on dune slopes and crests throughout TEP, on the grey brown dystric regosols. Soils are slightly acidic (pH 5.8) sand with very little clay, the lowest percentage clay of all soils examined.

This plant community is characterised by the presence of species group J (Table 3). Diagnostic consistent species include the woody forb *Helichrysum kraussii* and the geoxylic suffrutex *Dichapetalum cymosum*. Prominent species (>50% constancy) include the shrub *Dalbergia obovata*, the grasses *Trichoneura grandiglumis*, *Panicum kalaharensis* and the geoxylic-suffrutex *Parinari capensis* subsp. *incohata*. Another species showing a strong affinity to this community is *Terminalia sericea*, which attains its highest abundance in this sub-community. Other species are the shrub *Strychnos madagascariensis*, the geoxylic-suffrutices *Salacia kraussii*, *Eugenia mossambicensis*, the grasses *Pogonarthria squarrosa*, *Themeda triandra*, *Diheteropogon amplexans*, *Perotis patens*, *Aristida stipitata* subsp. *spicata*, *Digitaria eriantha*, the forb *Corchorus junodii* and the woody creeper *Rhoicissus revouillii*. Three of the last-mentioned species come from species group O, this group representing grassland areas associated with Sand Forest edges, a clear link between woodland and these areas. On average 37 species per sample plot were recorded.

This community is similar to what is called 'woody grassland' (Matthews *et al.* 1999) — a type of grassland characterised by an abundance of species with the geoxylic-suffrutex growth form.

#### 4. *Andropogon schirensis-Tephrosia longipes* subsp. *longipes* grassland associated with Sand Forest

A community which is found directly neighbouring on the Sand Forest patches, throughout TEP, on the grey brown dystric regosols. Soils are slightly acidic (pH 5.47) sand with very little clay. These soils have been shown to possibly retain some allelopathic properties that are present in the Sand Forest community (unpublished results).

This plant community is characterised by the presence of species group M (Table 3). Diagnostic consistent species include the grass *Andropogon schirensis* and the forb *Tephrosia longipes* subsp. *longipes*. Prominent species (>50% constancy) include the forbs *Indigofera inhambanensis*, *Trachyandra* cf. *salti*, the grasses *Bewsia biflora*, *Urelytrum agropyroides* and the sedge *Cyperus obtusiflorus*. Another species showing a strong affinity to this community is the grass *Perotis patens* that is very consistent (100%) and attains its highest cover-abundance value in this community. *Perotis patens* is a characteristic pioneer species. *Strychnos madagascariensis* also has an affinity to this community, but takes the form of a stunted shrub. Other species are the grasses *Diheteropogon amplexans*, *Aristida stipitata* subsp. *spicata*, and *Digitaria eriantha*. The first two mentioned species come from species group N, which includes species common to open woodland, showing that this community has a close association with the open woodland areas. On average 23 species per sample plot were recorded. Ten MC endemic/near-endemic species were recorded, of which two are restricted to this community (Table 4).

This community is open grassland with little or no trees and shrubs, and is always found directly bordering on the Sand Forest community. These characteristic grasslands do not extend very far from Sand Forest edges and exhibit a gradient; further from the Sand Forest patches these grasslands gradually acquire an open woodland character.

#### 5. *Nidorella auriculata-Justicia flava* hygrophilous grassland on clay-rich soils

A community which is often found next to pans and marshy areas as well as clay-based thickets, throughout TEP, on the grey brown to brown orange planosols. This community has soils with the highest percentage clay in the study area.

This plant community is characterised by the presence of species group S (Table 3). Diagnostic consistent species include the forbs *Nidorella auriculata*, *Justicia flava* and *Kyllinga erecta*. Prominent species (>50% constancy) include the grasses *Panicum maximum*, *Aristida congesta* and the forb *Commelina* cf. *erecta*. On average 26 species per sample plot were recorded. One MC endemic species has been recorded in this community, to which it is also restricted (Table 4).

This community can be associated with 'wet areas' as water collects in these clayey areas after rain, resulting in temporary pans. Therefore, much moister soils occur here than are found on the sands where the water drains away. The Muzi Swamp on the other hand is also clay-based but is fed mostly by outside ground water sources.

Based on floristics, this community is subdivided into two sub-communities.

##### 5.1 *Waltheria indica-Sporobolus pyramidalis* grassland on clay between thicket and pan marsh edges

A sub-community which is often found next to or surrounding pans and marshy areas as well as clay-based thickets, throughout TEP, on the grey brown planosols. These soils have a high percentage of clay.

This sub-community is characterised by the presence of species group Q (Table 3). Diagnostic consistent species include the forbs *Waltheria indica* and the grass *Sporobolus pyramidalis*. Prominent species (>50% constancy) include the grass *Eragrostis ciliaris*, the forbs *Monechma debile* and an *Indigofera* sp. On average 29 species per sample plot were recorded.

##### 5.2 *Acacia borleae-Kohautia virgata* shrubland on clay soils often associated with calcrete

A sub-community which is found next to marshy areas as well as the clay-based thickets associated with the Muzi Swamp, on the orange grey brown planosols. These soils are alkaline (pH 9) with a high percentage of clay.

This sub-community is characterised by the presence of species group R (Table 3). Diagnostic consistent species include the shrub *Acacia borleae* and the forb *Kohautia virgata*. Prominent species (>50% constancy) include the grass *Eragrostis heteromera* that attains its highest cover/abundance values in this sub-community. *Eragrostis heteromera* associated with species group U, which represents the common species of the Muzi Swamp. On average 23 species per sample plot were recorded.

#### 6. *Imperata cylindrica-Eragrostis lappula* grassland on sandy clay soils associated with Muzi Swamp and other marsh/pan areas

A community which is found neighbouring the Muzi Swamp as well as marshy areas associated with sand, on the dark brown grey humic gleysols to planosols.

This plant community is characterised by the presence of species group T (Table 3). Diagnostic consistent species include the grasses *Imperata cylindrica*, *Eragrostis lappula* and *Dactyloctenium geminatum*. Prominent species (>50% constancy) include the shrub *Acacia nilotica*, the grass *Panicum genuflexum* and the forb *Nidorella anomala*. Other species showing a strong affinity to this community are the grass *Eragrostis heteromera* (species group U) and the sedge *Cyperus natalensis*. *Cyperus natalensis* comes from species group W, linking this community with the clay-based communities. On average 21 species per sample plot were recorded. Seven MC endemic/near-endemic species were recorded of which six are restricted to this community (Table 4).

#### 7. *Oxalis* cf. *semiloba-Nymphaea nouchali* aquatic vegetation of standing water in marshes and pans

A community which is found associated with the many

perennial and permanent pans and marshes occurring in the clay-based areas (duplex soils), throughout TEP. This community is found in the water of inundated planosol soils.

This plant community is characterised by the presence of species group V (Table 3). Diagnostic consistent species include the forb *Oxalis* cf. *semiloba* and the hydrophyte *Nymphaea nouchali*. Prominent species (>50% constancy) include the sedges *Cyperus distans*, the grasses *Digitaria didactyla* and *Echinochloa pyramidalis*. Another species showing a strong affinity to this community is the sedge *Cyperus natalensis*. On average 13 species per sample plot were recorded, the lowest of all samples. No MC endemic species were recorded for this community.

#### 8. *Phragmites australis* reed beds of the Muzi Swamp

One particular community that was sampled but not included in Table 3 is the reed beds of the extensive Muzi Swamp, which crosses the eastern side of the reserve and extends northwards to Maputo Bay in Mozambique. This is a well-described community that is widespread and associated with water bodies throughout South Africa and the world. Here along the entire length of the Muzi Swamp, dense stands of *Phragmites australis* occur, although in some places these are mixed with *Typha capensis*. Some of these areas are utilised by the local community for harvesting of reeds. The Muzi Swamp is the only source of permanent water in TEP, even in the driest years. This community is rather similar to the *Phragmito-Magnocaricetea* Klika in Klika and Novak (1941) described for Europe (Mucina 1997). However, its precise relationship to this class of swamp vegetation is uncertain and requires further study.

### Discussion

#### Ordination

Distribution of the sample plots (relevés) along the X and Y1 axis as well as X and Y2 axis of ordination is given in the form of scatter diagrams (Figures 4 and 5). The scatter diagrams illustrate a moisture gradient along the horizontal axis, with the wetter habitats to the right and the drier habitats to the left. Arenosols and regosols communities base themselves on the left of the diagram, while planosols and histosols communities base themselves on the right. On the X and Y1 axis, a distinct discontinuity exists between the communities of the Sand Forest (A), woodlands (B), Muzi Swamp grassland and the perennial pans (H). Grassland communities associated with clays (G) do not show a discontinuity, but do form a strong group restricted to a specific area of the scatter diagram.

There is no discontinuity in the distribution of the sample plots representing the woodland and associated communities on the X and Y1 axes. However, on the X and Y2 axis a clear separation with discontinuities can be seen within the woodland communities, namely, closed woodland associated with duplex soils and grassland associated with Sand Forest. The rest of the woodland communities show no discontinuities but each community group recognised in the proposed classification is more or less restricted to a specific

area of the scatter diagram, thus supporting their treatment as closely related sub-communities. They also show a gradient of density from top to bottom, with the more open communities at the top and the thickets at the bottom.

This pattern of one woodland community merging with another woodland community can clearly be seen in the field. On the other hand, communities such as Sand Forest are quite distinct with sharp boundaries.

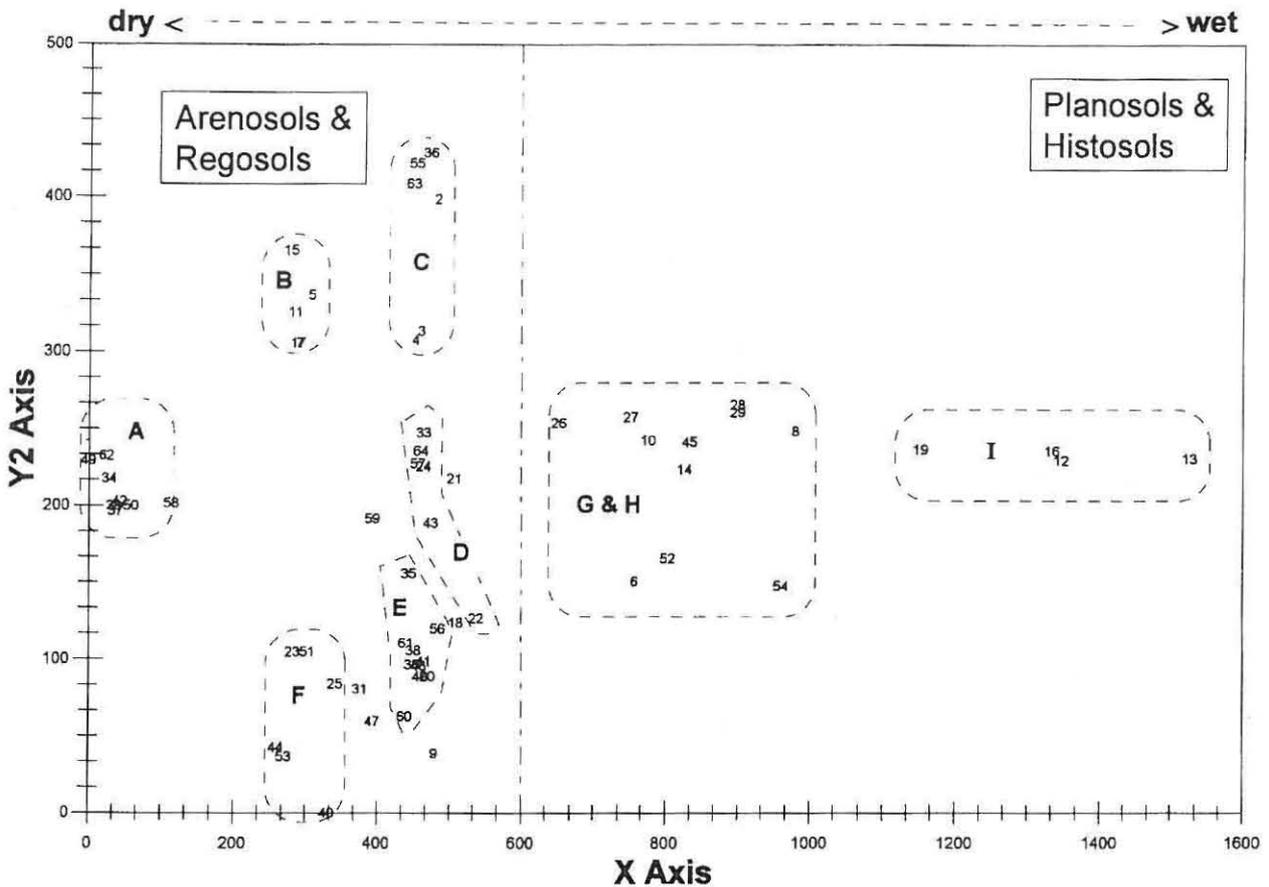
#### Plant community relationship

Eight ecologically-interpretable plant communities have been distinguished, described and mapped. This information can be used in reserve and area management, land-use planning, and extrapolation to other parts of Maputaland, as well as in further ecological studies. Results of the ordination not only confirm the classification, but also give an indication of floristic and associated habitat gradients. Dynamics of water in the landscape clearly control the structure of the community at the first physiognomic level. This is a common phenomenon in savanna areas (Solbrig 1993).

All the proposed communities are distinguishable in the field based on structure, growth form, general species composition and character species — this is despite the gradual environmental gradients that cause communities to merge into one another, particularly so in the case of the woodlands. The different woodland sub-communities often can be difficult to distinguish based on floristics alone, but structure and density help to distinguish between them.

Except for the broad-scale classification of the coastal grasslands of southern Mozambique (Myre 1964, 1971) and the detailed classification of coastal and inland communities elsewhere in Maputaland (Lubbe 1996, Matthews *et al.* 1999), the present study is a further attempt at a more detailed, larger scale phytosociological classification of some of the Maputaland coastal plain communities. A correlation between the plant communities of the present study and the various syntaxa described by Myre (1964, 1971) and other workers has been attempted. Myre (1964) did not formally describe any of the closed woodland or forest and related communities, but rather concentrated on the grassland and related communities. He did, however, give a basic species composition list for what he called Licuati Forest. The composition of this Licuati Forest in southern Mozambique corresponds closely with what is called Sand Forest in South Africa. Included in this species list are also some species associated with thicket vegetation on sand and clay, e.g. *Spirostachys africana* and *Euphorbia ingens*. This is also the case for the Sand Forest type described for Sileza Nature Reserve, namely the *Artabotrys monteiroae-Dialium schlechteri* forest, the coastal form of Sand Forest (Matthews *et al.* 1999). The last mentioned variation compares well with typical Sand Forest, although it also contains a few species which are associated with what is referred to as thicket or closed woodland in the present study (e.g. *Commiphora neglecta*). Such species are, however, very few in the case of the *Artabotrys monteiroae-Dialium schlechteri* forest. Lubbe (1996) found a degree of similarity with Sileza 'Sand Forest' with what he described as *Tricalysia delagoensis-Dialium schlechteri* inland forest.





**Figure 5:** Ordination (X and Y2) of the relevés from the Tembe Elephant Park and surrounding areas. A, *Drypetes arguta-Uvaria lucida* subsp. *virens* Sand Forest of deep sandy areas (dry sands). B, *Spirostachys africana-Berchemia zeyheri* closed woodland on duplex soils (clays). C, *Andropogon schirensis-Tephrosia longipes* subsp. *longipes* grassland associated with Sand Forest. D, *Helichrysum kraussii-Dichapetalum cymosum* sparse woodland. E, *Andropogon gayanus-Albizia versicolor* open woodland on sand. F, *Zanthoxylum capense-Clausena anisata* closed woodland and thicket on sand. G, *Nidorella auriculata-Justicia flava* hygrophilous grassland on clay-rich soils. H, *Imperata cylindrica-Eragrostis lappula* grassland associated with sandy clay soils associated with the Muzi Swamp and other marsh/pan areas. I, *Oxalis* cf. *semi-loba-Nymphaea nouchali* of standing water in marshes and pans

past, it is probable that fires would have taken place annually to tri-annually, depending on biomass build up. These fires would occur during the dry season (winter to early spring), when the grasses are dormant and at that time of year when lightning frequencies are the highest.

Margins of Sand Forest are often exposed to fire, which in some cases has a low impact, but at other times can be quite destructive. Many of these 'negatively' fire-impacted Sand Forest patches and margins do not regenerate at all. This leads us to the assumption that Sand Forest is decreasing as a result of fire. However, a comparison of aerial photographs of TEP taken in 1942, 1959, 1969 and 1975 indicates that the Sand Forest patches we see today are very stable. There has been no increase in Sand Forest distribution, this being in contrast to the areas neighbouring Sand Forest which show a distinct increase in woody plants. There is indication of slight reduction of Sand Forest patches, as would have been predicted. This reduction is very slight and depending on Sand Forest dynamics in other areas and over the long term, should not be looked on negatively. However, the negative impact of large herbivores,

such as elephant, which in the past were not closely associated with Sand Forest, in combination with fire, could promote Sand Forest shrinkage. Under the time scale at which Sand Forest dynamics seems to operate, these added impacts could negatively affect Sand Forest conservation within TEP.

### Endemism

About 2 500 species, but probably more, of vascular plants occur in the Maputaland Centre of Endemism (Van Wyk 1996). Of these, at least 230 species or infraspecific taxa and three genera are endemic or near-endemic to the region (Van Wyk 1996). Eighty-four of these Maputaland Centre endemics/near-endemics were recorded in the study area (Table 4), but the actual number present is expected to be slightly higher due to incomplete sampling. Most endemics were associated with only two of the seven major plant communities. Forty-two taxa are associated (27 restricted) with *Drypetes arguta-Uvaria lucida* subsp. *virens* forest (Sand Forest) and 37 (13 restricted) to the *Strychnos madagas-*

*carriensis-Combretum molle* woodland. Most of the *Salacia kraussii-Themedea triandra* open woodland sub-communities' endemics have the geoxylic suffrutex growth form. Hence this community shows a strong association with the *Themeda-Salacietum* woody grasslands described from the Sileza Nature Reserve and surrounding area (Matthews *et al.* 1999). *Themeda-Salacietum* woody grassland, which occurs closer to the coast, is another plant community noted for its high numbers of MC endemics. Another community relatively rich in endemics is the *Spirostachys africana-Berchemia zeyheri* closed woodland on clay, where 20 MC endemic/near-endemic species have been recorded. This is a restricted community in TEP, many of the endemics having a wider distribution outside the park on similar clay-based substrates. In the study area, by far the majority of plant endemics are confined to non-hygrophilous plant communities. The observed low species diversity and paucity of regional endemics in hygrophilous grassland communities is a common phenomenon throughout southern Africa.

The geological history of Maputaland suggests that the current ecosystems in the region may be of recent derivation. This part of the Mozambican Coastal Plain was last inundated by the ocean approximately 3–1.8 million years ago. In fact, many endemic plant taxa comply with the concept of neoendemics (young taxa). Thus, the MC comprises a unique environment in Africa in that it is geologically young with biological evolution (notably speciation) being actively driven.

Maputaland Centre endemics/near-endemics recorded in the study area, and even more so for the Centre as a whole, represent a wide spectrum of growth forms, including trees, shrubs, suffrutices, lianas, forbs, geophytes and annual herbs (Van Wyk 1996). Maputaland Centre endemics are also well represented in Sand Forest, woodland and grassland, with Sand Forest, on a regional basis, being perhaps the single richest community in MC plant endemics. In contrast, the Pondoland Centre of Endemism, located on the Pondoland Plateau to the south of the MC, is particularly rich in woody palaeoendemics associated with forest (Van Wyk 1994). It is hypothesised that one of the reasons for this marked difference in growth form and vegetation-type partitioning of endemics between these two centres of endemism is the relatively youthful (Quaternary) age of the exposed sandy Maputaland Coastal Plain and its associated plant communities. The species and plant communities had to adapt to more arid conditions inland as a result of sea level changes and resultant decrease in rainfall and soil moisture (water table drop); the lowering of the water table from deeper sand deposits rather than diminished rainfall.

The southern Kalahari, similarly associated with sand deposits, is also a relatively youthful ecosystem. Accumulation of Kalahari sands began towards the end of the Cretaceous, approximately 65 million years ago (Partridge and Maud 1987). Today many Kalahari sand plant endemics are to be found on the mesic northern areas of these sand deposits (Angola/Zambia/Democratic Republic of Congo/Zimbabwe). In contrast, the arid southern Kalahari sands (South Africa/Namibia/Botswana) contain very few local endemics. The southern Kalahari has been subjected to two major arid events, the second beginning in the Late

Pleistocene, although there have been intermitted wetter periods during this time (Malherbe 1984). The most recent arid period began approximately 10 000 years ago — consequently little time was available for speciation. The southern Kalahari also borders on ancient arid areas (e.g. Namib Desert and Karoo); thus there has been the opportunity for pre-adapted arid species establishing themselves through migration in Kalahari areas subjected to aridification. The latter invasions may have hindered *in situ* speciation and the development of neoendemics. On the other hand the southern portion of the Mozambican Coastal Plain (Maputaland) were at the time of its most recent exposure from the ocean apparently not bordered by any significant pre-adapted, arid, psammophilous floras. This may have resulted in the availability of many vacant niches on the sandy coastal plains subsequently occupied by newly evolved taxa derived from the available regional floras, hence the preponderance of neoendemics in the MC.

Four Maputaland Centre endemic/near-endemic bird species, namely, Neergaard's sunbird (*Nectarinia neergaardii*), Rudd's apalis (*Apalis ruddi*), Pinkthroated twin-spot (*Hypargos margaritatus*) and Woodward's batis (*Batis fratum*) are to be found in the study area. They are closely associated with Sand Forest (Van Rensburg 1998).

#### **Sand Forest (= Licuati Forest)**

Floristically, White (1983) classified the southern Africa forests as mainly belonging to two phytochoria, namely the Afromontane Archipelago-like Regional Centre of Endemism (which extends to the northeastern African uplands) and the Tongaland-Pondoland Regional Mosaic (which is largely restricted to the eastern coastal belt of southern Africa). His mapping was not at a fine enough scale to separate the 'Sand Forest' of northern KwaZulu-Natal and southern Mozambique from other Tongaland-Pondoland vegetation types. Moll and White (1978) considered many typical Sand Forest species (e.g. *Balanites maughanii*, *Cleistanthus schlechteri* and *Newtonia hildebrandtii*) to be Zanzibar-Inhambane linking species (the Zanzibar-Inhambane Region is the coastal phytochorial mosaic extending from southern Mozambique to east Africa). This phytochorion, together with the Tongaland-Pondoland Regional Mosaic, form White's (1983) Indian Ocean Belt. Low and Rebelo (1996), on the other hand, divide the southern African forests into three main types: Afromontane, Coastal and Sand Forest. These are then further subdivided. Van Rooyen *et al.* (1981) also recorded typical Sand Forest species (e.g. *Pteleopsis myrtifolia*, *Cleistanthus schlechteri*, *Hymenocardia ulmoides* and *Monodora junodii*) in the Sandveld communities (thicket) described from the Punda Milia-Pafuri-Wambiya area in the Kruger National Park.

Sand Forest occurs under drier conditions than most other forest types, and is thus classified as tropical dry forest. Marker and Russel (1984) have stated that the presence of mixed forest in low rainfall areas of the Eastern Cape can partly be ascribed to the presence of fog and the water holding capacity of deep sand, which sustain forest growth. Sand Forest in Maputaland is also found on deep sand, periodically experiencing heavy dews and low-level mists, espe-

cially in winter. This could effectively increase the rainfall.

In southern Africa forest at a local and regional scale generally shows low levels of tree endemism (White 1983, Cowling 1993, Matthews *et al.* 1993). Similarly, few forest tree species are rare (MacDevette *et al.* 1989), and uncommon species are generally those in ecosystems such as Sand Forest that just penetrate South Africa from the north-east. A notable exception is the forests of the Pondoland Centre of Endemism. These forests are rich in endemic plant species, several of which appear to be palaeoendemics (Van Wyk 1990, 1994, 1996). Tinley (1971) mapped the distribution of a dry semi-deciduous forest type (probably equivalent to Sand Forest) as a thin zone from northern KwaZulu-Natal up to Quissico (approximately 100km south of Inhambane), Mozambique. The northern limit (from Maputo–Quissico) of this dry semi-deciduous forest is still unclear, as Tinley (1971) noted a change in species composition in the area north of Maputo Bay. Our work has shown that Sand Forest is also an exception in being a forest type rich in endemic species (though in this case mainly neoendemics). These neoendemic species are centred in an area south of Maputo–Quissico (Mozambique) and north of St Lucia in northern KwaZulu-Natal (the core area of the Maputaland Centre). Hence, as far as is known, Sand Forest (as floristically defined in this paper) is more or less confined to the MC.

In many parts of southern Africa and rest of Africa, the boundary between forest and adjacent vegetation types (usually grassland or woodland, rarely fynbos) is very abrupt and in nearly all cases this transition does not follow environmental discontinuities. The abruptness of forest boundaries is chiefly ascribed to fire (Hopkins 1979, Midgley *et al.* 1997), an important determinant of forest boundaries and forest edge composition. Forest rarely burn, the fires usually stops at the forest margin. In the case of Sand Forest, not only does it have distinct boundaries, but it also has a narrow zone (1–2m) of nearly bare soil immediately adjacent to it. There are indications that allelopathic effects may play a role in the establishment of these narrow fringes of plant inhibition. Sand Forest, through allelopathic effects, possibly establishes a unique environment for itself, which also results in specific grassland communities neighbouring the Sand Forest. The resulting zone of plant inhibition may also protect Sand Forest against fire by acting as a kind of natural firebreak. Coetzee (1983) found similar abrupt boundaries (but no zone of plant inhibition) to one of the communities that he described from the central areas of the Kruger National Park, the *Androstachetum*. This community is composed of dense stands (forest) of the evergreen tree *Androstachys johnsonii* (Euphorbiaceae) on arid substrates in areas periodically experiencing heavy winter fog. The sharp boundaries observed here can not be attributed to fire, but were hypothesised to be due to the ability of the stands of *Androstachys johnsonii* to absorb water from the winter fogs, thus out-competing other species in this environment. It has now been established that the hairs in the dense indumentum on the leaves and twigs of this species can take up moisture (Alvin 1987).

In most parts of Africa forest types form mosaics with moist grassland and woodland. Relict patches of

Afromontane and Coastal Forest may occasionally be associated with savanna, but this is because of a restricted refuge, and the type of savanna more mesic. In the Cape Floristic Region Afromontane Forest is associated with wet or mesic evergreen sclerophyllous shrubland (fynbos). However, in the case of Sand Forest it occurs in a mosaic with dry woodland and thicket.

Midgley (1993) claimed that Sand Forest is dominated by species with wind-dispersed seeds, whereas other Indian Ocean coastal forests are dominated by fleshy-fruited species. From an analysis of unpublished data of dispersal patterns in the Sand Forest of TEP, it can now be shown that only 5% of the species are definitely wind-dispersed. This also applies to the more coastal Sand Forest types. Leaf attributes are generally fairly similar in all forests. Sand Forest is generally evergreen, non-spinous, with the leaves predominantly simple, micro- or mesophyllous and entire. Semi-deciduous trees do occur in Sand Forest, but these species are not dominant.

### Threats and conservation

Conservation efforts in the Maputaland Centre have hitherto centred mainly on areas containing species of large game. The vegetation of nearly all existing nature reserves and game reserves in KwaZulu-Natal is dominated by various types of savanna. A notable exception is the TEP that contains well-preserved stands of MC endemic-rich Sand Forest.

Outside conservation areas, the main threats to the Sand Forest habitat are uncontrolled fires used in clearing areas for agriculture, as well as selective species utilisation for traditional medicines, construction, fuel and other purposes. Examples of species selected for are *Cassipourea mossambicensis* that is used for cosmetic purposes (Brenton-Styles pers. comm.) and *Cleistanthus schlechteri* that is used in the wood carving trade. Uncontrolled cattle grazing, random uncontrolled fires, as well as selective species utilisation also have an effect on the other woodland areas outside conservation areas.

Inclusion of Sand Forest in conservation areas is no guarantee of the future persistence of this vegetation type. The effects of large herbivores, regular fires and Sand Forest dynamics can lead to disappearance of this vegetation type. One such threat to Sand Forest within a conservation area is highlighted in TEP, the conservation area in South Africa with the greatest amount of protected Sand Forest. The two primary reasons for the proclamation of TEP were that of Sand Forest conservation and the protection of the natural elephant population of Maputaland. This has led to a clash of interests between Sand Forest and elephant. Although these elephants prefer plant species from woodland habitats, they are increasingly utilising Sand Forest species. This is mainly due to the fact that old movement patterns have been fenced off and the elephants are now confined to a relatively small reserve. Since the old elephant movement routes were closed off in 1989, negative effects on Sand Forest and associated vegetation types in TEP have increased markedly (Matthews and Page unpublished results).

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