

**Contributions to the ecology of Maputaland, southern Africa, with
emphasis on Sand Forest**

by

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Submitted in partial fulfilment of the requirements for the degree

Philosophiae Doctor

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Promoter: Prof. Dr. A.E. van Wyk
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“No man crosses the same river twice. It is impossible for two reasons. The second time it is not the same river, and the second time it is not the same man. In the interval of time between the first and second crossing, no matter how short, both the river and man have changed.”

Heraclitus of Ephesus, 540–486BC

*Dedicated to my family and friends. . .
Specifically to those friends who stopped me from throwing this thesis into the dustbin*

ABSTRACT

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Keywords

Braun-Blanquet classification, endemism, Maputaland, Sand Forest, Woody Grassland, allelopathy, elephant, forage preference indices, evolution, vegetation dynamics

The principal hypothesis of this thesis was that the Maputaland Centre of Plant Endemism [MC] is characterised by plant communities that match a particular set of environmental variables, and their rich biodiversity with endemic and rare taxa reflecting the geomorphological history of the region. Data assembled supports the hypothesis. Vegetation studies highlighted two plant communities, endemic to the MC as being an important component of the region's biodiversity, namely Sand Forest and Woody Grassland.

A broad approach to the floristic classification of vegetation was adopted for information on the floristics patterns and diversity of the endemic/rare plants and plant communities of the MC. A hierarchical classification, description and ecological interpretation of the plant communities of the Tembe Elephant Park, Sileza Nature Reserve and surrounding areas are presented. Much of the vegetation distribution can be ascribed to the level of the water table, vegetation dynamics and historic evolution of the geomorphology of the region.

The hypothesis is presented that Sand Forest may have allelopathic effects on its environment. Data of exploratory germination trials are presented to test this hypothesis. Sand Forest soil inhibits the emergence of seedlings, the inhibiting effect decreasing progressively from Sand Forest through grassland to woodland.

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Sand Forest was defined as a community, and its possible dynamics are described. Ideas were formulated (albeit largely hypothetical) on the likely origin of this vegetation type. It is proposed that ancient Dune Forest is the precursor of Sand Forest, but that Sand Forest has subsequently become a separate functioning plant community on its own. Sand Forest appears to be a relictual vegetation type of which the historical factors responsible for its original establishment and expansion are currently no longer present in the region.

The use of woody species by elephant in different vegetation types in Tembe Elephant Park was investigated. A classification of species into utilization categories was produced which enabled assessment of the importance of different species to elephants, and also of the potential impact of elephants on different tree species. Management implications are highlighted.

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SUMMARY

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This study focused on aspects of the vegetation of Maputaland, an area with a rich biodiversity located in the extreme northeast of KwaZulu-Natal, South Africa, and adjacent parts of southern Mozambique. The principal hypothesis of this thesis was that the Maputaland Centre of Plant Endemism [MC] is characterised by plant communities that match a particular set of environmental variables, with a rich biodiversity including endemic and rare taxa reflecting the geomorphological history of the region. Data assembled supports the hypothesis. Vegetation studies highlighted two plant communities, both endemic to the MC, as being important components of the region's biodiversity, namely Sand Forest and Woody Grassland. Knowledge of the vegetation and flora of the MC and the role that large herbivores (specifically elephant) and fire may play in the dynamics of the different vegetation communities can help facilitate the formulation of management strategies. Notable for their richness in MC endemic/near-endemic taxa, the conservation of Sand Forest and Woody Grassland, should be a high priority.

A broad approach to the floristic classification of vegetation was adopted to address the need for information on the distribution patterns and diversity of the endemic/rare plants and plant communities of the MC. A hierarchical classification, description and ecological interpretation of the plant communities of the Tembe Elephant Park, Sileza Nature Reserve and surrounding areas are presented. The classifications resulted in mainly Sand Forest, woodland and grassland communities. Much of the vegetation distribution can be ascribed to the level of the water table, vegetation dynamics and historic evolution of the geomorphology of the region, either directly or indirectly, through its role in soil formation on the geologically young sandy substrate. Fire is an essential factor, particularly in maintaining the Woody Grassland. Geoxyllic suffrutices abound in

the Woody Grassland, raising questions about whether this vegetation type is best considered as grassland or extremely stunted savanna.

The hypothesis is presented that Sand Forest may have allelopathic effects on its environment, hence the characteristic zonation of the surrounding vegetation. Data of exploratory germination trials, as well as inorganic and organic soil analyses, are presented to test this hypothesis. Sand Forest soil inhibits the emergence of seedlings, the inhibiting effect decreasing progressively from Sand Forest through grassland to woodland.

Sand Forest was defined as a community, and its possible dynamics are described. Many biophysical factors were considered to formulate ideas (albeit largely hypothetical) on the likely origin of this vegetation type. It is proposed that ancient Dune Forest is the precursor of Sand Forest, but that Sand Forest has subsequently become a separate functioning plant community on its own. Sand forest appears to be a relictual vegetation type of which the historical factors responsible for its original establishment and expansion are currently no longer present in the region.

The use of woody species by elephant in different vegetation types in Tembe Elephant Park was investigated using a modified Point-centred Quarter sampling design. A classification of species into utilization categories was produced which enabled assessment of the importance of different species to elephants, and also of the potential impact of elephants on different tree species. Ninety of the 137 plant species encountered in the study were utilized. Thirteen species were selected for, 32 were used at random, 35 were avoided and at least nine were rejected. Management implications are highlighted.

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CURRICULUM VITAE

Wayne Sidney Matthews was born in 1961 and grew up in Springs, South Africa. He received his school education there, and completed his tertiary education at the University of Pretoria. In 1988 he did his National Service, followed by an MSc, which he received with distinction. His thesis dealt with the phytosociology of the North-eastern Mountain Sourveld. In 1992 he joined the then KwaZulu Bureau of Natural Resources as a Regional Ecologist for Maputaland. This post he still holds today in the Ezemvelo KwaZulu-Natal Wildlife where he is based in Tembe Elephant Park, Maputaland. Wayne has worked as a natural history tour guide for Trialblazers and Lapalala Wilderness Trails. He has travelled widely on advisory trips (compiling plant species lists, wildlife carrying capacities, biodiversity, ecological methodologies) and is familiar with the flora and fauna of many areas, such as Transkei/Pondoland, Southern Namibia/Richtersveld, Botswana/Okavango and Kalahari, Zimbabwe highlands, Western Zambia (Kafue area) and Maputaland (northern KwaZulu-Natal/southern Mozambique). He is an avid photographer and has had many of his photographs published. A list of his publications follows:

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CHAPTER 1

GENERAL INTRODUCTION

1.1 Background

When the European hunters and explorers arrived in the region today known as Maputaland in the early eighteenth century, they found a sparsely inhabited area, known for disease and infested by tsetse fly. As the French explorer Delegorgue (1838–1844) expresses that periods' European sentiments for this region: "In addition to the insurmountable dangers to the health of explorers in the Makazanes (a reference to the Mabhudu-Tsonga people living south of Maputo Bay) country, must be added the treachery of these locals, whose reputation as poisoners is known far and wide and appears to be deserved" (Delegorgue 1990). The presence of the tsetse fly prevented the keeping of cattle and other domestic livestock. Tsetse flies in Maputaland were only reduced to a point where livestock could be kept after the spraying with insecticide and game eradication programmes in the 1940s and 1950s. Today Maputaland is an area with considerable ecotourism potential containing several major provincial and tribal conservation areas.

Historically the name Maputaland has been applied, in a broad sense, to the coastal plain stretching from Maputo in Mozambique southwards to near the Mkuzi River in northern KwaZulu-Natal (Bruton & Cooper 1980). In recent times the southern boundary of the region has, for convenience, been extended to the estuary of Lake St Lucia so as to include the greater part of a biogeographical region. In South Africa, politically Maputaland covers an area of approximately 10 000 km² in the north of KwaZulu-Natal. Until recently this portion of Maputaland was known as Tongaland, but this name has now fallen into disuse. A further 10 000 km² extends into southern Mozambique. The combined area has been referred to as the *Greater Maputaland* by Smith (2001). As a biogeographical region the boundaries of Maputaland are well defined, except in the north, where the line is arbitrary (Van Wyk & Smith 2001). Maputaland is extremely biodiverse and includes a large number of endemic/near-endemic plant and animal species.

Earliest biological inventories for Maputaland came from mariners, hunters, traders and settlers. The first systematic collections and scientific surveys were, however, only conducted around 1900, such as by the missionaries R.B. Woodward and J.D.S. Woodward. They collected birds in the Lebombo Mountains and discovered many tropical species, including what is today called

Woodward's Batis (*Batis fratrum*). The Maputaland region was first studied from a biological point of view by the botanists R.D. Aitken and G.W. Gale (Aitken & Gale 1921) and the first descriptions of the ecology of the area was done by the zoologist Austin Roberts (Roberts 1936). The first mammal survey of the region was carried out in 1914 by the then Transvaal Museum (Rautenbach *et al.* 1980).

1.2 Maputaland Centre of Endemism

Southern Mozambique and the northern part of KwaZulu-Natal are recognised as a Centre of Plant Endemism, namely the Maputaland Centre (Van Wyk 1994, 1996). The boundaries of the Maputaland Centre (MC) were defined by Van Wyk (1994), who also provided information on the rich biodiversity of the centre (Van Wyk 1996; Van Wyk & Smith 2001). Biogeographically the core area of the Maputaland Centre has been defined (Van Wyk 1994, 1996; Van Wyk & Smith 2001) as that part of southern Mozambique and northeastern KwaZulu-Natal bounded by the Inkomati and Limpopo Rivers in the north, by the Indian Ocean in the east, by the western foothills of the Lebombo Mountains in the west and by the St Lucia Estuary in the south, from where it extends further southwards along the coast to near Mtunzini (including the transitional Ngoye Range). Biogeographically the boundaries of the centre are clear except in the north, where the line is arbitrary. Maputaland is also known for its rich fauna and flora which includes the high levels of endemism. Current knowledge is that about 2 500 species (but probably more) of vascular plants occur in the Maputaland Centre; of these at least 230 species/infraspecific taxa are endemic or near-endemic to the region (Van Wyk 1996). Other endemics are one species and 14 subspecies of mammal, 23 reptile species, three frog species and eight fresh water fish species. The Maputaland centre also corresponds with the southern part of the south-eastern African coast Endemic Bird Area [EBA]. The Important Bird Areas [IBA] programme of southern Africa (Barnes 1998) identified seven areas for KwaZulu-Natal, which fall into the Maputaland region. Of the more than 472 taxa of birds in the Maputaland Centre (almost 60% of South Africa's total), five are endemic/near endemic to the centre.

The rich biodiversity of Maputaland is partly due to the large number of habitats found in the region, including internationally recognised wetlands. High levels of endemism are spread across virtually the whole taxonomic spectrum, involving both plant and animals. White (1983) treated the area geographically as part of his larger Tongaland-Pondoland Regional Mosaic. In addition to being a Regional Mosaic, this floristic region was considered a Transition Zone (Moll & White 1978; White 1983). However, for a long time this emphasis on Maputaland as a transition (tropical

subtraction) zone has obscured its status as a centre of endemism in its own right. The Maputaland Centre, as part of the Maputaland-Pondoland Region (Site Af59), is acknowledged as one of the important centres of plant diversity/endemism in Africa (Davies *et al.* 1994). Recently the Maputaland Centre was incorporated in the larger Maputaland-Pondoland-Albany Hotspot, one of the 36 such regions of global conservation significance (Steenkamp *et al.* 2004).

Maputaland is also of exceptional biogeographical interest because of the sharp biogeographical transformation of both plant and animal taxa in the region (Poynton 1961; Bruton & Cooper 1980). Maputaland is at the southern end of the tropics in Africa and many tropical organisms reach the southernmost limit of their range here. The flora and fauna of the Maputaland Centre are predominantly of Palaeotropical and Afrotropical derivation respectively. Cape floristic elements are very rare among the endemics of the region (e.g. *Restio zuluensis* and a form of *Aspalathus gerrardii* with minute flowers). Curiously, some of the coastal grasslands contain grass species usually associated with the Drakensberg-Afromontane region (e.g. *Monocymbium ceresiiforme*). However, these grasses are most probably distinct ecotypes.

Elephants have been recorded on the Maputaland coastal plain more or less continuously since 1840 (Harris 1852, Baldwin 1895; Bulpin 1966). Southern Mozambique and northern KwaZulu-Natal, Maputo Elephant Reserve [MER], Futi Corridor and Tembe Elephant Park [TEP] presently hold elephant populations separated from each other either through electric fences or social political barriers imposed by the presence of man. These subpopulations represent remaining fragments of the coastal plain population that, until 1855, roamed as far south as the White Umfolozi River (Klingelhoefer 1987). Both the MER and TEP elephant populations suffered from heavy poaching during the last 30 years. The last free roaming population of elephants in South Africa was fenced-in with the proclamation of Tembe Elephant Park in Maputaland in 1983. This protected area was established in response to the increasing levels of human-elephant conflict and the need to protect the biodiversity of the region, which was under-represented within the protected areas of KwaZulu-Natal. At present the elephant population in TEP comprises some 185 animals (Matthews 2004) while the MER harbours approximately 200 animals, which are essentially free roaming. At present an unknown number of elephants are resident in the Futi Corridor but they are under a constant man-induced threat (Ostrosky & Matthews 1995). The post-war (Mozambique Civil War) return of agricultural activity to the region resulted in elephants causing significant crop damage around the MER (De Boer & Baquete 1998). This is leading to renewed pressure on the local elephant population.

1.3 Sand Forest

Sand Forest (Licuáti Forest) only occurs in South Africa and Mozambique, and is a unique inland feature of Maputaland. It has over the years been referred to as:- Licuáti Forest (Myre 1964), Tongaland Sand Forest, Msinga Bush (Moll 1968), Sand Forest (Moll 1978, Mucina *et al.* 2005), *Artabotrys monteiroae-Dialium schlechteri* Forest (Matthews *et al.* 1999), Western Sand Forest (Kirkwood & Midgley 1999), Sand Thicket and Forest (Smith 2001); Eastern Sand Forest, and Licuati Sand Forest (Mucina & Geldenhuys 2004).

Sand Forest harbours many rare and unusual types of plant and animals, many of which are Maputaland Centre endemics taxa. Because of its restricted occurrence and unusual species complement, Sand Forest is one of the most important habitat types in Maputaland. The biggest stand of Sand Forest (perhaps best described as thicket in this area) is found in southern Mozambique (north of Tembe Elephant Park) it is ~ 25 km long and ~8 km wide.

Structurally Sand Forest is a relatively dense vegetation type with different strata. The forest is generally low-grown, 5 to 12 m tall, a closed canopy with few large emerging species and a noticeable lack of undergrowth including a low abundance of herbs. The emergent trees in most places are covered by epiphytic plants such as orchids and lichens. These forests have a relic character and do not regenerate actively. They also show floristic and faunistic links to the tropics further north. In most cases the forests are delimited by narrow zones of sparse grass-vegetated or bare-sand areas directly adjacent to the forest margin.

1.4 Rational and motivation

Maputaland, a region of great scenic beauty and rich biodiversity, shows considerable ecotourism potential, and this could be used as a basis for economic growth in the region. Several important conservation areas are to be found in the region, Tembe Elephant Park, Ndumo Game Reserve, Mkuzi Game Reserve and Maputo Elephant Reserve in Mozambique also including the Greater St Lucia Wetland Park, a World Heritage Site that includes Kosi Bay Coastal Forest Reserve. Currently initiatives for establishing a transfrontier conservation area and the so-called “peace parks” between northern KwaZulu-Natal, Swaziland and southern Mozambique are underway, effectively linking the northernmost KwaZulu-Natal parks (Tembe Elephant Park and Ndumo Game Reserve) and tribal conservation areas, with the southernmost Mozambican parks and conservation areas. Management of these areas will require a sound

understanding of the biological processes and intricacies of the region.

Efficient biological surveys are a fundamental requirement for the effective management of biological resources and constitute the most basic activity in the field of conservation biology (Margules & Austin 1991). Conservation priorities in Maputaland were identified after a series of reports, including surveys by Bruton & Cooper (1980), Tinley & Van Riet (1981) and Klingelhoef (1987), which discuss the natural biotic riches of the region and indicate the need to safeguard these attributes. In 1994, the Maputaland-Pondoland Region was recognised as an International Centre of Plant Diversity (Davis & Heywood 1994) and in 2005 was incorporated in the Maputaland-Pondoland-Albany Hotspot (Steenkamp *et al.* 2004). Van Wyk (1996) has shown that the Maputaland Centre is an area of high plant species diversity with relatively high numbers of endemic and near-endemic species. It harbours a rich and diverse mega fauna and also abounds in invertebrates, which at this stage are not well documented. Although many biological surveys have been carried out in the Maputaland region, most have not tried to define or identify critical sites of biodiversity for protection and/or conservation management. Recently conservation planning studies have been initiated and are currently in progress (Smith 2001, Goodman 2003). One method being employed is systematic conservation planning, which involves mapping the distribution of different conservation features and existing Protected Areas [PA], setting representation targets for each feature, measuring the effectiveness of the present PA system in meeting these targets and, using computer-based selection algorithms to identify additional sites (Margules & Pressey 2000). In addition, this process incorporates a range of socio-economic and threat data on threatened species to increase the relevance of the planning exercises (Smith 2001).

Because of the significant number of endemic plant species associated with Sand Forest, the latter is perhaps the most remarkable plant community in the Maputaland Centre (Wild & Barbosa 1968, Moll 1977, 1980, Moll & White 1978, Van Wyk 1996, Van Wyk & Smith 2001). Equally important in terms of endemism is the Woody Grassland (not to be confused with “wooded”) of the coastal plains (Matthews *et al.* 1999). Both Sand Forest and Woody Grassland are endemic to the Maputaland Centre. By better understanding the distribution and determinates of Sand Forest, Woody Grassland and associated habitats, appropriate management can be put in place in and outside reserves.

Key statements addressed in the present study include;

- i) *Maputaland Centre of Plant Endemism is characterised by plant communities*

specific to its heterogeneous environmental factors.

- ii) *Maputaland Centre of Plant Endemism exhibiting a specific relationship between habitats, species and the geomorphological history of the region.*
- iii) *Maputaland Centre of Plant Endemism has a high plant diversity (compared with surrounding areas), including endemic and near-endemic plant taxa, which exhibit relationships with specific habitats.*
- iv) *knowledge of the vegetation and flora of the Maputaland Centre of Plant Endemism, and the role of large herbivores (specifically elephant *Loxodonta africana*) and fire makes it possible to formulate management strategies.*

These statements were used to formulate specific objectives to test ideas/hypothesis, to contribute to ecology and vegetation science and to inform management options.

1.5 Objectives

The principle objectives of the present study are to:

- collate and make a synthesis of available information on the functioning of the terrestrial plant communities of Maputaland, with emphasis on Sand Forest;
- refine the classification and description of the vegetation of Maputaland as well as the environmental determinants of these habitats;
- record ecological and floristic data for the Sand Forest and associated woodland habitat of a part of Maputaland by identifying, characterising, interpreting, describing and mapping the major vegetation units and their variations that occur in the Tembe Elephant Park and surrounding areas;
- record ecological and floristic data for the Woody Grassland and associated vegetation of a part of Maputaland by identifying, characterising, interpreting, describing and mapping the major vegetation units and their variations that occur in the Sileza Nature Reserve and surrounding areas;
- identify primary determinants of community composition and distribution, with emphasis on Sand Forest;

- assess the floristic richness and the level of endemism in Maputaland in the context of the Maputaland Centre;
- record ecological and floristic data to construct a classification of woody species in terms of their abundance, their importance in the elephant diet, and the potential effect of feeding by elephant on the major vegetation types that occur in Tembe Elephant Park;
- propose and evaluate specific hypotheses on the dynamics, function and evolution of Sand Forest and its relationships and affinities with other plant communities in the region;
- propose and evaluate hypotheses regarding the origin and evolution of Sand Forest with respect to the geological and geomorphological evolution of the region; and
- propose and evaluate existing management directives for the region, be it for conservation of the biodiversity, for sustainable utilisation of the region's natural resources, or for ecotourism, with emphasis on Sand Forest and related communities.

1.6 Layout

This thesis consists of a collection of contributions on the phytosociology, vegetation dynamics, herbivore interactions and ideas and hypotheses on the evolution and dynamics of the vegetation of Maputaland. Contributions are in the form of manuscripts, of which some have been published, as well as contributions in preparation for possible publication in scientific journals. Although details of the study area, methods, results, discussion and references are presented in the individual contributions, brief descriptions of the study area (Chapter 2) and the methodological approach (Chapter 3) are supplied separately. References for all Chapters are grouped together under References at the end of the thesis. A synthesis of the principal findings, management implications of the work and conclusions are presented in Chapter 9, 10 and 11.

The reprints/manuscripts included in this thesis show some stylistic irregularities and repetitiveness. These are primarily due to differences in layout and style required by the various scientific journals and the fact that each manuscript is an entity in itself. To get manuscripts accepted for publication, conformation to some idiosyncrasies of referees and editors was

sometimes unavoidable.

Additional specific data, references and publications in which the author was involved, and that contribute to the subject matter dealt with in the thesis and that may assist in the understanding of specific topics, are presented as Annexures.

CHAPTER 2 STUDY AREA

2.1 Locality

This study mainly focused on the South African section of the Greater Maputaland (Figures 1 & 2), a region henceforth referred to as Maputaland, and specifically the coastal plain, a low lying region covered by Cenozoic to Recent marine deposits. The northern limits were the Mozambique border and the southern limits the northern end of Lake St Lucia, bordered by the Lebombo Mountains in the west and the Indian Ocean in the east. The core area of the southern portion of the Maputaland Centre of endemism [MC] as defined by Van Wyk (1994, 1996) and Van Wyk & Smith (2001) is congruent with the study area (Figure 1).

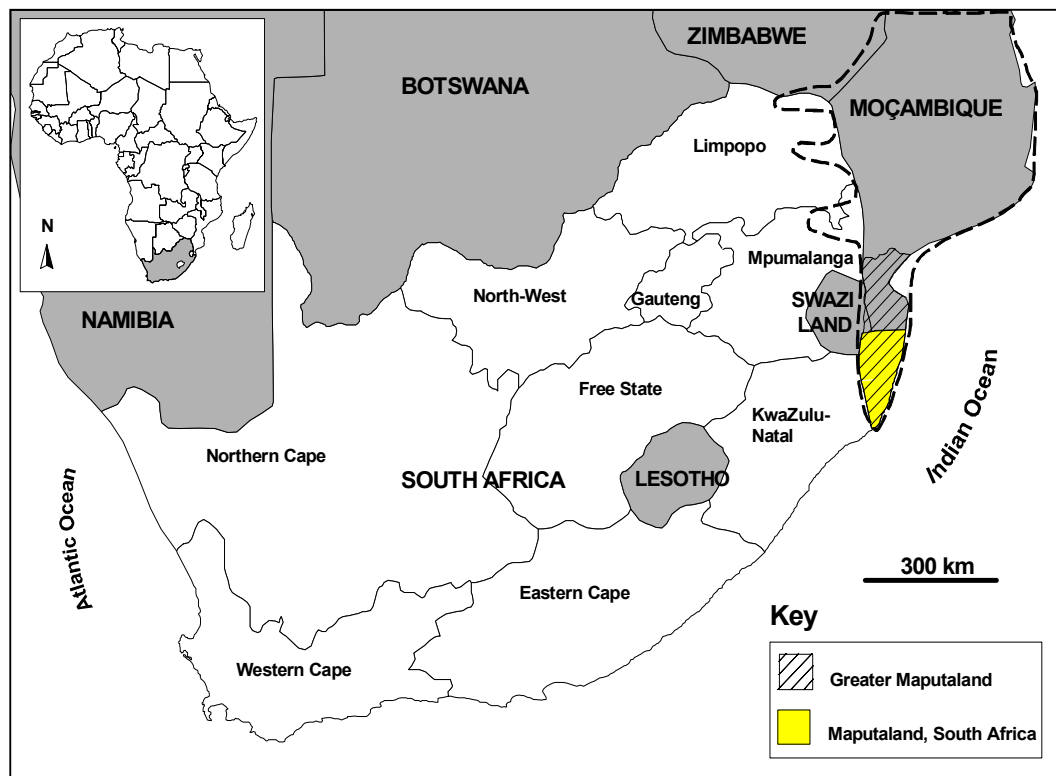


Figure 1. Location of Greater Maputaland and Maputaland, South Africa (from Smith 2001). Dashed line represents area of influence of the Maputaland Centre (Van Wyk 1994).

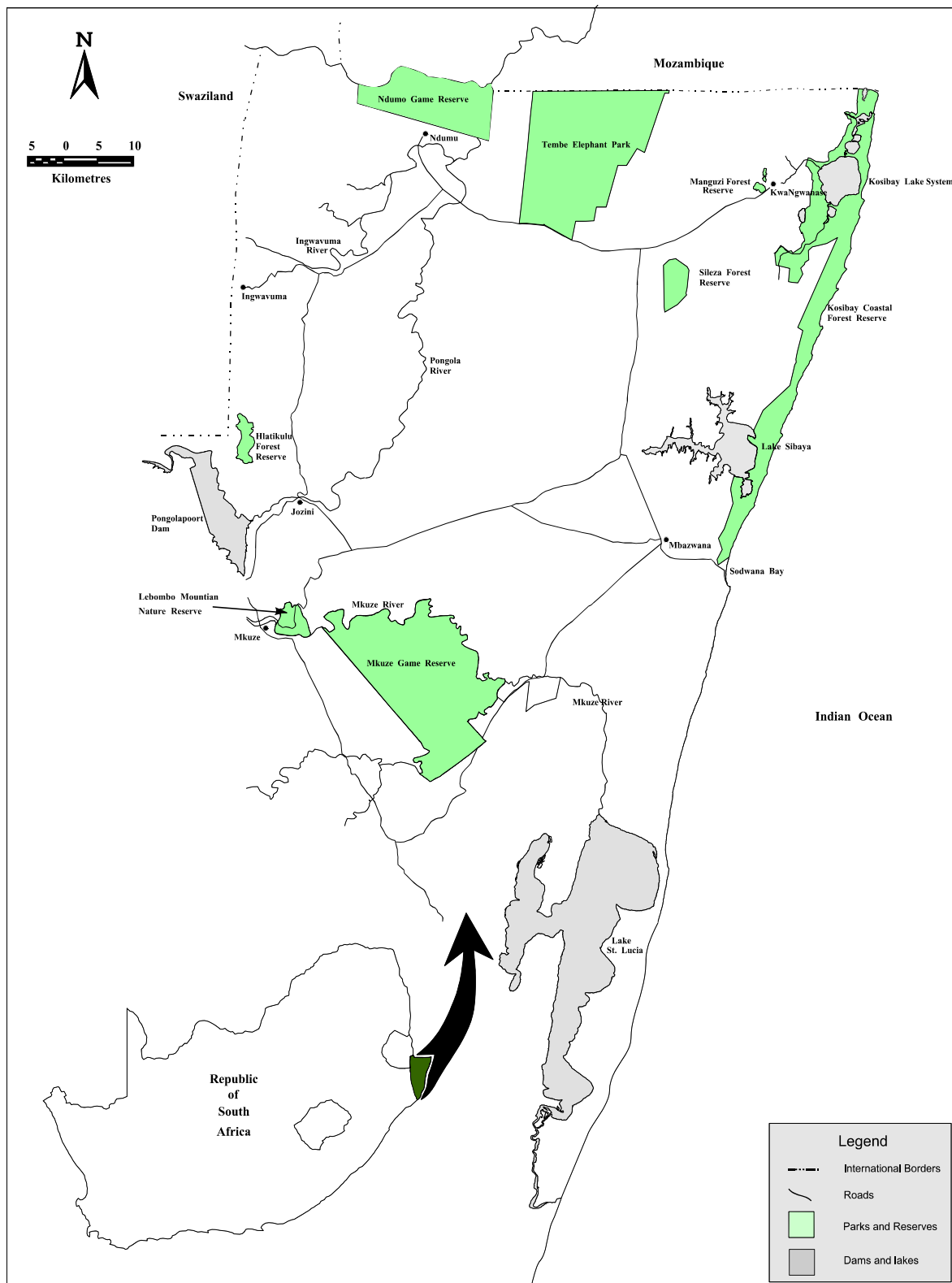


Figure 2. A simplified locality map showing main towns, parks, reserves, dams, lakes and roads of Maputaland in northern KwaZulu-Natal, South Africa as relevant to the study.

2.2 People of Maputaland

Maputo, the Capital City of Mozambique, and also Maputaland, is named after Chief Mabhudu of the Thonga people. He was a powerful chief at Lourenço Marques (now Maputo also formerly known as Delagoa Bay) during the 1770s and 1780s (Kloppers 2001). The Tembe people are ethnically linked to the Thonga, who occupy vast areas in southeastern Africa. The Tembe or Tembe-Thonga historically occupied the entire area from the present-day Maputo in Mozambique to the Mkhuze River in the south (Figures 1 & 2). The western boundary of the tribe's distribution was the Pongola River (Kloppers 2001). The Tembe take their name from the founder of the clan, Mthembu, who migrated from Kalanga to settle near Maputo around 1554. The word Thonga is of Zulu origin and means dawn. The Zulu used this name to refer to all the people living north of them (the Zulu people) who were not of Sotho or Nguni origin. The word Thonga also has a negative connotation to it and was used by the Zulu to denote slaves. Until recently the Maputaland region was known as Tongaland, but this name has now fallen into disuse.

The Portuguese were the first Europeans who made contact with the Tembe people. Portuguese sailors referred to the east coast of what is now known as Maputaland as 'Terra de Fumo' (the land of smoke) because of the large amount of smoke from wild fires seen. Portuguese interests in trade with Delagoa Bay (now Maputo Bay) led to the colonisation of southern Mozambique. According to Kloppers (2001), Britain also laid claim to the southernmost part of Mozambique, as did other white settlers such as the Portuguese. The issue was eventually settled in 1875 through international arbitration by the then French President, Mac Mahon. The border between Mozambique and South Africa was drawn along a straight line from Kosi Bay to the confluence of the Pongola and Usuthu Rivers, and from there along the river to the Lebombo Mountains, the exact position of the line is still today questioned by many sources (Kloppers 2001). The Tembe were not consulted and their tribal area was split in two. Today the Tembe tribal area falls in the Ingwavuma District of South Africa and in the Matutuine District of Mozambique. The Tembe Authority in Mozambique has largely been broken down during the Mozambican Civil War (September 1964–August 1974), but it still exists and has been gaining more influence since peace has been established (Lusaka Accord signed in September 1974).

By and large, environmental characteristics of Maputaland are such that it compels those who settle there to follow a particular pattern of natural resource utilisation. For example, the region is not ideally suited for keeping cattle. Considering the immense importance of cattle in Nguni

(Zulu) culture it is easy to see why the Zulu did not wish to settle here. The main source of protein available to the people is fish. The Zulu, and many other tribes in South Africa, do not eat fish except the Tembe-Thonga. These, and other ecological conditions, such as the practise of shifting agriculture in the nutrient-poor soils, made Maputaland an unattractive area for the Nguni people to settle.

Most Tembe people today still follow a traditional way of life, relying heavily on the natural resources of Maputaland for their survival. Although there are some economic developments in the area, the people still catch fish as they had always done in the fish kraals at Kosi Bay and in huge *fonyo* fishing drives in the pans around the area. Most people still collect wild fruits and many people are still involved in tapping the sap of the *ilala* palm (*Hyphaene coriacea*) to prepare the alcoholic drink called *ubusulu* (with all its intoxicating values).

However, the human population of the area has steadily increased forcing many people to over-harvest the resources. It has led many people to clear the natural vegetation to grow crops and to harvest firewood to sell to tourists and other users. This is a non-sustainable short-term solution that also impacts on the region's biodiversity. One potential long-term solution is to encourage the local people to establish sustainable eco-tourism projects and to set quotas for the sustainable harvesting of the available natural resources. However, the only way that this can be achieved is by reducing the rate of the present habitat destruction, this can only be done based on monitoring and information gathered on the biodiversity and its driving forces in the region.

2.3 Physical environment

2.3.1 Topography

With the exception of the narrow Lebombo range which rises to an elevation of some 600 m, the Maputaland Centre is a nearly flat, low-level coastal plain with a maximum elevation of about 150 m. Ancient linear north-south trending dunes, some of which may reach an altitude of 129 m, occur in the central part of the coastal plain (Wright 1997). The high coastal dune ridge along the shoreline rises to almost 200 m above sea level in places in KwaZulu-Natal, and is said to be amongst the tallest vegetated dunes in the world. The Maputaland Centre contains some extensive wetlands, particularly marshes, lakes and estuaries. In the study area there are three major natural lake systems, all of which are found in the east of the region. Lake Sibaya is the largest natural freshwater lake in South Africa and covers an approximate area of 70 km²

(Pitman 1980; Miller 2001). The Kosi Lake system consists of four interconnected lakes, which range in salinity from close to seawater concentrations in the tidal basin, to freshwater in Lake Amanzimnyama (Wright 2002). Lake St Lucia is 40 km long, up to 10 km wide and it has an average depth of 0.9 metres. It is connected to the sea by The Narrows, a tidal channel of about 20 km that together with the lake forms the largest estuary in Africa (Taylor *et al.* 2004). There are a number of other, smaller natural water bodies in Maputaland, many of which have associated wetlands.

2.3.2 Climate

Maputaland can be described as having a warm to hot, humid sub-tropical to tropical climate. Average monthly humidity is relatively high (fluctuating between 65–85%), even in the drier inland parts of the region. Winters are drier than summers and there is a pronounced dry season (April to September), although rain is received throughout the year. A tropical to subtropical climate prevails, with no frost occurring in winter.

2.3.2.1 Moisture and rainfall

The most striking feature of the climate of Maputaland is the variation in rainfall across the region. In the east, along the coast, the annual rainfall ranges from 1000 to 1300 mm. This decreases progressively inland, so that the mean annual rainfall is approximately 500 mm at the foot of the Lebombo Mountains. Rainfall then increases with altitude with the crest of the Lebombo Mountains receiving approximately 800 mm annually (Bruton & Cooper 1980; Maud 1980; Schulze 1982). However, these annual rainfall values can vary dramatically between years. The area is subject to extreme rainfall events caused by tropical cyclones or cut-off low-pressure systems. Northeasterly and southwesterly winds predominate in the region, with the rain-bearing winds coming from the southwest.

Mist frequently occurs on the Lebombo Mountains and, through inversion, locally on the plains (particularly in winter). The relative air humidity is generally high on the plains, even away from the coast. The high relative air humidity coupled with high summer temperatures result in a high discomfort index during the summer months.

2.3.2.2 Temperature

The southern boundary of the Maputaland Centre seems to follow the 18°C mean midwinter isotherm (Poynton 1961) quite closely and thus forms the southerly tip of the Tropical Climate Region, which is characterised by the coldest month (July) having a mean temperature of above 18°C. Being in essence an ecotonal region, climatic conditions in the study areas are often referred to as tropical/subtropical. The existence of this tropical peninsula is due to the low-lying topography of the Mozambican coastal plain east of the Lebombo Mountains, and the proximity of the warm Agulhas Current (Bruton & Cooper 1980). Sea temperatures are maintained at above 21°C by this warm current that also plays a significant role in the narrow temperature range between summer and winter of the northern KwaZulu-Natal coastline.

2.3.2.3 Fire

Regular fires are a natural phenomenon in the region and are important for the maintenance of many of the vegetation types, notably the coastal grasslands. In these coastal grasslands, topography, regular fire and water table depth are key ecological determinants (see Chapter 4). The woodlands also experience fires on a regular basis, and many of the species in the woodlands are adapted to fire. The Sand Forest on the other hand, is not adapted to fire and in cases when fire has penetrated the forests it has had a detrimental impact on the intact forest patches (see Chapter 5). Dune Forest is also not adapted to fire although it can recover and re-establish itself relatively quickly after severe damage from fire.

2.3.3 Hydrology

Water table and ground water movements play an important role in maintenance of many of the vegetation types in parts of Maputaland, as deep sand deposits cover the area. The water table varies from on the surface (Muzi Swamp and hygrophilous grassland) to depths of 60 m or more, below ground surface. The shallow water table feeds the marshes and pans in the area. The ground water is almost exclusively replenished by rainwater. After rains immediate fluctuations in local water levels can be experienced for a period of time. It was estimated by Kruger (1986) that vertical seepage rates were in the order of 0.1 m/day. Water movements through the sands were at a mean transmissivity of 20 m²/day and a co-efficient of storativity of 1x10⁻³. The only other source of surface water is the seasonal pans that occur on the duplex soils. These pans are usually dry during the winter (April–September).

2.3.4 Geology

The following account of the geology of the region is based mainly on Botha (1994) and Momade & Achimo (2004). Refer to Figures 3 & 4. Parts of the Maputaland coastal plain are geologically quite recent, especially in the east where it continues to expand, chiefly as a result of sand deposition. The formation of this plain, together with the topography of the region, has had a major influence on the abiotic and biotic characteristics of Maputaland. The cover sands of the Maputaland region are mainly aeolian in origin and consist of thin veneers of sandy topsoil. The underlying geology consists of Cretaceous age siltstones unconformably overlain by sediments of Miocene and Pleistocene origin. These Cretaceous sediments are considered to comprise the hydrogeological bedrock. The overlying sediments are more permeable, with the highest values found in the Miocene deposits. The latter are however present in the form of long north-south trending ridges, possibly representing old beach terraces, and may be completely absent in some areas. The Pleistocene sediments were deposited in a back-barrier lagoonal environment. These sediments in general have a lower permeability than the Miocene sediments, and are believed to contribute to constraining the permeability for regional groundwater movement. The permeability of the cover sands is relatively high.

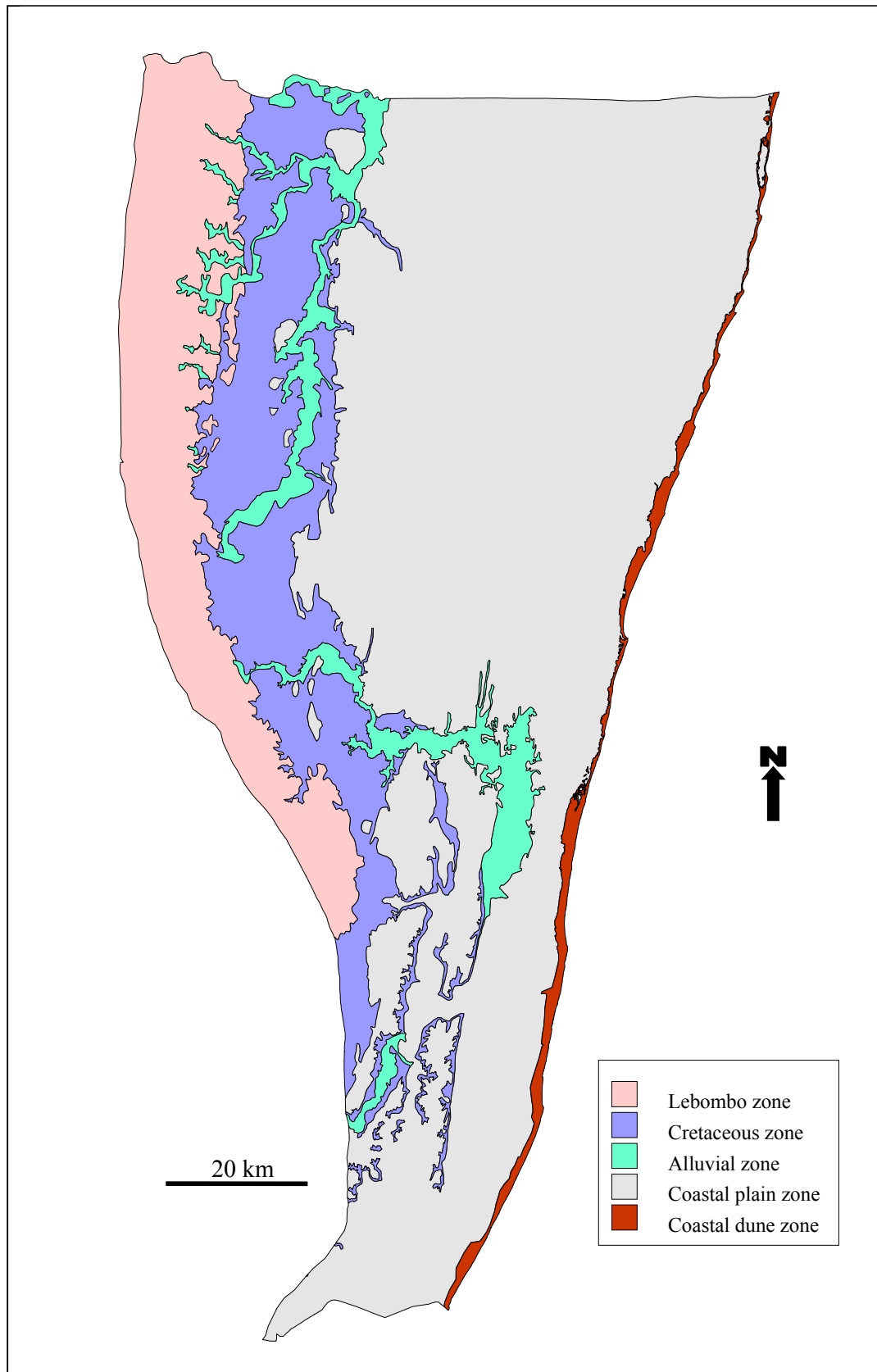


Figure 3. Main geological zones of Maputaland (Smith 2001). The study area conforms to the Coastal plain zone.

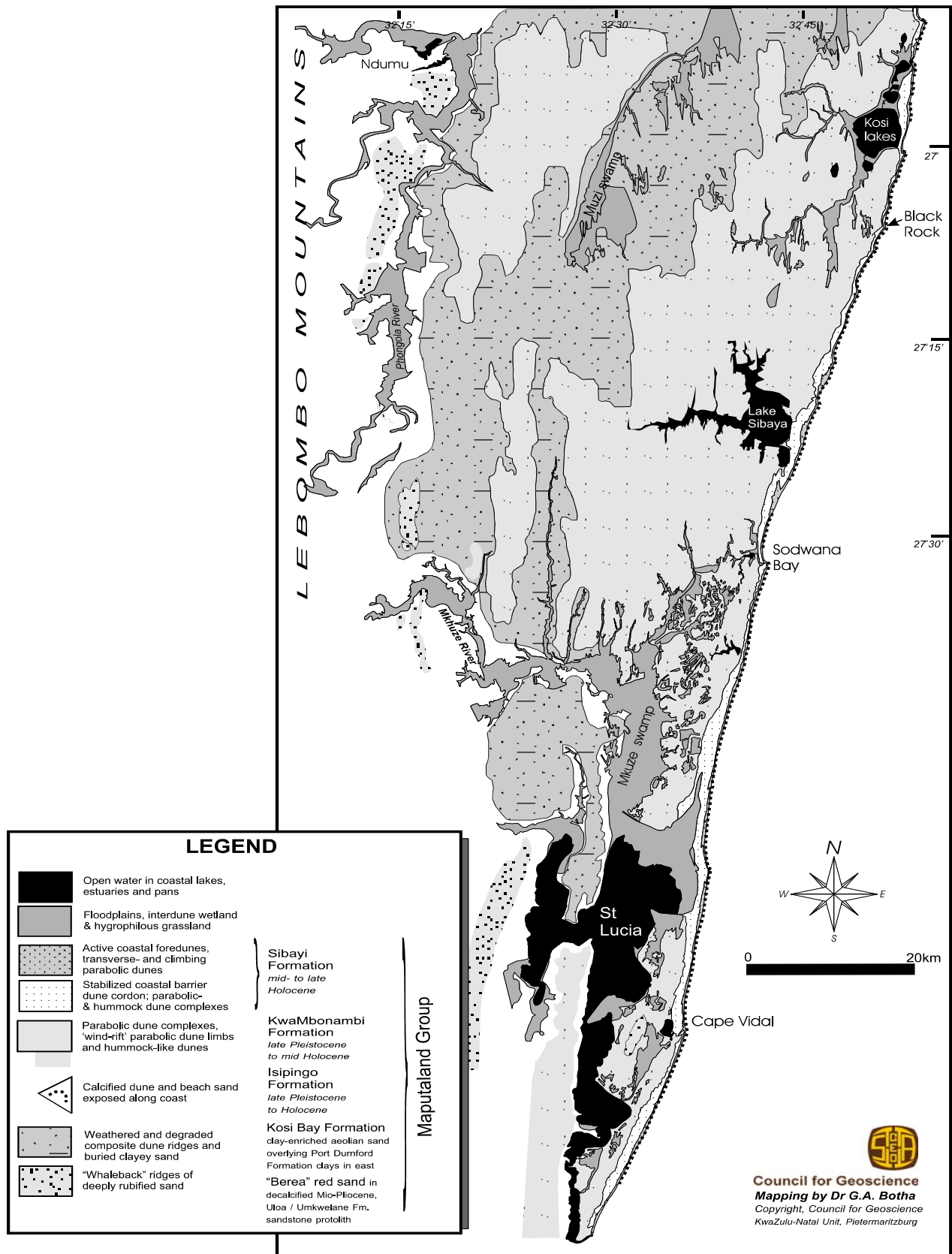


Figure 4. Geological map showing the distribution of aeolian sand stratigraphic units relative to incised drainage lines linked to coastal water bodies (Botha *et al.* 2003).

2.3.4.1 Condensed Geological history

Gondwana records

The break-up of Gondwana is an event that commenced in the Jurassic and is continuing today. There is an almost complete geological record of this period preserved in the offshore basin on the continental shelf around southern Africa (Watkeys 1997). Onshore, however, the records are sparse. Watkeys (1997) describes five stages of break-up.

The first stage, during the Jurassic (180–179 Ma), break-up in South Africa is marked by some rifting along the Lebombo mountains at the time of the Karoo volcanism. There was an attempted continental separation as indicated by the eruption of the Jozini rhyolites (179 Ma), which now form the Lebombo mountains.

Stage two (179–155 Ma) involves the linkage and movement along a fracture system (Gastre Fault). This fracture system separated the Patagonia block from Africa and the rest of South America.

During Stage three (155–135 Ma), another fracture system developed from the Somali Basin, past the Lebombo to the Weddell Sea and the Proto-pacific Ocean. Motion along this system split Gondwana into two plates: East Gondwana (Antarctica, Madagascar, India and Australia) and West Gondwana (South America and Africa). The Msunduze Formation (consisting of conglomerates is probably part of a rift succession), Mipilo basalt and Moveene basalt found in the southern parts of Mkuzi Game Reserve all formed during this stage.

Stage four (135–115 Ma) was the onset of sea floor spreading in the rift, involving the separation of South America and Africa (extraction of the Falkland Plateau which at that stage was located along the southeast coast of South Africa). Also during this time India rifted away from Australia and Antarctica. The Makatini Formation was deposited on the Maputaland platform from about 120 to 114 Ma, consisting of alluvial and fluvial deposits interfingering with estuarine and shallow marine sediments.

During Stage five (115–90 Ma), continuing extraction of the Falkland Plateau and opening of the South Atlantic occurs. Madagascar reached its present position (105 Ma) and the split between Antarctica and Australia took place. In Maputaland, the Mzinene Formation was deposited (112–

91 Ma). It consists of a general monotonous sequence of shallow marine silts and sands, which are glauconitic and locally pebbly, with sandy and shelly concretions. It is overlain by the shallow marine St Lucia Formation, rich in invertebrate fossils, which were deposited between 85 to 64 Ma.

Dune Cordons

The following account is based on Wright (2002) and refers to Figures 5 and 6a–6d. Late Cretaceous rifting associated with Gondwanaland break-up formed a shallow sea with the beach raised approximately 130 m above present sea levels. Steep gradient/short length rivers out of the Lebombo mountains formed large fluvial outwash fans which were worked into beaches by wave action (~ 65 Ma) (Zululand group: Makatini, Mzinene and St Lucia Formations). The dominant south-easterly wave direction prevails through to present times. Marine sediments are rich in fossils (e.g. ammonites, gastropods, bivalves and echinoides).

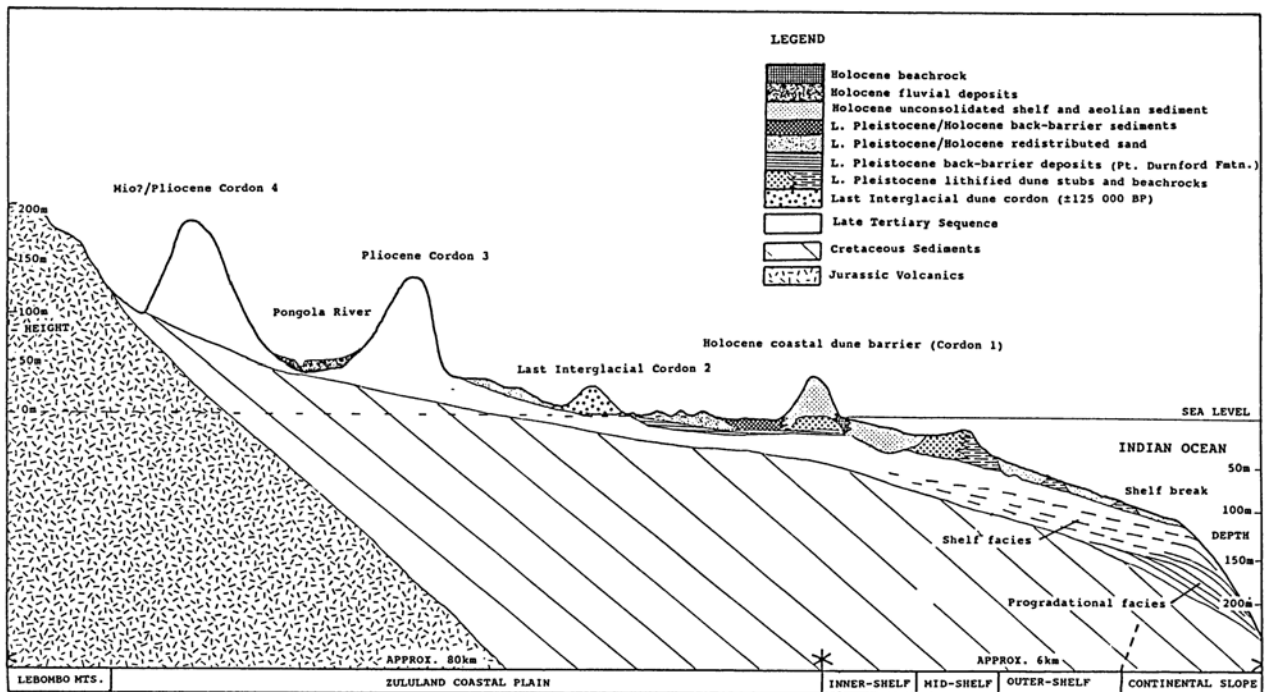


Figure 5. An idealised west to east cross-section through the northern KwaZulu-Natal Coastal Plain showing the geomorphological relationship of the different palaeodune cordons (from Wright 2002).

Figures 6a–6d. An idealised overview of the Cenozoic evolution of the northern KwaZulu-Natal palaeodune cordons (from Wright 2002).

Figure 6a.
Late Cretaceous (~65ma)
Legend
A= Lebombo Mt volcanism
B= shallow sea
C= fluvial outwash fans
D= dominant wave direction
E= Marine sediments rich in fossils

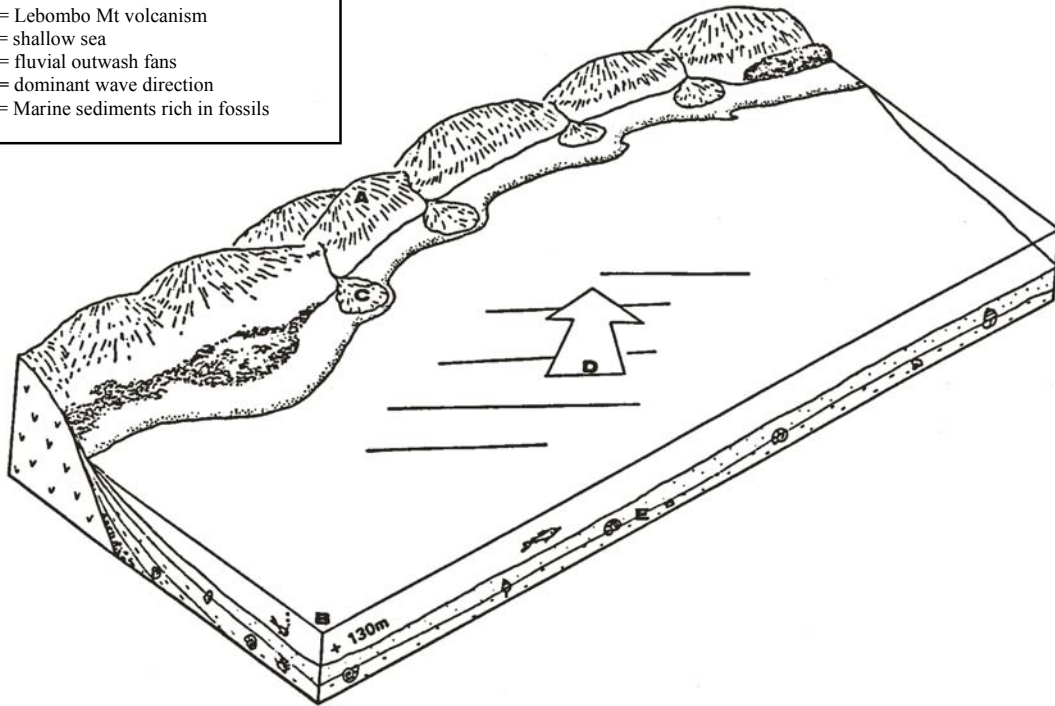
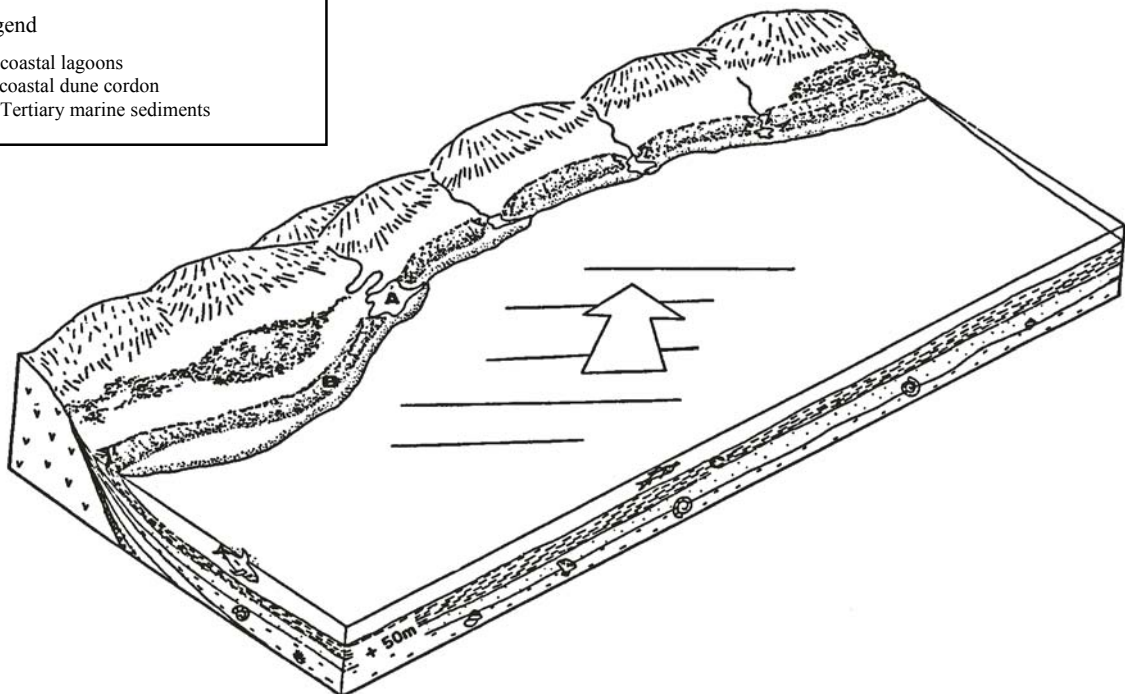


Figure 6b.
Late tertiary (~3ma)
Legend
A= coastal lagoons
B= coastal dune cordon
C= Tertiary marine sediments



Figures 6a–6d (continued). An idealised overview of the Cenozoic evolution of the northern KwaZulu-Natal palaeodune cordons (from Wright 2002).

Figure 6c.

Late Pleistocene (125 000BP)

Legend

A= shallow sea

B= tidal flats

C= coral fossil deposits

D&G&F= new coastal dune cordons

E= eroded Lebombo mountains and dune cordon

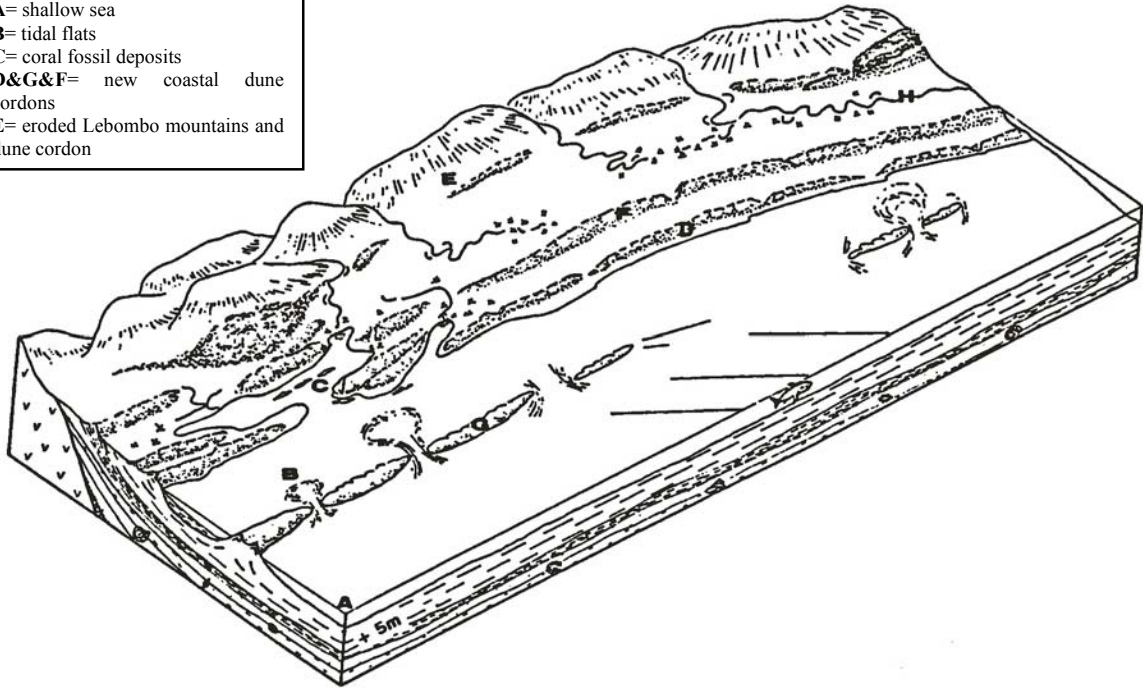


Figure 6d.

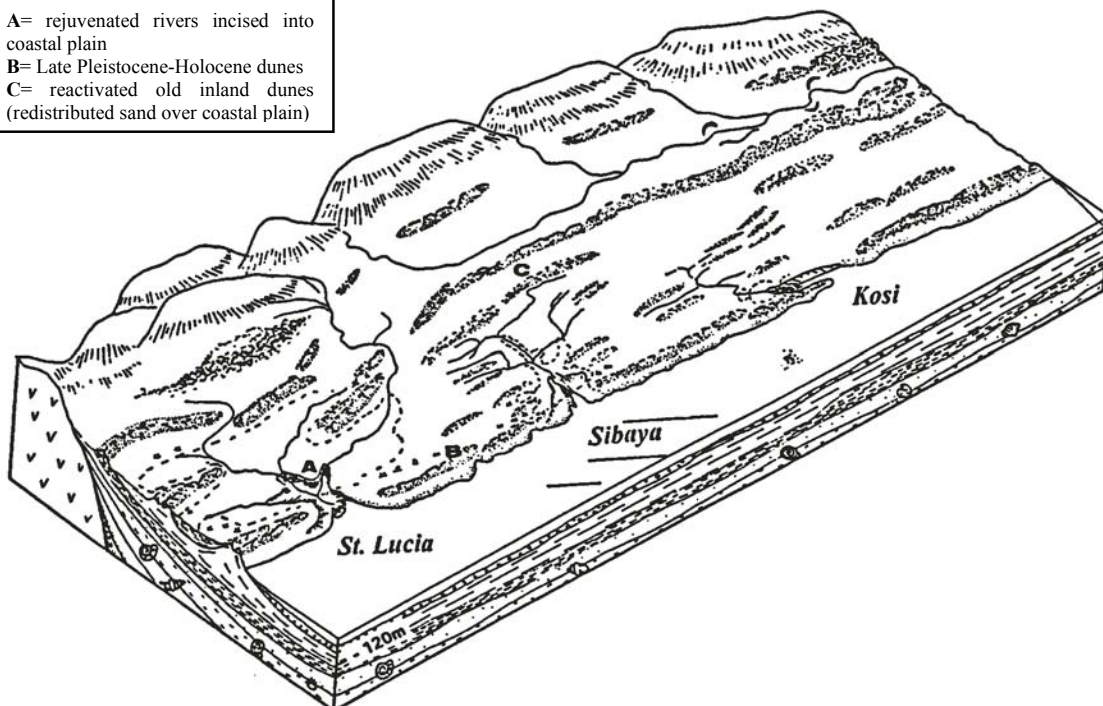
Late Pleistocene, last glacial maximum (18 000BP)

Legend

A= rejuvenated rivers incised into coastal plain

B= Late Pleistocene-Holocene dunes

C= reactivated old inland dunes (redistributed sand over coastal plain)



By the Miocene–Pliocene (~3 Ma) the mountains had eroded down and the rivers further decreased their gradients, forming lagoons at the coast (Figure 6b). Beach sediments were reworked by the prevailing winds into a large coastal dune cordon. Sediments include terrigenous and marine deposits, marine fossils and reworked Cretaceous fossils that were deposited into the shallow sea.

During the last Interglacial (~125 000 BP) sea levels had dropped approximately 125 m from a level that is 5 m above present day levels. The sea became shallower with offshore archipelagos (similar to Bazaruto in Mozambique) and tidal flats were common. Coral communities thrived leaving fossil deposits at what are now False Bay and St Lucia (Figure 6c). The Lebombo Mountains and the Miocene-Pliocene dune cordon eroded down. A new cordon (Late Pleistocene shoreline) was formed seaward of the Miocene-Pliocene dune cordon. This cordon approximates the Sihangwana dune cordon today. The archipelagos formed the basis for the more recent dune complexes. Decreasing river gradients and the formation of the barrier dune complex forced the rivers to migrate northward, resulting in the palaeo-Pongola system.

A sudden drop in sea level of 135 m (130 m below present levels) approximately 18 000 BP, rejuvenated the rivers causing them to incise into the coastal plain (Figure 6d). The very Late Pleistocene/Holocene coastal dunes formed on the old archipelagos. A change in the climate reactivated the old inland dunes, redistributing sand over the coastal plain. A rise in sea-level (130 m) to present day levels caused many of the rivers to be blocked by lagoonal barrier environments.

The precise ages of these dune cordons are still in contention. They are difficult to age, as top layers have been remobilised, possibly many times.

2.3.4.2 Main formations

Jurassic

Jozini Formation (Volcanic rhyolites): ~179 Ma.

Cretaceous

Msunduze (conglomerates), Mipilo (basalt) and Movene (basalt) Formations (155–135 Ma).

Makatini Formation (alluvial, fluvial with estuarine and shallow marine sediments): 120–

114 Ma.

Mzinene Formation (sequence of shallow marine silts and sands, locally pebbly with sand and shelly concretions): 112–91 Ma.

St Lucia Formation (rich in invertebrate fossils): 85–64 Ma.

Tertiary (65–1.8 Ma)

Miocene to Pliocene

The Uloa Formation is a source of controversy as the formation records are problematic (large time gaps present, missing records). A mid-Miocene transgression was followed by a marine regression during the late Miocene-Pliocene. A sequence of calcified conquina (cemented unsorted shelly debris, similar to conglomerate), shelly conglomerates and beach sands/gravels (Uloa Formation) and overlying aeolian calcarenite deposits (Umkwelane Formation) were deposited along the Lebombo foothills and towards the coast. A series of sea still stands during this regression are marked by remnants of dune cordons that are now deeply weathered to form Berea-type red sand e.g. Ndumo Hill.

Quaternary (1.8 Ma–0)

Pleistocene and Holocene.

The Port Durnford Formation

These deposits comprises 20–25m succession of estuarine clays, lacustrine (lake deposits) peat and aeolian sediments. A basal sand stone is overlain by grey or black mud with sandy laminae, which contain tracks, *Ophiomorpha nodosa* (trace fossil name for mud prawn), burrows and wood fragments, as well as a variety of fossils including crustacean and fish remains, foraminifera, marine molluscs, fragments of turtles and a crocodile (Hobday 1974; Scott 1992). NOTE: This formation seems to correspond to inland water bodies, vleis, swamp forest, sediments with hippo tracks and churned-up mud, etc. A Port Durnford coastal lake may have occupied a similar perched position in the landscape relative to sea levels at different geological times.

The following deposits follow the sequence of regressions and transgressions associated with sea level changes and uplift which took place from ~130 000 – ~70 000 BP till now.

The Kosibay Formation comprises orange or grey, weathered dune sands that are widespread inland of the coastal zone. (Cross-bedded sand and local calcarenite; Mid to

Late Pleistocene: ~130 000–10 000 BP).

The KwaMbonambi Formation dune systems derived from aeolian reworking of older dune sands, and inter-dune wetland deposits (inland-stabilised dunes and redistributed sand (non-calcareous); diatomite). This formation is associated with the marine regression, rivers incisions in response to the lowering sea level (~120 m) during the cool, drier phase associated with the last glacial maximum (~18 000 BP) which exposed most of the continental shelf (exposed bedrock ~70m below current sea level).

Sibayi Formation high coastal dune cordon including the current dunes, made up of calcareous sand. The Mid-Holocene marine transgression flooded coastal valleys and lakes, with alluvial sedimentation infilling many bedrock valleys near the coast. This high sea level is recorded by beach rock along the coast beach ridges within the coastal lakes systems.

The beach rock and aeolianite outcrops (some submerged) parallel coast and coastal facies extend semi-continuously from –5 m to –95 m and delineate the Late Pleistocene palaeo-coastline events. The Pleistocene, post-last Interglacial regressions resulted in deposition and cementation of coast-parallel beach rocks and aeolianites, which defines a series of four distinct paleo-coastline episodes with possible ages between 117 000 and 22 000 years BP.

2.3.5 Sea level records

This account of sea level changes is based on Ramsy (1995, 1997) and Momade *et al.* (2004). The shelf in the Maputaland region is extremely narrow (~3 km) compared to the global average of 75 km, and is characterised by submarine canyons, coral reefs and steep gradients on the continental slope (Ramsy 1995, 1997). The shelf break occurs 3 km offshore at -65 m depth. Three submarine canyons occur off Sodwana Bay. The origins of these canyons are not related to the position of modern river mouths but can probably be linked to palaeo-outlets of the Pongola and Mkuzi River systems. It is suggested that the canyons are mass wasting features, which were exploited by paleo-drainage during regressions. These canyons seem to be associated with first, the Late Pliocene (5.3–1.8 Ma) and secondly to the Late Pleistocene (~ 18 000 BP), when a sharp fall in sea level occurred and rejuvenated rivers.

Beachrock/aeolianite is carbonate-cemented beach sand which forms on sandy beaches in

tropical and subtropical climates (Miller 1997). The carbonate cement that binds the beach rocks is formed by repeated wetting and drying cycles driven by tidal activity. It is not only restricted to the tidal zone but also occurs in the supratidal zone where salt-water spray facilitates cementation. Beach rock forms during sea stillstands or during minor regression events, therefore its presence or absence can provide information regarding past sea levels and coastline morphology.

Summary of main sea level changes according to diagrams of Ramsy (1997) and a Quaternary sea level curve for southern Africa is given below. The sea levels are discussed in relation to present day sea level, taken as 0 m.

Mid Pleistocene (130 000–200 000 BP). Little is known.

Late Pleistocene (130 000–10 000 BP).

At:	+5 m	~124 000 BP.	
Dropped to	-45 m	~118 000 BP.	Last interglacial high stand
Rose to	+5 m	~106 000 BP.	
Remained at this level	0 m	~98 000 BP	(~12 000 yrs).
Slowly dropped to	-35 m	~58 000 BP.	Records between ~58 000 &
		~86 000 BP.	unclear.
Remained at this level	0 m	~44 000 BP	(for a period of ~12 000 yrs)
Dropped to	-130 m	~18 000 BP	Last Glacial Maximum
Rose sharp to	0 m	~8 000 BP	(Holocene)

Holocene sea levels according to diagrams of Ramsy (1997) are given below. Based on dating a series of Holocene beachrocks and planation (planning erosion, cutting into rock by wave action to form wave cut platforms) episodes on the southeast African coastline.

Gradual rise to	+1.5 m	~6 000 BP	
Remained at this level	0 m	~5 000 BP	
Rose sharp to	+3 m	~4 480 BP	
Dropped sharp to	0 m	~3 880 BP	
Remained at this level	0 m	~3 200 BP	
Dropped to	-2 m	~3 000 BP	Records unclear
Rose to	+1.5m	~1 610 BP	Records unclear

Dropped to 0 m ~900 BP
Remained at this level till today.

The first more relatively recent time that the sea level reach its present level along our coastline was at ca. 6 500 BP (Ramsy 1995).

2.3.6 Soils

The coastal dune sands consist mainly of quartz with local concentrations of heavy minerals such as ilmenite, rutile and zircon (Hobday 1979). Recent sands are whitish, while older sands tend to be reddish to brownish, with higher clay contents. Older dunes with stabilised woody vegetation tend to have a high humus content in the soils (Weisser & Cooper 1993).

In contrast to the infertile soils over most of Maputaland, weathering of rhyolite and basalt on the Lebombo Mountains has produced relatively fertile soils with high clay contents. Soil derived from the rhyolite and basalt to the west was deposited on the coastal plain as clayey but shallow lithosols. To the east there is a belt of rich clay-loam soils formed primarily *in situ* on the Cretaceous strata. These vary from red loamy to clayey soils on the higher-lying areas to black vertisols on lower-lying valley bottoms.

The three main soil types present on the coastal plain areas, are dystrophic regosols (Namib soil form), histosols (Champagne soil form) and humic gleysols (Soil Classification Working Group 1991; Soil Survey Staff 1996; FAO-UNESCO 1974). The regosols cover most of the region and are Quarternary sand deposits of generally low fertility (Watkeys *et al.* 1993). Dystrophic regosols are moderate to well-drained (leached) acidic sands found in elevated places such as dune crests and slopes. Histosols are acidic organic soils with an organic rich A horizon thicker than 400 mm and are found in marshy areas and pans. Humic gleysols are wet acidic sands with an abnormal accumulation of organic matter and are found in depressions where a high water table occurs. Duplex soils consisting of a clay layer beneath a sandy horizon occur in depressions, which become waterlogged in the wet season and sometimes form pans. 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.

2.4 Vegetation and flora

The southern boundary of the Maputaland Centre seems to follow the 18°C mean midwinter isotherm quite closely. This line also marks a zone where the fauna (and to a lesser extent the flora) changes from predominantly tropical to predominantly temperate (Poynton 1961). Plants display the same transitional pattern, although slightly more gradual. Maputaland is a transitional (ecotonal) area between tropical and subtropical climates and many plant and animal taxa find either their southern limit or their northern limit in the region.

The geological history of Maputaland suggests that the current ecosystems in the region may be of recent derivation. Many Maputaland Centre endemic plant taxa (Van Wyk & Smith 2001) comply with the concept of neo-endemics (recently developed). Thus, the Maputaland Centre comprises a unique environment in Africa in being geologically young and active with biological evolution (notably speciation) still in a very active phase. Although potential palaeo-endemics are present in the region (e.g. *Encephalartos ferox*, *Helichrysoptis septentrionale*, *Raphia australis*), many of the Maputaland Centre endemics appear to be of fairly recent diversification, an impression supported by the fact that some are differentiated at the infraspecific level only, with nearest relatives still extant. The Maputaland Centre is outstanding for its richness in neo-endemics. It is a remarkable region in which biological evolution, including speciation, appears to be particularly active amongst both plants and animals. All of these deductions would be consistent with the postulated geologically relatively recent (Quaternary) origin of the sandy, low-lying coastal plain comprising the greater proportion of the Maputaland Centre.

The interpretation of the current geographical range of a species is much more complex than just the climatic variables which determine the broad vegetation types in the region. To explain individual floristic patterns of distribution, a complex combination of biotic and abiotic factors may be taken into account including those present today and those from the past.

The general vegetation of the study area was broadly classified by Acocks (1953, 1988) as Coastal Forest and various Thornveld and Lowveld savanna veld types. The Coastal Forest and Thornveld was subdivided into the Typical Coast-belt Forest (1), Zululand Palm Veld (1b), Dune Forest (1d) and Mangrove Forest. According to Low & Rebelo (1996) the vegetation of Maputaland is part of both the Savanna and Forest Biomes. Savanna vegetation types recognised by them in the area are Sweet Lowveld Bushveld and Natal Lowveld Bushveld, and Coastal Bushveld-Grassland. The Sand Forest and Coastal Forest belong to the Forest Biome.

At least fifteen broad vegetation types were described for the KwaZulu-Natal portion of Maputaland by Moll (1977, 1980). However, with the exception of the pioneering work of Myre (1964) 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. Tinley (1971, 1976, 1985) did some pioneering work on the vegetation along the coast including mapping much of the southern Mozambique vegetation. Detailed vegetation descriptions have, however, been published for Ndumo Game Reserve (De Moor *et al.* 1977) and Mkhuzi Game Reserve (Goodman 1990) but these areas are not chiefly on sand. Klingelhoeffer (1987) did some work on the vegetation of the Tembe Elephant Park, but this was a broad-scale study related to elephant in the area. Lubbe (1996) completed a comprehensive vegetation study of the coastal strip from the Mozambique border down to Sodwana Bay, and included all the estuarine and lake systems in this area. Kirkwood & Midgley (1999) analysed the floristics and structure of Sand Forest.

2.4.1 Unique plant communities

Two noteworthy vegetation types, Sand Forest and Woody Grassland occur in Maputaland and are considered endemic to the Maputaland Centre. In this study emphasis was put on Sand Forest specifically as there are many intriguing aspects and management questions related to this Forest type. For example it is the forest type in the Maputaland Centre with the highest number of plant and animal types that are endemic to the Maputaland Centre, many of which are rare plants and animals. Sand Forest is the habitat for rare types of animals such as suni (*Neotragus moschatus*), four-toed elephant shrew (*Petrodromus tetradactylus*), Neergaard's sunbird (*Nectarinia neergaardi*), bluethroated sunbird (*Anthreptes reichenowi*), African broadbill (*Smithornis capensis*) and many different species of butterfly. Sand Forest shows low regenerating capabilities and certain of the large tree species like *Newtonia hildebrandtii* seem only to occur as mature plants. There are also management questions about the impact that elephants have on Sand Forest in Tembe Elephant Park. The Woody Grassland also has relatively high numbers of plant and animal types that are endemic to the Maputaland Centre, many of which are rare plants and animals. Intriguing aspects of this habitat is the suffrutex growth form that is so prevalent among many of the woody plant species.

2.4.1.1 Sand Forest (also named Licuáti Forest)

This forest type occurs in both South Africa and Mozambique. Sand Forest, also known as Licuáti Forest in Mozambique, is a very distinctive forest type with a unique combination of plant and animal taxa. This vegetation type is more or less restricted to ancient coastal dunes in northern KwaZulu-Natal and the extreme southern portion of Mozambique (Maputaland). Sand Forest harbours many rare and unusual types of plant and animal, including several Maputaland Centre endemics. Because of its restricted occurrence and unusual species complement, Sand Forest is one of the most important habitat types in the Maputaland Centre. It occurs in patches from False Bay in the south to just south of Maputo in Mozambique (Myre 1964; De Moor *et al.* 1977; Moll 1978; Moll & White 1978; Goodman 1990; Matthews *et al.* 1991, 2001; Everard *et al.* 1995; Lubbe 1997; Kirkwood & Midgley 1999; Siebert *et al.* 2002). The biggest stand of Sand Forest (perhaps best described as thicket in this area) is found in southern Mozambique (north of Tembe Elephant Park) ~ 25 km long and ~8 km wide (Siebert *et al.* 2002; Izidine 2003).

Structurally Sand Forest is from 5 to 12 m tall and forms a dense vegetation with different strata. The forest is generally low-grown, with a closed canopy of *Cleistanthus schlechteri*, *Dialium schlechteri* and *Hymenocardia ulmoides*. *Newtonia hildebrandtii* is one of the tallest species emerging above the forest canopy. *Croton pseudopulchellus*, *Pteleopsis myrtifolia*, *Drypetes arguta*, *Uvaria lucida* and *Cola greenwayi* are the most common shrubs in the understorey; while *Eragrostis moggii* is the most abundant grass species. The emergent trees are covered in places by epiphytic plants such as orchids and lichens. These forests have a relic character showing links to the tropical forest flora further north. The patches of Sand Forest are characterised by very sharp boundaries towards the surrounding vegetation (generally sandy woodland) and a distinct surrounding 'fringe' of thicket-like vegetation. In most cases the forests are delimited by narrow zones of sparse grass-vegetated or bare-sand areas directly adjacent to the forest margin, and these in turn are surrounded by open woodland communities.

The word "Licuáti" is a Mozambican (Ronga word) term that locally (locally referring to southern Mozambican areas, Maputaland) refers to thick bush that in most cases is what on the South African side is known as Sand Forest. Myre (1964) was the first to use the term "Licuáti Forest" formally to refer to a type of forest of which the composition corresponds closely with what is now called Sand Forest. A distinction has been made between so-called tall and short sand Licuáti Forest. Izidine (2004) referred to the short, dense form of Sand Forest and proposed

to call it Licuáti Thicket, based on Edward's (1983) structural classification of vegetation. The 14 000 ha of the Licuáti Forest Reserve, Mozambique, is a fine example of this form of Sand Forest. The tall form continues to be referred to as Licuáti Forest.

2.4.1.2 Woody Grassland

This unique grassland type is endemic to the Maputaland Centre, and is shared by South Africa and Mozambique. The Name Woody Grassland is applied to an unusual type of grassland characterised by the abundance of dwarf woody plant species with annual or short-lived woody shoots sprouting from a massive perennial underground system (so-called geoxylic suffrutices). The Woody Grassland is characterized by the dwarf shrubs *Parinari capensis* subsp. *incohata*, *Eugenia albanensis*, *Ancylbotrys petersiana*, *Diospyros galpinii*, *Gymnosporia markwardii*, *Eugenia capensis* (suffrutex form) and *Salacia kraussii*. Grass species include *Themeda triandra*, *Cymbopogon plurinodis*, *Diheteropogon amplexans*, *Trachypogon spicatus* and *Urelytrum agropyrioides*. This rather uncommon growth-form appears to be best developed in Africa, with the greatest concentration of such taxa occurring in the Zambesian Region (White 1976, 1983). These dwarf woody plants can be compared with extremely stunted trees, a fact which led White (1976) to refer to them as the "underground forests of Africa". Woody Grassland is found widespread on the dune crests and slopes elevated above the low-relief plains. It also occurs in open areas on sandy soils in woodlands and the Palmveld of Moll (1978).

CHAPTER 3 GENERAL METHODS

3.1 Methodological approach

The general methodology discussed here are broad outlines of the methods employed in each of the chapters. For more details on specific methods, please refer to the respective chapters.

3.1.1 Phytosociology

Groups of species tend to occur in associations determined by their ecological tolerance of abiotic and biotic factors, combined with interspecific and intraspecific interactions. Phytosociological classification of syntaxa seeks to investigate the interrelationships between plant species and their distribution patterns. Classification procedures employed in the Braun-Blanquet method, and modified by Mueller-Dombois & Ellenberg (1974) and Bredenkamp (1982), have been used to indicate the correlation between specific environmental conditions and plant communities. Thus, by utilizing the Braun-Blanquet method, hypotheses of the relation between the vegetation and environmental factors can be generated, the end product being an ecological classification.

The Braun-Blanquet classification procedure consist of two phases. During the first or analytical phase, environmental and floristical data are collected during fieldwork. The second phase (synthetic phase) results in the delimitation of the plant communities based on the classification of the field data. These plant communities (syntaxa) are then organized along environmental gradients (Moore *et al.* 1970; Deall 1985; Matthews 1991; Westfall 1992) to determine the most important environmental factors contributing towards the differentiation of each vegetation assemblage (plant community).

3.1.2 Phytosociological sampling strategy

Subjectively versus objectively placed sample sites have been both criticised and endorsed (Coetzee 1974; Mueller-Dombois & Ellenberg 1974; Werger 1974). The approach taken in the present study was of a more objective based method, namely stratified random sampling (Coetzee 1974; Bredenkamp & Theron 1978; Deall 1985; Matthews 1991; Westfall 1992). This approach allows for efficient sampling in heterogeneous vegetation but relies a great deal on

good reconnaissance of the area and aerial photograph analyses for the initial stratification. Using this sampling approach one is less likely to over- and under-sample as well as exclude certain vegetation types. The distribution of the sampling sites was based on the random stratification concept to ensure that all the different types of vegetation assemblages were sampled (Mueller-Dombois & Ellenberg 1974). The element of subjectivity was considered essential so as to place the sample plots in the most representative physiologically and floristically homogeneous vegetation stands to avoid ecotonal areas. This subjective placement would always be within proximity of the original sample placement.

3.1.3 Germination trails

The seedling emergence method was used as basis for all germination trails, using this method provided a standard by which all sample responses could be judged. By using this method different soil samples could be compared against each other based on the emergence and subsequent growth responses of a standard bioassay namely, lettuce (*Lactuca sativa* cv. Great Lakes) and wheat (*Triticum aestivum* cv. Inia).

3.1.4 Soil analyses

For most plant ecological field studies a basic understanding of the geomorphological and geological characteristics of a sample site is adequate. Soils, however, are one of the direct controls of plant distribution and performance, therefore requiring more detailed consideration. There is no single international terminology for soil classification and description. Most descriptions are variants, with more or less traits of the soil used in formulating the nomenclature. In the present study the more commonly used classification systems in South Africa and internationally are used, namely the FAO soil classification system (FAO-UNESCO 1974) and the South African soil classification (Soil Classification Working Group 1991).

Soil is an extremely complex medium and its variability causes many challenges in analysis and interpretation. Standard soil analyses were undertaken where appropriate. This included pH, electrical conductivity, as well as the nitrogen, phosphorus, calcium, potassium, magnesium and sodium content of the soil. Where additional chemical information was available for the soil of a site, it was also included in the data set. In the case of the bioassay investigation, a detailed soil chemistry analysis was undertaken which also include atomic absorption spectroscopy so as to give an indication of organic compounds present in the soil samples.

3.1.5 Elephant vegetation utilisation

Food selection has been studied in elephants using a wide range of techniques. The direct methods include field observation of feeding, animal gut content analysis and faecal analysis. Indirect field methods include counting of the frequencies of use of individuals of different plant species and estimates of the intensity of use of individuals of different species sampled in transects and quadrats. As one of the objectives of the elephant utilisation study was to determine the intensity of use of different species of plants in different vegetation/habitat types, a sample method was selected. Manpower and time are always constraints and because of this a plot-less sampling technique was chosen as they are usually less time consuming than plot-based ones (Walker 1970). The Point-centred-quarter [PCQ] method (Cottam & Curtis 1956) was selected as an appropriate strategy, but this was modified so that the sample sizes required for accurate estimates of density of each species and the intensity of utilisation could be reduced by reducing the sampling bias towards individuals in the smaller height classes. The PCQ method usually requires samples larger than 250 PCQ points for estimating the densities of species in a particular vegetation type (Heyting 1968). Because both the variance of distance measurements and the variation in relative abundance was decreased by sub-sampling in the five height categories, the sample size was considered adequate to obtain the estimates of density required.

Sample sites were distributed in a stratified random manner throughout the Tembe Elephant Park, in the seven broad vegetation/habitat types (Matthews *et al.* 2001) based on the Park's road network and aerial photographs.

Preference indices of various vegetation types which express the proportion that a plant species makes up in the diet as a fraction of the proportion that it makes up in the habitat, have been used in several studies on feeding in elephants, as well as in studies on food selection in a wide range of other animal species (Manly *et al.* 1993). Three different indices were calculated in this study (a) The Forage Ratio, (b) Manly's Alpha and (c) Ivlev's Electivity Index (Krebs 1989). The purpose of using preference ratios in this study is twofold i.e. to establish which plant species elephant feeding might threaten, and secondly to establish how both the absolute and relative abundance of a particular plant species in different habitats influenced the degree of selection. An index was therefore required which would allow comparisons between vegetation types. To determine the importance of any plant species to elephant and at the same time establishes what impact elephants might have on any particular species, the values for three parameters were

used, namely the volume utilized from each different plant species, the preference for different plant species, and the density of each plant species.

3.1.6 Literature review

The literature study consisted of two parts. The first part focussed exclusively on the study area. This pertained to basic inventories, biological and environmental, and includes geomorphological studies. The second part focused on gaining an understanding of possible processes that are pertinent to the formation and functioning of the different habitats in the study area. Aspects of the ecological and geomorphological processes of the region were analysed. The vegetation dynamics, evolutionary processes and related issues was also examined. All these biological inventory data, geomorphological and other processes were interpreted based on an understanding of the role time played. Some unpublished information was gained from current researchers working in the study area. Various books, reports, papers were consulted on appropriate topics.

CHAPTER 4

VEGETATION OF SILEZA NATURE RESERVE AND NEIGHBOURING AREAS

PUBLISHED MANUSCRIPT

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Vegetation of the Sileza Nature Reserve and neighbouring areas, South Africa, and its importance in conserving the woody grasslands of the Maputaland Centre of Endemism

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Keywords: Braun-Blanquet classification, endemism, grassland, Maputaland, phytosociology, sand forest, suffrutex, synecology, vegetation, water table

ABSTRACT

An analysis of the plant communities of the Sileza Nature Reserve and surrounding areas ($\pm 4\,124$ ha) is 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. A TWINSPLAN classification, refined by Braun-Blanquet procedures, revealed 12 distinct, mainly grassland plant communities. A hierarchical classification, description and ecological interpretation of these communities are presented. The level of the water table, either directly, or indirectly through its role in soil formation, is the deciding factor in defining plant communities on the geologically young sandy substrate. Fire is an essential factor, particularly in maintaining the woody grasslands, a rare vegetation type rich in geoxyllic suffrutices, and unique to the Maputaland Centre. A comparison between the endemic complement in the subtropical coastal grasslands of Maputaland and the high-altitude Afromontane grasslands of the Wolkberg Centre of Endemism shows marked differences in growth form and vegetation type partitioning between the two centres. This can probably be ascribed to the relative youth (Quaternary) of the Maputaland coastal plain and its associated plant communities. Notable for their richness in Maputaland Centre endemic/near-endemic taxa, the conservation of sand forest and woody grasslands should receive high priority. Afforestation with alien trees is the most serious threat to the biodiversity of the Maputaland coastal grasslands, not only because of habitat destruction, but also through its expected negative effect on the hydrology of the region.

INTRODUCTION

Maputaland, previously known as Tongaland, comprises the northernmost sector of the Tongaland-Pondoland Regional Mosaic, one of the main African phytochoria recognised by White (1983). Most of this phytochorion falls within the Maputaland-Pondoland Region, a centre of plant endemism (Van Wyk 1994). Situated at the southern end of the tropics in Africa, emphasis on Maputaland as a region of biotic transition has largely obscured its status as a regional centre of endemism in its own right (Figure 1). Recent formal recognition of the Maputaland Centre [MC] (Van Wyk 1994, 1996) acknowledges the high levels of endemism and remarkable biodiversity of this region.

The vegetation of the MC is diverse, with at least fifteen broad vegetation types described for the KwaZulu-Natal portion of the region (Tinley 1976; Moll 1977, 1980). However, with the exception of Myre's (1964, 1971) pioneering studies on the vegetation of southern Mozambique, very little quantitative work has been done on the grasslands of the centre. The present study on the vegetation of the Sileza Nature Reserve [SNR], an area dominated by grasslands, presents more specific information on the phytosociology of one of the MC's comparatively little-known vegetation types.

With a large, impoverished and rapidly increasing human population in Maputaland, there is an urgent need to improve people's living standards by utilising the region's readily available natural resources on a sustainable

basis. The SNR, an area under the control of the KwaZulu Department of Nature Conservation, is currently being developed as part of a community-driven ecotourism initiative aimed at local community upliftment and development. Also included in the project are sections of the surrounding Endlonlweni Communal Area, which comprises both undeveloped land and a section previously used for commercial plantations by the KwaZulu Department of Forestry. The bordering Nguni Cattle Area, which is being used for the breeding of pedigree Nguni cattle, will eventually be linked to form a single conservation unit that will be jointly managed by the KwaZulu Department of Nature Conservation and local communities.

Knowledge of the vegetation of a region forms the basis for understanding and managing its plant resources and other aspects of the environment. One of the main problems facing the plant conservationist is the lack of sound information on which to base conservation strategies. The present study aims to provide ecological and floristic data for the woody grasslands of Maputaland by identifying, characterising and interpreting the major vegetation units and their variations that occur in the SNR and surrounding areas. Floristically rich (high biodiversity/endemism) and interesting habitats will also be highlighted together with comment on some of the unusual structural features of the Maputaland grasslands.

STUDY AREA

Location

The location of the study area ($27^{\circ} 06' S$, $32^{\circ} 36' E$) is shown in Figure 1. It covers $\pm 4\,124$ ha (2 124 ha of the proclaimed SNR and $\pm 2\,000$ ha of communal land), and is an extensive, low-relief, sandy plain, covered mostly by grassland with relatively small patches of

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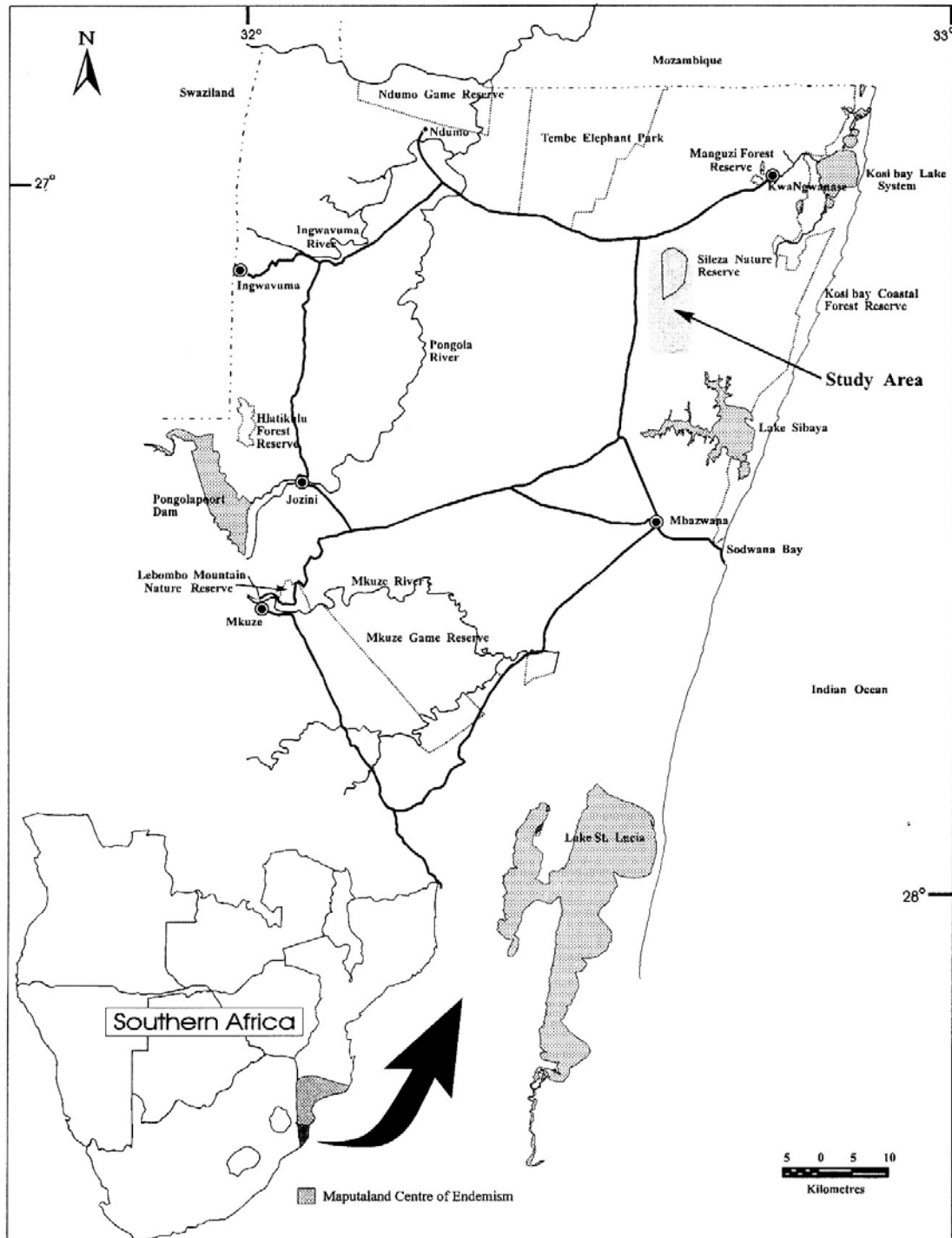


FIGURE 1.—Map showing the Maputaland Centre of Endemism and the location of the study area.

short or tall forest, usually bordered by woodland. Moll & White (1978) have categorised this area as Coastal Grassland, although in many ways this is a mosaic of Moll & White's (1978) Coastal Grassland and Palm Veld. Most of the area is undeveloped and is utilised as grazing land for cattle. An important local industry is the making of palm wine from the sap of *Hyphaene coriacea*

and *Phoenix reclinata* (Cunningham & Wehmeyer 1988; Cunningham 1990a, b).

Geology

Geologically the study area is very similar to the rest of the Maputaland and southern Mozambican coastal

plain. The principal stratigraphic units are unconsolidated Quaternary grey aeolian sands and Quaternary yellowish redistributed sands, underlain by a multi-layered sedimentary sequence of Quaternary, more clayey consolidated sands (Port Durnford Formation) and Tertiary white sandy limestone with basal conglomerate, all resting unconformably on an undulating impermeable Cretaceous siltstone floor which slopes downwards to the east (Hobday 1979; Maud 1980; South African Committee for Stratigraphy 1980).

Topography and climate

The study area is characterised by undulating sand ridges (linear north-south-trending dunes) interspersed with depressions which may form pans or swamps due to the poor drainage and high water table of the region. The highest dune in the study area reaches 98 m asl. The lowest point lies at ± 76 m asl—a difference of only 22 m. Of the few pans to be found in the study area, Gonde-tembe (± 50 ha²) is the largest.

Maputaland has a warm to hot, humid, subtropical climate (Schultze 1982). Average annual humidity is high, even in the drier inland parts of the region. Winters are drier than the summers, although rain is received throughout the year. Rainfall data are given in Table 1, with Phelendaba being the weather station nearest to the study area (± 2.5 km). This station is compared to Sihangwana and Ndumo (both from drier inland areas) as well as the much wetter Kosi Bay on the coast. Owing to the undeveloped nature of much of Maputaland, there is a shortage of certain environmental data, such as temperature.

Hydrology

A shallow water table (ground level to a depth of 7–15 m) exists within the aeolian sands and its level varies according to ground water movements, topography and rainfall. The exact ground water levels (more specifically, the deeper ones), are difficult to determine and fluctuate greatly over time. Values deeper than 2 m are, therefore, approximate. Ground water is almost exclusively replenished by rainwater. This shallow water table feeds all the marshes and pans in the study area. After rains, quick fluctuations in local water table levels can be experienced, with an estimated vertical seepage rate in the order of 0.1 m/day (Kruger 1986). Fluctuations unrelated to the season's rains are ascribed to water movements through the sands, with Kruger (1986) reporting an average transmissivity of 20 m²/day and a co-efficient

of storativity of 1×10^{-3} . The general flow direction is from west to east, away from the watershed which lies more centrally in Maputaland.

Soils

Soils are developed from the relatively homogeneous, grey, siliceous, aeolian sands. Soil types are limited, but soil patterns are intricate, though predictable, as a result of the relationship between topography and water table levels (areas subjected to periods of inundation). Soil nomenclature follows the FAO soil classification system (FAO-UNESCO 1974) and Soil Classification Working Group (1991). Most of the soils show signs of high levels of leaching (dystrophic) as well as being relatively acidic [approximate pH (water) 6.1]. An unusual feature is the presence of above average levels of the micronutrient Boron (G. Mann pers. comm.).

Three main soil types (forms) are present in the study area, namely dystric regosols (SA-Namib), histosols (SA-Champagne) and humic gleysols. Dystric regosols are moderate to well-drained acidic sands found in elevated places such as dune crests and slopes. Histosols are sour organic soils with an organic rich A horizon thicker than 400 mm and are found in swampy areas and pans. Humic gleysols are wet acidic sands with an abnormal accumulation of organic matter and are found in depressions (areas with a high water table). The regosols cover most of Maputaland and are Quaternary sand deposits of generally low fertility (Watkeys *et al.* 1993).

METHODS

Fifty 100 m² sample plots (10 × 10 m) were distributed in a stratified manner throughout the study area. As far as was possible, plots were equally distributed in the different physiographical-physiognomically homogeneous units, distinguished on the basis of physical environment, physiognomy, as well as dominant plant species composition and abundance. Sampling was carried out from January to May 1993. Scientific names of plant taxa follow Arnold & De Wet (1993). The following information was recorded for each plot: 1, total floristic composition and cover-abundance value for each species, according to the Braun-Blanquet cover-abundance scale as described by Mueller-Dombois & Ellenberg (1974); 2, water table depth/level at the time of sampling, using a 2 m soil auger; 3, signs of grazing pressure, mainly by cattle; 4, soil type/form (FAO-UNESCO 1974; Soil Classification Working Group 1991) and basic colour; 5, amount of organic material

TABLE 1.—Mean annual and absolute maximum and minimum rainfall for four weather stations in the region (based on Weather Bureau records)

Station	Period (yrs)	Mean	Annual rainfall (mm)	
			Absolute max. (year)	Absolute min. (year)
Kosi Bay	42	944	1 552 (1985)	506 (1959)
Sihangwana	28	726	2 105 (1975)	245 (1960)
Phelendaba	5	699	958 (1991)	449 (1992)
Ndumo	71	614	1 160 (1938)	276 (1931)

ranked as distinct or indistinct and its depth of occurrence; 6, herbaceous biomass estimates by means of a disc pasture meter (Trollope & Potgieter 1986), following calibration as explained by these authors; 7, topographical position based on terrain types (Land Type Survey Staff 1986), namely (a) crests, (b) scarp, (c) mid-slope, (d) footslope and (e) valley bottom or floodplain; 8, geology, according to 1:250 000 geological survey maps (Geological Survey 1986) and locally at a larger scale through personal observations in the field; 9, land type according to 1:250 000 land type map (Land Type Survey Staff 1986); 10, a 50 point species count using the step-point method (Mentis 1981).

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 & 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 to Detrended Correspondence Analysis (DECORANA) (Hill 1979b).

Maputaland Centre endemics and near-endemics mentioned in the text are based mainly on the work of Van Wyk (1996). The term 'endemic' refers to a taxon limited in its range to a restricted geographical area, or a particular substrate; when a taxon is also marginally present elsewhere (sometimes in the form of distant satellite populations), it is referred to as a 'near-endemic' (Matthews *et al.* 1993).

RESULTS

Classification of vegetation

A classification of the vegetation is presented in a phytosociological table (Table 2). Five major plant communities were identified. These communities closely reflect differences in water table depth (soil moisture) which is directly correlated with the regional topography (Figure 2). Soil type also plays an important role, particularly in the case of hygrophilous communities. The number of species per plot (= species richness) ranges from a minimum of seven to a maximum of 60, with an average of 25. Hierarchical classification of the vegetation reinforces the correlation between habitat and communities (Figures 2 & 3). The distribution among plant communities of MC endemic/near-endemic taxa, is listed in Table 3. A summary of selected community attributes is supplied in Table 5.

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

1. *Artabotrys monteiroae*–*Dialium schlechteri* forest of deep water table areas (relatively dry sands).
2. *Themedito*–*Salacietum* M. Myre (1964); woody grasslands of relatively dry sandy areas.
 - 2.1. *Catunaregam spinosa*–*Acacia burkei* woodland and woodland areas of forest edges.
 - 2.2. *Themedito*–*Salacietum Parinarietosum* M. Myre (1964); woody grasslands of deep water table areas (relatively dry sands), e.g. dune crests and slopes.
 - 2.2.1. *Eugenia capensis*–*Mundulea sericea* woody grassland of relatively deep water table areas.

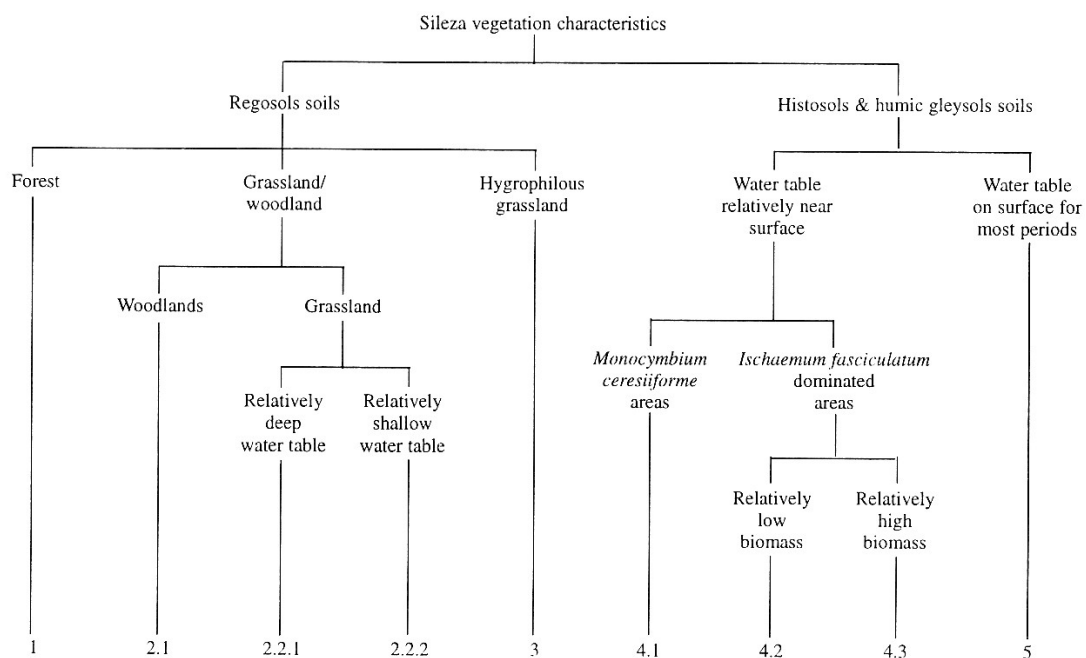


FIGURE 2.—Dendrogram illustrating the habitat relationships of the different communities. Community numbers correspond with descriptions in the text.

TABLE 2.—Phytosociological table of the vegetation of the Sileza Nature Reserve and neighbouring areas (species with an occurrence of 1 have been omitted)

COMMUNITY NUMBER	1		2		3		4		5								
	2.1	2.2	2.2.1	2.2	3	4.1	4.2	4.3	5								
RELEVÉ No.	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0							
SPECIES PER RELEVÉ	4 4 3 4 0	2 1 1 0 0 4 4	1 1 5 4 4 1	3 2 0 1 2 4 1	2 3 3 2 1 2	4 1 3 2 3	0 0 2	0 1 2 0 3 0	3 1 9 7 6	1 6 3 8 2 6	5 2 1 7 3 5 9	3 8 0 0 4 7	7 6 1 6 2 8 0	9 1 2 1 4 0	7 5 4 4 5	9 2 8	4 9 3 8 0 5
SPECIES	3 4 3 4 3	6 4 4 4 4	4 4 3 1 3 4 2	3 4 2 3 2 3	2 2 2 1 2 2 1	1 1 1 1 1 1	1 1 1 1 1 1	1 1 1 1 1 1	1 1 1 1 1 1	1 1 1 1 1 1	1 1 1 1 1 1	1 1 1 1 1 1	1 1 1 1 1 1	4 2 6 4 0 5	7 5 5 3 7	1 7 0	2 3 2 6 1 2
SPECIES GROUP A	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Ariabotrys monticola</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Commiphora neglecta</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Dialium scheuchteri</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Acacia kraussiana</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Tricholysis lanceolata</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Achyranthes cf. aspera</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Diospyros natalensis</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Mimusops caffra</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Strychnos henningsii</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Albericia delagayense</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Albizia anthelmintica</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Asperagus falcatus</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Grewia occidentalis</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Cyperus albostriatus</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Erythroxylum emarginatum</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Pteleopsis myrtilloides</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Dombolola oblongifolia</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Sansevieria coronata</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Sarcostemma viminale</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Ochna barbosae</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Pleuroxylon obliquum</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Dovyalis caffra</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Pyrenacantha scandens</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Maytenus undata</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Tarenna junodi</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Eragrostis moggi</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Croton pseudopuchelii</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Ficus natalensis</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Isoglossa woodii</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Canissa tetrameria</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
SPECIES GROUP B	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Calumetragm spinosa</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Panicum maximum</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Conchocarpus junodi</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Sapum integerrimum</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Acacia burkei</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Vangueria infausta</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Indigofera vicicoides</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Antidesma venosum</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Lineum cf. viscosum</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Phyllanthus sp.</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Asystasia gangetica</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Canthium inerme</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+

TABLE 2.—Phytosociological table of the vegetation of the Sileza Nature Reserve and neighbouring areas (species with an occurrence of 1 have been omitted) (cont.)

COMMUNITY NUMBER	1		2		3		4		5	
	21	22	22.1	22.2	4.1	4.2	4.3			
RELEVÉ No.	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0
3 4 3 2 3	4 4 3 4 0	2 1 1 0 0 4 4	1 1 5 4 4 1	3 2 0 1 2 4 1	2 3 3 2 1 2	4 1 3 2 3	0 0 2	0 1 2 0 3 0		
3 1 9 7 6	6 3 8 2 6	5 2 1 7 3 5 9	3 8 0 0 4 7	7 6 1 6 2 8 0	9 1 2 1 4 0	7 5 4 4 5	9 2 8	1 4 9 3 8 0 5		
3 4 3 4 3	6 4 4 4 4	4 4 3 1 3 4 2	3 4 2 3 2 3	2 2 2 1 2 2 1	1 1 1 1 1 1	1 1 1 1 1	1 0 1	1 1 1 1 1 1		
3 7 8 8 4	0 9 8 3 5	6 6 3 6 8 6 8	9 1 4 0 2 4	1 0 0 4 0 2 4	4 2 6 4 0 5	7 5 5 3 7	1 7 0	2 3 2 6 1 2		
SPECIES GROUP E (cont.)										
<i>Rhynchosia combusa</i>		+	+	+						
<i>Cissampelos hirta</i>		+	+	+						
<i>Ochna natalitia</i>		+	+	+						
<i>Sporobolus fimbriatus</i>		A	+	+						
<i>Xylotheca kraussiana</i>		+	+	+						
SPECIES GROUP F										
<i>Phaleria capensis</i> ssp. <i>incobata</i>		T	1	A	A	+	A	T	A	
<i>Dactyloctenium aegyptium</i>		+	+	+	+	+	+	+	+	
<i>Oxygonum robustum</i>		+	+	+	+	+	+	+	+	
<i>Valeriana oligosperma</i>		+	+	+	+	+	+	+	+	
<i>Eugenia arbanensis</i>		+	+	+	+	+	+	+	+	
<i>Ureyrum agropyroides</i>		+	+	+	+	+	+	+	+	
<i>Trichoneura grandiglumis</i>		+	+	+	+	+	+	+	+	
<i>Ethanasia muticus</i>		+	+	+	+	+	+	+	+	
<i>Dichrostachys cinerea</i>		+	+	+	+	+	+	+	+	
<i>Ancylobotrys petersiana</i>		+	+	+	+	+	+	+	+	
<i>Salaica kraussi</i>		1	A	1	1	3	+	+	+	
<i>Sporobolus mauritanicus</i>		+	+	+	+	+	+	+	+	
<i>Eragrostis sclerantha</i>		+	+	+	+	+	+	+	+	
<i>Diospyros lycoides</i>		+	+	+	+	+	+	+	+	
<i>Triliceras mossambicensis</i>		+	+	+	+	+	+	+	+	
SPECIES GROUP G										
<i>Themeda lanata</i>		+	A	B	A	B	A	B	A	1
<i>Aristida stipitata</i>		+	+	+	+	+	+	+	+	
<i>Abidaandia hygrophila</i>		+	+	+	+	+	+	+	+	
<i>Hypochaeris conacea</i>		+	+	+	+	+	+	+	+	
<i>Pennisetum patens</i>		+	+	+	+	+	+	+	+	
<i>Helichrysum kraussii</i>		+	+	+	+	+	+	+	+	
<i>Agathisanthemum bojeri</i>		1	1	+	+	+	+	+	+	
<i>Terminalia senecia</i>		1	1	A	1	1	1	+	+	
<i>Phoenix nictitans</i>		+	A	+	+	+	+	+	+	
<i>Diospyros gajani</i>		+	+	+	+	+	+	+	+	
<i>Marsdenia albomarginata</i>		A	+	+	+	+	+	+	+	
<i>Syzygium cordatum</i>		+	+	+	+	+	+	+	+	
<i>Commelina africana</i>		+	+	+	+	+	+	+	+	
SPECIES GROUP H										
<i>Chamaecrista plumosa</i>		+	+	+	+	+	+	+	+	R
<i>Cyperus tenax</i>		+	+	+	+	+	+	+	+	+
<i>Bulbosylis contorta</i>		+	1	1	+	+	+	+	+	+
SPECIES GROUP I										
<i>Helichrysum septentrionale</i>		+	+	+	+	+	+	+	+	+
<i>Wahlerbergia abyssinica</i>		+	+	+	+	+	+	+	+	+
<i>Vahlia capensis</i>		+	+	+	+	+	+	+	+	R

TABLE 2.—Phytosociological table of the vegetation of the Sileza Nature Reserve and neighbouring areas (species with an occurrence of 1 have been omitted) (cont.)

COMMUNITY NUMBER	1					2					3					4					5											
	2.1	2.2	2.2.1	2.2.2	2.2.3	2.1	2.2	2.2.1	2.2.2	2.2.3	2.1	2.2	2.2.1	2.2.2	2.2.3	2.1	2.2	2.2.1	2.2.2	2.2.3	2.1	2.2	2.2.1	2.2.2	2.2.3	2.1	2.2	2.2.1	2.2.2	2.2.3		
RELEVÉ No.	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0		
SPECIES PER	3 4 3 4	3 1 9 7	6 3 8 2	6 1 5 2	7 3 5 9	3 8 0 4	7 1 1 5	4 4 1 1	5 4 4 1	1 1 5 4	4 4 1 1	3 2 0 1	2 4 1 1	3 2 0 1	2 4 1 1	3 2 0 1	2 4 1 1	3 2 0 1	2 4 1 1	3 2 0 1	2 4 1 1	3 2 0 1	2 4 1 1	3 2 0 1	2 4 1 1	3 2 0 1	2 4 1 1	3 2 0 1	2 4 1 1	3 2 0 1		
RELEVÉ	3 7 8 4	0 9 8 3	5 6 3 6	8 6 8 9	1 4 0 2	4 1 4 0	2 4 1 1	4 0 2 4	1 0 0 4	0 2 4 1	0 0 4 0	2 4 1 1	4 0 2 4	1 0 0 4	0 2 4 1	0 0 4 0	2 4 1 1	4 0 2 4	1 0 0 4	0 2 4 1	0 0 4 0	2 4 1 1	4 0 2 4	1 0 0 4	0 2 4 1	0 0 4 0	2 4 1 1	4 0 2 4	1 0 0 4			
SPECIES GROUP I (cont.)																																
<i>Hypericum laetandii</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Striga junodii</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Helichrysum</i> sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
SPECIES GROUP J																																
<i>Eragrostis lapuja</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Sporobolus subtilis</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
SPECIES GROUP K																																
<i>Monocymbium ceresilloforme</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Panicum genuiflexum</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Pycnus aribulus</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
SPECIES GROUP L																																
<i>Sorghastrum stipoides</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Fuirena pubescens</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Lobelia erinus</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Polygala capillaris</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Andropogon eucomus</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
SPECIES GROUP M																																
<i>Ischaemum fasciculatum</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Eragrostis inamoena</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
SPECIES GROUP N																																
<i>Cyperus sphaerospermus</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Desmodium dregeanum</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Centella asiatica</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
SPECIES GROUP O																																
<i>Leersia hexandra</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Hemerithia altissima</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Pycnus polystachyos</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Acroceras macrum</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Fuirena obcordata</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Oldenlandia cephalotes</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Hydrocotyle bonariensis</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Eleocharis dulcis</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Cyperus</i> sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Cyperus fastigiatus</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Nymphaea capensis</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
SPECIES GROUP P																																
<i>Cyperus obtusiflorus</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Cyperus natalensis</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		

- 2.2.2. *Urelytrum agropyroides*–*Trichoneura grandiglumis* woody grassland of relatively shallower water table areas.
3. *Eragrostis lappula*–*Helichryopsis septentrionale* hygrophilous grassland on humic gleysols (inter-dune depressions).
4. *Ischaemum fasciculatum*–*Eragrostis inamoena* hygrophilous grasslands on Champagne soils.
- 4.1. *Monocymbium cerasiiforme*–*Eragrostis lappula* grassland of areas not as regularly inundated by water as 4.2.
- 4.2. *Ischaemum fasciculatum*–*Cyperus sphaerospermus* grassland of depressions scattered throughout the grassland areas or directly bordering on marshes/pans.
- 4.3. *Ischaemum fasciculatum* grassland representing low species diversity but relatively high biomass, dominated by *Ischaemum fasciculatum*.
5. *Leersia hexandra*–*Hemarthria altissima* grassland of marsh/pan areas (water-table on surface during most years).

Description of plant communities

1. *Artabotrys monteiroae*–*Dialium schlechteri* forest of deep water table areas (relatively dry sands)

Found on dune crests and slopes, this community is associated with grey dystric regosols in places with the deepest water table. In four of the five investigated plots the water table could not be reached with the soil auger (>2 m deep). Biomass measurements were not undertaken in this community as the field layer in most instances was mainly short shrubs with very few grasses and forbs.

Characterised by species group A (Table 2), diagnostic species include the trees *Dialium schlechteri* and *Commiphora neglecta*, understory shrub *Tricalysia lanceolata* and the lianas *Artabotrys monteiroae* and *Acacia kraussiana*. Prominent species (>50% constancy) include the trees *Mimusops caffra*, *Albizia anthelmintica*, *Strychnos henningsii* and *Erythroxylum emarginatum*, shrubs *Diospyros natalensis*, *Grewia occidentalis*, *Pteleopsis myrtifolia* and *Deinbollia oblongifolia*, understory perennial *Achyranthes* cf. *aspera*, rhizomatous succulent *Sansevieria concinna*, sedge *Cyperus albostriatus* and lianas *Albertisia delagoense*, *Asparagus falcatus* and *Sarcostemma viminalis*. *Synaptolepis kirki*, with a high constancy in this community, is a character taxon of species group C. Species group C links the present community with the woodland community (2.1). On average 40 species per plot were recorded. No less than 12 MC endemic/near-endemic species were found in these forests, thus making this one of the richest communities for such taxa (Table 3).

TABLE 3.—Maputaland Centre endemic or near-endemic plant species (according to Van Wyk 1996), and the plant communities with which they are associated (* = diagnostic species for community)

Endemic/near-endemic taxon	Family	Plant community number									
		1	2.1	2.2.1	2.2.2	3	4.1	4.2	4.3	5	
<i>Acacia kraussiana</i>	Mimosaceae	×*	×								
<i>Acridocarpus natalitius</i> var. <i>linearifolius</i>	Malpighiaceae			×							
<i>Albertisia delagoensis</i>	Menispermaceae	×*		×	×						
<i>Brachystelma tenue</i>	Asclepiadaceae			×							
<i>Cissampelos hirta</i>	Menispermaceae		×	×							
<i>Corchorus junodii</i>	Tiliaceae	×	×*	×							
<i>Crotalaria monteiroi</i> var. <i>monteiroi</i>	Fabaceae	×	×								
<i>Dialium schlechteri</i>	Caesalpinaceae	×*	×								
<i>Dovyalis longispina</i>	Flacourtiaceae	×									
<i>Encephalartos ferox</i>	Zamiaceae	×									
<i>Eragrostis moggii</i>	Poaceae	×									
<i>Erythroxylum delagoense</i>	Erythroxylaceae	×									
<i>Eugenia capensis</i> (' <i>mossambicensis</i> ' form)	Myrtaceae		×	×*	×						
<i>Grewia microthyrsa</i>	Tiliaceae	×	×								
<i>Gymnosporia markwardii</i> ms.	Celastraceae		×	×	×						
<i>Helichryopsis septentrionale</i>	Asteraceae				×						
<i>Helichrysum adenocarpum</i> subsp. <i>ammophilum</i>	Asteraceae					×					
<i>Helichrysum tongense</i>	Asteraceae					×					
<i>Indigofera inhambanensis</i>	Fabaceae				×						
<i>Ochna barbosae</i>	Ochnaceae	×									
<i>Ochna natalitia</i> (suffruticose form)	Ochnaceae			×	×						
<i>Oxgonum robustum</i>	Polygonaceae		×	×	×						
<i>Ozoroa engleri</i>	Anacardiaceae		×	×	×						
<i>Parinari capensis</i> subsp. <i>incohata</i>	Chrysobalanaceae		×	×	×	×					
<i>Podocarpus falcatus</i> (sand/swamp forest form)	Podocarpaceae	×									
<i>Restio zuluensis</i>	Restionaceae						×		×	×	
<i>Salacia kraussii</i>	Celastraceae		×	×	×						
<i>Sansevieria concinna</i>	Dracaenaceae	×									
<i>Striga junodii</i>	Scrophulariaceae					×	×				
<i>Syzygium cordatum</i> (suffruticose form)	Myrtaceae			×	×						
<i>Tarenna junodii</i>	Rubiaceae	×									
<i>Tricliceras mossambicensis</i>	Turneraceae		×	×	×						
<i>Vahlia capensis</i> subsp. <i>vulgaris</i> var. <i>longifolia</i>	Vahliaceae				×	×					
<i>Vernonia centuarioides</i>	Asteraceae				×						
TOTAL NUMBER OF TAXA	34	14	13	13	14	6	2	0	1	1	

This community is structurally a forest, the canopy varying from as low as 5 m up to about 20 m. The species composition is unique and other authors have referred to this community as Sand Forest (e.g. Moll 1977, 1980; Moll & White 1978; Ward 1981), typical elements of which include *Dialium schlechteri*, *Pteleopsis myrtifolia*, *Ptaeroxylon obliquum*, *Croton pseudopulchellus* and *Ochna barbosae*. Pendulous lichens (*Usnea* spp.) are particularly abundant in the protruding crowns of many of the trees. Sand forests in the study area lie at the eastern limits of their distribution and are floristically notably impoverished compared with their inland counterparts (unpublished data). Because of their proximity to the coast, they also contain species more characteristic of coastal dune forest, such as *Mimusops caffra*, *Acacia kraussiana* and the understory herb *Isoglossa woodii*.

2. *Themeda*-*Salacietum* M. Myre (1964); woody grasslands of relatively dry sandy areas

An association restricted to grey dystric regosols on dune crests, slopes and relative high-lying level plains. Average water table depth was ± 1.8 m, whereas in many of the other sampling sites it could not be reached by the soil auger (>2 m). Average biomass was 2091.1 kg.ha⁻¹.

Characterised by species group G (Table 2), diagnostic species include the grasses *Themeda triandra* and *Aristida stipitata*, sedge *Abildgaardia hygrophila* and the palm *Hyphaene coriacea*. Prominent species ($>50\%$ constancy) include the palm *Phoenix reclinata*, geoxylic suffrutex *Diospyros galpinii*, grass *Perotis patens*, woody forb *Helichrysum kraussii*, rhizomatous forb *Agathisanthemum bojeri* and *Terminalia sericea*, which varies from a dwarf shrub to a large tree. On average 39 species per plot were recorded.

This association is subdivided into two subassociations on the basis of structure and floristic composition, thus indicating a strong correlation between the tall woodlands and the woody (suffrutex-rich) grasslands.

2.1. *Catunaregam spinosa*-*Acacia burkei* woodland and woodland areas of forest edges

A subassociation of grey dystric regosols on crests and slopes of dunes. Average water table depth was ± 1.8 m, with two samples deeper than the soil auger length (>2 m). Average biomass was 2291.5 kg.ha⁻¹, a value slightly higher than those of related grassland communities and attributable to a slightly higher woody component.

Characterised by species group B (Table 2), prominent diagnostic species include the shrubs *Catunaregam spinosa* and *Vangueria infausta*, shrubs/trees *Acacia burkei* and *Sapium integerrimum*, grass *Panicum maximum* and the forb *Corchorus junodii*. *Terminalia sericea* is consistent as well as achieving its highest abundance. Other prominent species ($>50\%$ constancy) are the shrubs/trees *Antidesma venosum*, *Canthium inerme*, *Strychnos spinosa*, *Ozoroa obovata* and *Garcinia living-*

stonei, forbs *Indigofera vicioides*, *Limeum* cf. *viscosum*, *Phyllanthus* sp. and *Asystasia gangetica* and the grass *Andropogon gayanus*. On average 49 species per plot were recorded, the highest average number of species among all the communities, with 11 MC endemic or near-endemic species (Table 3).

2.2. *Themeda*-*Salacietum Parinarietosum* M. Myre (1964); woody grasslands of deep water table areas (relatively dry sands), e.g. dune crests and slopes

A subassociation of grey dystric regosols on dune crests, slopes and low-relief plains. Average water table depth was ± 1.9 m, with the depth in many samples extending further than the soil auger length (>2 m). Average biomass was 1990.9 kg.ha⁻¹.

Characterised by species group F (Table 2), diagnostic species include the geoxylic rhizomatous suffrutex *Parinari capensis* subsp. *incohata*, which in places can attain a high canopy cover, the grass *Diheteropogon amplexens* and forb *Oxygonum robustum*. Other prominent species ($>50\%$ constancy) include the forb *Vernonia oligocephala*, rhizomatous suffrutices *Eugenia albanensis*, *Ancylobotrys petersiana* and *Salacia kraussii*, a dwarf shrubby form of *Dichrostachys cinerea*, as well as the grasses *Urelytrum agropyroides*, *Trichoneura grandiglumis*, *Elionurus muticus*, *Sporobolus mauritanus* and *Eragrostis sclerantha*. *Themeda triandra* attains its highest cover values. On average 34 species per plot were recorded.

This subassociation is subdivided into two variants determined by differences in water table depth.

2.2.1. *Eugenia capensis*-*Mundulea sericea* woody grassland of relatively deep water table areas

A variant associated with grey dystric regosols on dune crests, slopes and sandy plains. Average water table depth nearly always exceeded 2 m. Only one of the water table samples did not extend deeper than the soil auger length (>2 m). Average biomass for this subcommunity was 1995.9 kg.ha⁻¹.

Characterised by species group D (Table 2), the geoxylic rhizomatous suffrutex *Eugenia capensis* (also referred to as *E. mossambicensis*) is one of the diagnostic species. Other prominent species ($>50\%$ constancy) are a dwarf shrub form of *Mundulea sericea*, the forbs *Stylosanthes fruticosa* and *Indigofera williamsonii*, prostrate creeper *Dicerocaryum eriocarpum* and the grass *Setaria sphacelata*. *Themeda triandra* attains its highest cover values in this variant. Other species showing a strong affinity to this variant (usually $>50\%$ constancy) are the forb *Vernonia oligocephala*, shrub *Strychnos madagascariensis* and grasses *Pogonarthria squarrosa*, *Eustachys paspaloides* and *Digitaria natalensis*. The last four species belong to group E, which represents the species shared between this and the woodland community (2.1). This again underscores the relationship between the woodlands and the woody grasslands. On average 36 species per plot were recorded, with 12 MC endemic or near-endemic species (Table 3).

2.2.2. *Urelytrum agropyroides*–*Trichoneura grandiglumis* woody grassland of relative shallower water table areas

A variant associated with grey dystric regosols on dune crests, slopes and sandy plains. Average water table depth was ± 1.8 m, with only one sample extending deeper than the soil auger length (>2 m). Average biomass for this subcommunity was $1985.8 \text{ kg}\cdot\text{ha}^{-1}$.

Although lacking a characteristic species group, this subcommunity is characterised by the absence of species group D (Table 2). Consistent species include the grasses *Urelytrum agropyroides* and *Trichoneura grandiglumis*. Other species which show a strong affinity to this community are the grasses *Themeda triandra* and *Aristida stipitata*, sedge *Abildgaardia hygrophila*, geoxylic rhizomatous suffrutex *Eugenia albanensis*, palm *Hyphaene coriacea* and the forb *Chamaecrista plumosa*. This forb comes from species group H, a group representing the species shared between the woody grassland communities (2.2) and the hygrophilous grasslands (4). This connection signifies a floristic relationship between the 'wetter' woody grasslands on dystric regosols (this variant) and the truly hygrophilous grasslands on Champagne soils. On average 32 species per plot were recorded, with 13 MC endemic or near-endemic species (Table 3), the highest number for all the investigated plant communities.

3. *Eragrostis lappula*–*Helichryopsis septentrionale* hygrophilous grassland on humic gleysols (inter-dune depressions)

This plant community is found in interdune depressions and other low-lying areas, and is associated with grey to dark grey sands (humic gleysols). These soils show signs of slightly higher organic matter accumulation than those of the preceding communities. Average water table depth was ± 1.2 m. Average biomass was $1758.3 \text{ kg}\cdot\text{ha}^{-1}$, the lowest value of all the plant communities and quite obvious to the naked eye in the field.

Characterised by species group I (Table 2), diagnostic species include the forbs *Helichryopsis septentrionale*, *Wahlenbergia abyssinica*, *Vahlia capensis*, *Hypericum lalandii* and the hemi-parasite *Striga junodii*. Species showing a strong affinity to this community are the sedges *Cyperus tenax* and *Cyperus obtusiflorus* and the forb *Desmodium dregeanum*. The grass *Eragrostis lappula* attains high cover values. On average 19 species per plot were recorded, with six MC endemic or near-endemic species (Table 3).

This community shows relationships with drier grasslands (species group H) as well as with wetter (hygrophilous) communities (species group J) on histosols.

4. *Ischaemum fasciculatum*–*Eragrostis inamoena* hygrophilous grasslands on Champagne soils

Found on wet, seasonally waterlogged, bottom lands and associated with dark grey to black histosols, with high levels of organic matter composition compared to the substrates of the preceding communities. Average

water table depth was ± 0.65 m. Average biomass was $3454.7 \text{ kg}\cdot\text{ha}^{-1}$.

Characterised by species group M (Table 2), diagnostic species include the grasses *Ischaemum fasciculatum* and *Eragrostis inamoena*. The former species attains some of the highest cover values in places and is very prominent. On average, 13 species per plot were recorded.

This community shows relationships with the hygrophilous grassland community on Namib soils (species group N). It is subdivided into three subcommunities on the basis of the prominence of *Ischaemum fasciculatum*, a species reflecting periods of inundation.

4.1. *Monocymbium cerasiiforme*–*Eragrostis lappula* grassland of areas not being as regularly inundated by water as the *Ischaemum fasciculatum*–*Cyperus sphaerospermus* grassland

A plant subcommunity of bottom lands, associated with dark grey to black soils (mixture of histosol and humic gleysols very rich in organic matter) and usually bordering on communities 4.2 and 4.3 (Figure 3). Average water table depth was ± 0.7 m, with three samples lying at a depth of 1 m. Average biomass was $2419.5 \text{ kg}\cdot\text{ha}^{-1}$.

Characterised by species group K (Table 2), the grass *Monocymbium cerasiiforme* is the most diagnostic species. Another diagnostic grass ($>50\%$ constancy) is the small-growing *Panicum genuflexum*. Other prominent species are the sedges *Cyperus obtusiflorus* and *C. sphaerospermus* and the grasses *Sporobolus subtilis* and *Eragrostis lappula*. The last two species are from group J and indicate a strong relationship between this subcommunity and the hygrophilous grasslands on humic gleysols (3). On average 14 species per plot were recorded, with two MC endemic or near-endemic species (Table 3).

4.2. *Ischaemum fasciculatum*–*Cyperus sphaerospermus* grassland of depressions scattered throughout the grassland areas or directly bordering on marshes/pans

A plant subcommunity of bottom lands, associated with dark grey to black histosols rich in organic matter and usually bordering on pans and marshes. Average water table depth was ± 0.5 m, with only one sample reaching a depth of 1 m. Average biomass was $2986.8 \text{ kg}\cdot\text{ha}^{-1}$.

Characterised by species group L (Table 2), the most prominent diagnostic species is the tall grass *Sorghastrum stipoides*. Other diagnostic species ($>50\%$ constancy) include the sedge *Fuirena pubescens*, forbs *Lobelia flaccida* and *Polygala capillaris* and the grass *Andropogon eucomus* and, although of lesser constancy, the grasses *Ischaemum fasciculatum* and *Eragrostis inamoena*. Also characteristic are the sedge *Cyperus sphaerospermus* and the prostrate forbs *Centella asiatica* and *Desmodium dregeanum*. The latter three species are from group N, thus showing a relationship between this subcommunity and other hygrophilous grasslands (3 & 4.1). On average 15 species per plot were recorded, with no MC endemic/near-endemic species (Table 3).

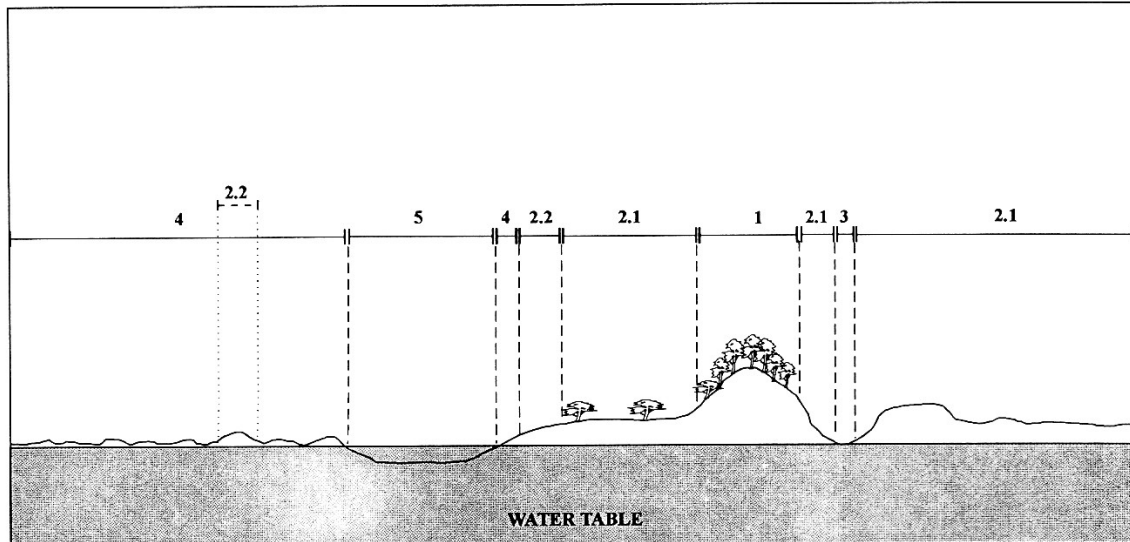


FIGURE 3.—Schematic representation of the distribution of the different plant communities in the Sileza Nature Reserve and surrounding community areas. Dotted lines indicate overlapping distributions. 1. *Arabotrys monteiroae*–*Dialium schlechteri* forest in deep water table areas (relatively dry sands). 2.1. *Catunaregam spinosa*–*Acacia burkei* woodland and woodland areas of forest edges. 2.2. *Themeda*–*Salacietum Parinarietosum*; woody grasslands in deep water table areas (relatively dry sands), e.g. dune crests and slopes. 3. *Eragrostis lappula*–*Helichrysois septentrionale* hygrophilous grasslands on humic gleysols (inter-dune depressions). 4. *Ischaemum fasciculatum*–*Eragrostis inamoena* hygrophilous grasslands of Champagne soils. 5. *Leersia hexandra*–*Hemarthria altissima* grassland of marsh/pan areas (water table on surface during most years).

4.3. *Ischaemum fasciculatum* grassland representing low species diversity but relatively high biomass, dominated by *Ischaemum fasciculatum*

Found in bottom lands on dark grey to black organic-rich soils (histosols). Average water table depth was ± 0.7 m (with one sample reaching 1 m), and is thus slightly deeper than that of the preceding two subcommunities. Average biomass was $4957.7 \text{ kg}\cdot\text{ha}^{-1}$, the highest value of all plant communities in the study area, which is remarkable considering that none of the grasses making up the major proportion of the biomass are particularly tall plants. The dominant grass, *Ischaemum fasciculatum*, only reaches a height of ± 400 mm.

Characterised by the absence of species group L (Table 2), the most prominent taxon is the grass *Ischaemum fasciculatum*, a species which contributes significantly to the high average biomass. There are few other prominent species, the most consistent perhaps being *Cyperus natalensis*, a sedge from group P, which is common to all communities. Other species showing $>50\%$ constancy include the forb *Desmodium dregeanum* and the grasses *Hemarthria altissima* and *Acroceras macrum*. The last two species are diagnostic for community 5, the very wet one. On average nine species per plot were recorded, the lowest number among the studied plant communities, with only one MC endemic/near-endemic (Table 3).

5. *Leersia hexandra*–*Hemarthria altissima* grassland of marsh/pan areas (water table on surface during most years)

A plant community of bottom lands and associated with dark grey to black histosols very rich in organic matter. Average water table depth was ± 0.1 m with only

two of the samples not having the water table present on the surface. Average biomass was $4584.4 \text{ kg}\cdot\text{ha}^{-1}$, making this the community with the second highest biomass. Not all plots were sampled for biomass because of the presence of surface water.

Characterised by species group O (Table 2), diagnostic species include the grasses *Leersia hexandra*, *Hemarthria altissima* and *Acroceras macrum*, the latter attaining constantly relative high cover values. Other diagnostic members ($>50\%$ constancy) are the sedges *Pycneus polystachyos*, *Fuirena obcordata*, *Eleocharis dulcis* and *Cyperus natalensis*, the latter being common to all communities. Diagnostic forbs include *Oldenlandia cephalotes* and *Hydrocotyle bonariensis*. Many of these species are also sporadically present in other hygrophilous grasslands, notably in localised patches of wetter conditions. On average 13 species per plot were recorded, with only one MC endemic or near-endemic species (Table 3).

Ordination

Distribution of the sample plots (relevés) along the first and second axes of ordination is given in the form of a scatter diagram (Figure 4). A third axis of ordination contributes little to the interpretation of the communities and will therefore not be considered further.

Figure 4 illustrates a water table depth (moisture) gradient along the horizontal axis, with the wetter habitats to the right and the drier habitats to the left. There is only a slight discontinuity in the distribution of the sample plots representing the deep (community 1) and the shallow water table areas (community 2). However, all plant communities are more or less restricted to specific areas of the diagram.

A distinct discontinuity exists between the communities of the dystric regosols (Namib soil) and the histosols (Champagne soil), with the intermediate communities being placed centrally in the diagram. Subcommunities of the areas with a deep (1) and shallow (2) water table show no separation, thus supporting their treatment as closely related subcommunities. This pattern of one community merging with another along a water table depth gradient can be clearly seen in the field. There can be no doubt that the level of the water table, either directly, or indirectly through its role in soil formation, plays the deciding role in defining plant communities on the coastal plain of Maputaland.

habitat gradients. Dynamics of water in the landscape, in this case the water table, clearly control the structure of the community at the first physiognomic level. This is a common phenomenon in savanna areas (Solbrig 1993).

All the communities are easily distinguishable in the field on the basis of growth form, general species composition and character species, despite the gradual environmental gradients. Variation in water table level, the overriding environmental factor, is much less easily distinguished and is best reflected by changes in plant community and the presence of different soil types. Water table levels fluctuate seasonally in accordance with rainfall as well as unseasonally because of non-rainfall related ground water movements (Kruger 1986). It is possible that water table levels rarely falls below 15 m.

DISCUSSION AND ADDITIONAL NOTES

Plant communities

Twelve ecologically interpretable plant communities have been distinguished and described. This information can be used in reserve and area management, land-use planning, extrapolation to other parts of Maputaland as well as in further ecological and floristic studies. The results of the ordination not only confirm the classification, but also give an indication of floristic and associated

With the exception of the excellent broad-scale classification of the coastal grasslands of southern Mozambique (Myre 1964, 1971), the present study is the first attempt at a more detailed, larger scale phytosociological classification of some of the Maputaland coastal plain grasslands. A correlation between the plant communities of the present study and the various syntaxa described by Myre (1964, 1971) has been attempted. Here we recognise his formally described *Themedo-Salacietum* and

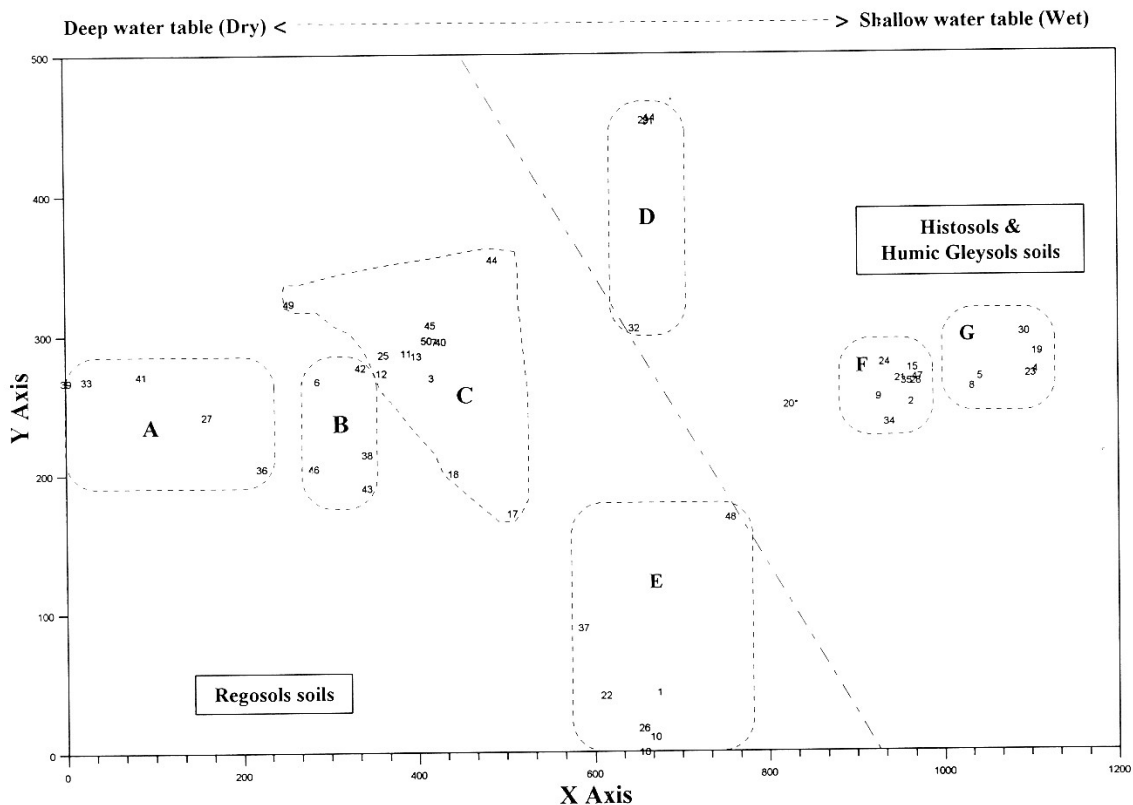


FIGURE 4.—Ordination of the vegetation of the Sileza Nature Reserve and surrounding community areas. A, *Artabotrys monteirouae-Dialium schlechteri* forest of deep water table areas (relatively dry sands). B, *Catunaregam spinosa-Acacia burkei* woodland and woodland areas on forest edges. C, *Themedo-Salacietum Parinarietosum*; woody grasslands of deep water table areas (relatively dry sands), e.g. dune crests and slopes. D, *Monocymbium ceresiiforme-Eragrostis lappula* grassland of areas not as regularly inundated by water as F, E, *Eragrostis lappula-Helichrysopsis septentrionale* hygrophilous grasslands on humic gleysols (inter-dune depressions. F, *Ischaemum fasciculatum-Cyperus sphaerospermus* grassland of depressions scattered throughout the grassland areas or directly bordering on marshes/pans or/as well as the *Ischaemum fasciculatum* grassland subcommunity representing low species diversity but relatively high biomass. G, *Leersia hexandra-Hemarthria altissima* grassland of marsh/pan areas (water table on surface during most years).

TABLE 4.—Geoxylic suffrutices occurring in the study area, together with the plant communities with which they are associated

Taxon	Plant community number								
	1	2.1	2.2.1	2.2.2	3	4.1	4.2	4.3	5
<i>Parinari capensis</i> subsp. <i>incohata</i>		×	×××	×××	×				
<i>Ancylbotrys petersiana</i>		××	×××	××					
<i>Eugenia albanensis</i>		××	××	×××					
<i>Eugenia capensis</i> (dwarf form)		×	×××	×					
<i>Diospyros galpinii</i>		××	××	××					
<i>Salacia kraussii</i>		×	××	××					
<i>Gymnosporia markwardii</i> ms.		×	××	××					
<i>Diospyros lycioides</i>			××	××					
<i>Terminalia sericea</i>			××	×					
<i>Syzygium cordatum</i>			×	××					
<i>Ochna natalitia</i>			××						

× = rare; ×× = average; ××× = abundant; blank = absent.

Themedo–Salacietum Parinarietosum, two syntaxa which are easily recognisable throughout the MC. We have, however, considered it premature to formally describe the other syntaxa. More phytosociological studies in other areas of the Maputland Coastal plain are needed to correlate results.

Geoxylic suffrutices

An outstanding feature of some of the Maputland grasslands (e.g. the *Themedeto–Salacietum* woody grasslands of the present study) is the abundance of geoxylic (often rhizomatous) suffrutices (e.g. Henkel *et al.* 1936; Myre 1964, 1971; Moll & White 1978). These dwarf woody plants can be compared with extremely stunted trees, a fact which led White (1976) to refer to them as the ‘underground forests of Africa’. Furthermore, in this type of grassland the phytomass of the suffrutices greatly exceeds that of the grasses (White 1976; unpublished data).

The geoxylic suffruticose habit is characterised by annual or short-lived woody shoots sprouting from massive or extensive woody, perennial, underground axes. This rather uncommon growth form appears to be best developed in Africa, with the greatest concentration in the Zambezi Region (White 1976, 1983). Despite White’s (1976) statement that relatively few suffruticose species are confined to the Tongaland-Pondoland Regional Mosaic, plants with this growth form are abundant in the study area where they are almost exclusively confined to the *Themedeto–Salacietum* woody grasslands (Table 4).

White (1976) suggests that in Africa the geoxylic suffrutex probably originated as a response to unfavourable edaphic conditions, notably in strongly oligotrophic, seasonally waterlogged sandy soils in regions of extremely low relief. He argues that this habit is not primarily an adaptation to fire or frost, as has been supposed by Burt Davy (1922), whilst acknowledging that for some species, at least occasionally, fire is necessary for vigorous growth.

The present study confirms the observation that geoxylic suffrutices are prevalent in areas of sandy soil and relatively low relief (Table 5). However, doubt is cast on the validity of White’s perhaps too simplistic claim that seasonally waterlogged soil is the primary determinant for the presence of this growth form. In the study area the distribution of geoxylic suffrutices rather reflects the depth of the water table, with these plants being most abundant in sites where it is high, yet still below 1.8 m. These sites comprise mainly those relatively high-lying, well-drained areas such as dune crests and slopes, the surface soils of which are never waterlogged. In fact, geoxylic suffrutices are noticeably absent from inter-dune depressions, the only areas which are clearly seasonally waterlogged.

Fire might have played a more significant role in the evolution of the suffruticose habit than suggested by White (1976). In the absence of fire, the above-ground shoots of the suffrutices in frost-free areas (such as the study area) become less floriferous, moribund, and may even die back. Flowering and the sprouting of new shoots in suffrutices are considerably enhanced by the frequent annual burning of the Maputland grasslands.

TABLE 5.—Environmental factors associated with the different plant communities. Other selected attributes are also presented

Plant community number	Average water table depth (m)	Predominant soil type	Average biomass (kg/ha)	Average number of plant species/sample plot	Number of suffrutex taxa	Number of endemics	Size* (ha)	% in Sileza N.R.
1	>2	dystric regosols	—**	40	0	14	90	4.2
2.1	1.76	dystric regosols	2292	49	7	13	90	4.2
2.2.1	>2	dystric regosols	1996	36	11	13	1000	47.2
2.2.2	1.76	dystric regosols	1986	32	10	14	1000	47.2
3	1.32	humic gleysols	1758	19	1	6	500	23.5
4.1	0.725	histosols	2420	14	0	2	400	18.8
4.2	0.52	histosols	2987	15	0	0	400	18.8
4.3	0.7	histosols	4958	9	0	1	400	18.8
5	0.11	histosols	4584	13	0	1	44	2.1

* = estimates only; ** = not determined.

Grassland or savanna?

Physiognomically, typical grassland is characterised by strong dominance of hemicryptophytes of the Poaceae. Savanna, on the other hand, has been defined as a vegetation type comprising an herbaceous, usually graminoid, layer with an upper layer of woody plants of which the canopy cover does not exceed 75% (Edwards 1983). A non-quantitative, more functional savanna definition is that it is a tropical vegetation type in which ecological processes, such as primary production, hydrology and nutrient cycling, are strongly influenced by both woody plants and grasses, and only weakly influenced by plants of other growth forms (Scholes & Walker 1993).

Due to the abundance of geoxyllic suffrutices, it is somewhat of a misnomer to refer to these communities merely as 'grassland'. We suggest 'woody grassland' as a more appropriate descriptive term. In a sense these woody grasslands imitate a savanna in which the tree stratum has been reduced to almost the same level as that of the graminoids and with many of the dwarf trees actually comparable to hemicryptophytes, particularly if fire is given its due recognition as a natural factor. Rutherford & Westfall's (1994) inclusion of the Maputaland grasslands under their Savanna Biome might therefore be more appropriate than would appear at first glance. Detailed comparative studies on the ecology of these unusual woody grasslands, in relation to conventional grassland and savanna, would be most instructive.

Fire

Growth in the coastal grasslands of Maputaland is not distinctly seasonal and herbage production is high, despite the infertile soils. Regular fires are a natural phenomenon in these grasslands, although today most are caused by humans. The same patch of grassland may be burned up to three times a year, with at least one fire a year being the norm. There can be no doubt that fire is an essential factor in maintaining the woody grasslands of coastal Maputaland. Margins of sand forest exposed to fire often acquire woodland elements and woodland character species. This, however, appears to be a temporary stage towards sand forest recovery.

An increase in burning frequency owing to an expanding human population over the last few decades has led to the commonsense assumption that tree-dominated vegetation types in the study area must be decreasing. However, a comparison of aerial photographs of the area taken in 1942, 1975 and 1991 indicates the contrary. In most cases the patches of woodland and sand forest have either increased in size (albeit slightly) or became more densely wooded. These forests and woodlands also turned out to be very stable features—all being strictly confined to the same sites over at least the past 50 years, although size and floristic composition might have changed.

It is hypothesised that the observed increase in size and the thickening-up of the forest/woodland patches could have been caused by changes in water table level. A drop in water table over the long term would be conducive towards the creation of habitats more suitable for the development of woodland, thicket and eventually

forest. The continued afforestation of the woody grasslands with pines, eucalypts, cashew nuts and other alien trees will, almost certainly, bring about such a drop in the level of the water table. This could result in a dramatic increase in the woody component of the vegetation of the region. Woody grasslands might, in future, have to be increasingly maintained by fire in order to keep them in their current 'underground savanna/forest' state.

Primary or secondary grassland?

Are the extensive coastal grasslands of Maputaland primary or secondary? Rutherford & Westfall (1994) do not include them in their Grassland Biome, but consider them part of the Savanna Biome. They differentiate the true Grassland Biome climatically from the Savanna Biome in terms of minimum winter temperature in conjunction with moisture levels, thus restricting it mainly to the grasslands of the high central plateau and eastern parts of the Great Escarpment of South Africa.

Moll & White (1978) and White (1983) distinguish two broad types of grassland in the Tongaland-Pondoland Regional Mosaic, namely edaphically controlled grassland associated with scattered palms on badly drained sandy soils and secondary fire-maintained grassland that has replaced anthropogenically destroyed coastal forest. On deeper soils along the coast, grassland has been considered a phase in the primary succession to coastal dune forest, a fire-subclimax. In the absence of fire, succession quickly proceeds from grassland to dune scrub and forest (Weisser 1978). This trend towards forest development diminishes inland and in the study area, which falls within the edaphic grasslands of White (1983), grassland appears to be a more stable feature.

Although the frequency of fire in the coastal grasslands of Maputaland has obviously increased due to human activities, floristic and morphological evidence clearly indicate that they have been edaphically controlled and/or fire-maintained for a very long time. The high incidence of endemics, several of which developed an obligate geoxyllic suffruticose habit (Tables 3 & 4), signifies a long evolutionary history for this particular vegetation type in the region.

As in the case of the Afromontane grasslands (Matthews *et al.* 1993), the presence of coastal grasslands in Maputaland is not the result of the relatively recent anthropogenic destruction of savanna or forest, although the presence of humans may have led to their expansion or contraction in certain parts. We contend rather that these grasslands are essentially primary in nature and not secondary in the sense of being 'unnaturally' degraded forest or savanna. In fact, the association between fire and these grasslands must be as old as the grasslands themselves, thus making fire a regular feature of the environment. Extensive afforestation with exotic trees, so-called conservation measures to curtail fire, woodcutting, grazing and shifting cultivation have already resulted in the all but total disappearance of grassland in many parts. Biodiversity has diminished accordingly, particularly in the southern coastal region of Maputaland (Weisser 1978).

Endemics

About 2 500 species (but probably more) of vascular plants occur in the MC. Of these at least 230 species or infraspecific taxa and three genera are endemic or near-endemic to the region (Van Wyk 1996; unpublished data). Thirty one of these MC endemics were recorded in the study area (Table 3), but the actual number present is expected to be slightly higher due to incomplete sampling. Most endemics were associated with only two of the five major plant communities. By far the majority of plant endemics are confined to non-hygrophilous grassland, a vegetation type hitherto usually considered secondary (anthropogenic) in origin (e.g. Henkel *et al.* 1936; Weisser 1978; White 1983). The observed low species diversity and paucity of regional endemics in hygrophilous grassland communities is a common phenomenon throughout southern Africa.

Four MC endemic/near-endemic bird species, Neergaard's sunbird (*Nectarinia neergaardi*), Rudd's apalis (*Apalis ruddi*), pinkthroated twinspot (*Hypargos margaritatus*) and Woodward's batis (*Batis fratrum*) are found mostly in sand forest. A subspecies of the pinkthroated longclaw (*Macronyx ameliae ameliae*), a rare MC endemic bird, is mainly associated with the *Ischaemum fasciculatum*-*Eragrostis inamoena* hygrophilous grasslands.

The present study enables comparison between the coastal plain grasslands of the MC and the high-altitude Afromontane grasslands of the Wolkberg Centre, a botanical centre of endemism along the northeastern Transvaal Escarpment (Matthews *et al.* 1993). Environmental factors associated with the montane plant communities are more diverse and include often complex interactions between lithology, soil type and depth, topography, precipitation (rain and mist), altitude, rockiness, slope and fire regime (Matthews *et al.* 1992a, b; 1994). A much simpler situation exists in the MC with the key determinants being the interconnected effects of water table, soil type and topography, upon which fire has been superimposed. The study on the Wolkberg Centre, however, covered a considerably greater area. Casual observations and comparison with other studies (notably Myre 1964, 1971) have nevertheless shown that the plant communities (and thus associated environmental factors) of the present study extend over most of the Maputaland coastal plain.

MC 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). Most noticeable among the more than 130 Wolkberg Centre endemics is the complete lack of annuals and large trees and the fact that nearly all these species are confined to grassland (Matthews *et al.* 1993; unpublished data). There is a conspicuous lack of local endemism in the associated patches of Afromontane forest. In contrast, MC endemics are well represented in both grassland and sand forest, with the latter, on a regional basis, being perhaps the single richest community in MC plant endemics. It is hypothesised that one of the reasons for this marked difference in growth form

and for the vegetation-type partitioning of endemics between the two centres of endemism is the relative youthful age of the sandy Maputaland coastal plain (Quaternary) and its associated plant communities.

Threats and conservation

Conservation efforts in the MC have hitherto centred mainly around areas containing species of large game. The vegetation of nearly all existing nature reserves is dominated by various types of savanna. A notable exception is the Tembe Elephant Reserve which contains well-preserved stands of endemic-rich sand forest. The grasslands in the region are particularly poorly conserved and managed.

Afforestation is currently the most serious threat to biodiversity on the coastal plain of the MC. Uncontrolled cattle grazing and random, uncontrolled fire certainly effects species composition and diversity, but probably do not change the structure of the grasslands. The planting of alien trees over large tracts of grassland, on the other hand, not only destroys the grassland habitat but is also expected to affect the hydrology of the region negatively. Further afforestation by the timber industry and private individuals is expected. The establishment of other extensive monocultures, for example cashew nuts, sugar cane and coconut palms, also threatens the grasslands of this relatively unspoiled part of Africa. With so little grassland formally conserved, the SNR, despite its small size, fulfils a crucial role in ensuring the preservation of the endemic-rich flora and fauna of the MC, one of the world's most unique centres of endemism.

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CHAPTER 5

VEGETATION OF TEMBE ELEPHANT PARK

PUBLISHED MANUSCRIPT

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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 TWINSPLAN 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.

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

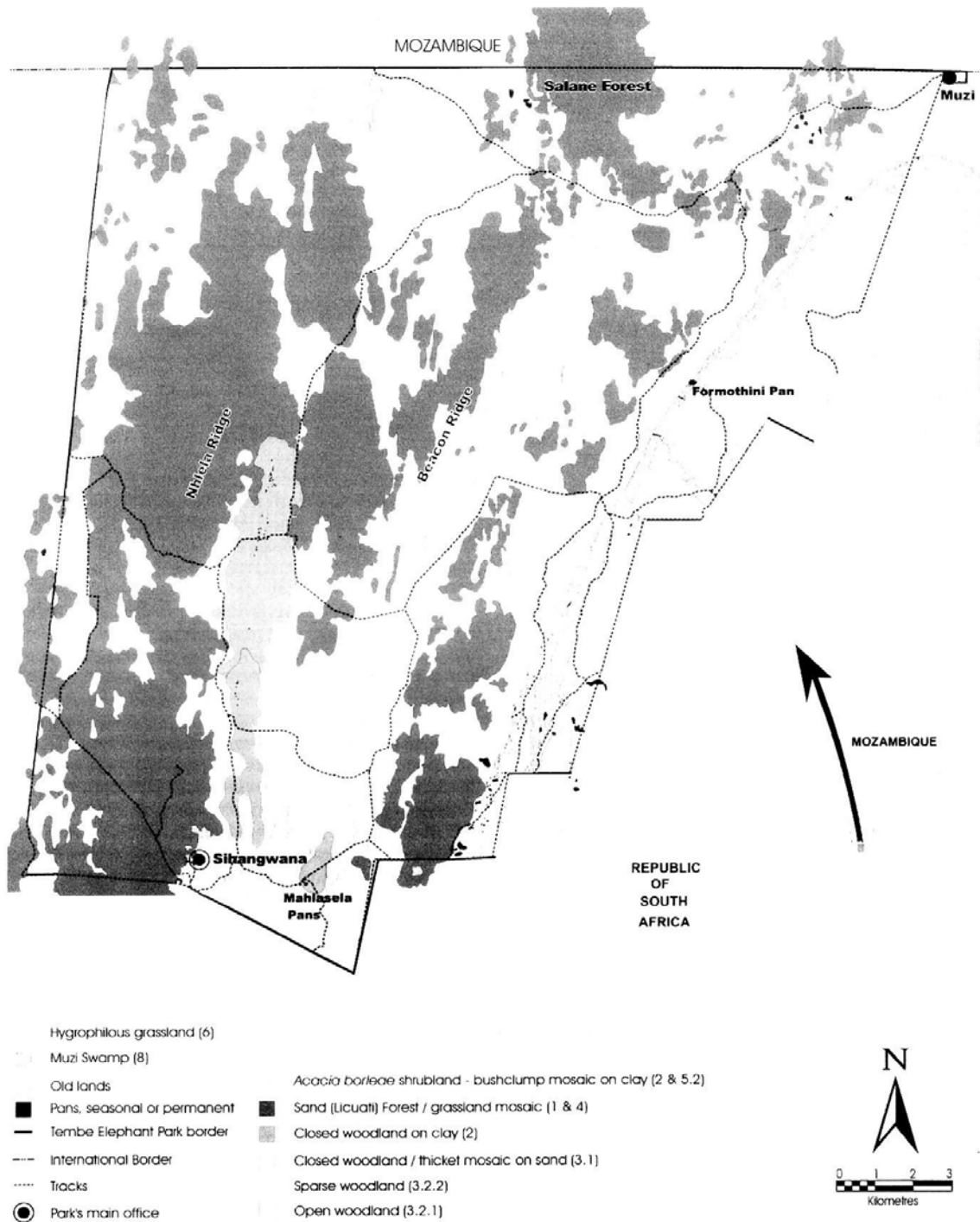


Figure 1: Map showing the location of the Tembe Elephant Park and its broad vegetation types. Numbers in brackets refer to the specific plant communities (see text) combined under that mapping unit

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)	Mean	Annual rainfall (mm)	
			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 20m²/day and co-efficient of storativity of 1⁻¹⁰⁻³. 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

Table 3: Phytosociological table of the vegetation of the Tembe Elephant Park and surrounding areas (species with an occurrence of 1 have been omitted throughout). Community 8 (reed beds of Muzi Swamp) is not included

COMMUNITY NUMBER	1		2	3		4	5		6	7		
	1.1	1.2		3.1.1	3.1.2		3.2.1	3.2.2			5.1	5.2
RELEVÉ No.	4 0 5 3 6	3 5 3 4	0 1 0 1 1	4 4 5 5 2 3	3 2 0 5	3 4 3 4 2 4 6 2 5 6	3 4 2 2 5 6 4	0 0 0 3 5 6	0 1 2	0 1 1	2 2 5 4 5 2	1 1 1 1
SPECIES PER RELEVÉ	8 1 0 4 2	7 8 9 2	5 5 7 1 7	4 0 3 1 3 0	1 5 9 9	8 6 5 1 0 8 0 1 6 1	3 3 4 2 7 4 7	2 4 3 6 5 3	6 8 6	8 0 4	9 8 4 5 2 7	3 2 6 9
	3 3 3 3 3	3 4 3 3	5 3 4 4 4	3 3 4 4 4 5	4 3 3 2	3 3 3 2 3 4 3 4 4 2	4 3 3 4 3 2 3	2 2 3 1 1 1	2 3 3	1 2 3	1 1 1 1 1 3	1 1 1 1
	5 6 2 6 4	6 1 0 3	5 8 5 6 0	6 8 3 5 2 0	8 2 1 8	5 6 8 7 6 7 2 3 3 9	1 6 8 4 5 9 6	5 9 6 8 8 3	0 6 2	8 2 0	9 8 4 8 8 8	9 1 2 1
SPECIES GROUP A												
Cola greenwayi	A 1 1 1 +	+										
Balanites maurhamii	+ + + + +											
Ptaeroxylon obliquum	+ + + + +											
Suregada zanzibaniensis	+ + + + +											
Haplocoelum gallense	+ + + + +											
Stychnos henningsii	+ + + + +											
Wrightia natalensis	+ + + + +											
Acacia kraussiana	R + 1											
Panicum latocomum	+ + + + +											
Strophanthus luteolus	+ + + + +											
Croton stenkampianus	+ + + + +											
Lankea antisorbiculata	+ + + + +											
Ochna arborea	+ + + + +											
Leptochloa uniflora	+ + + + +											
SPECIES GROUP B												
Pythax fragrantissima	+ + + + +											
Hyperacanthus microphyllus	+ + + + +											
Tricalysia junodi	+ + + + +											
Cassipourea mossambicensis	+ + + + +											
Grewia microthyrsa	+ + + + +											
Cyperus albostriatus	+ + + + +											
Combretum mikuzense	+ + + + +											
Phyllanthus sp. nov.	R											
Oxyanthus latifolius	+ + + + +											
Zanthoxylum leprieii	+ + + + +											
Tarenna littoralis	+ + + + +											
SPECIES GROUP C												
Drypetes arguta	A A + A 1	A + A 1										
Uvaria lucida ssp. virens	+ 1 1 + 1	+ + + + +										
Croton pseudopulchellus	+ + + 1 +	+ + + 1 +										
Pteleopsis myrtilloia	+ + + R +	+ + + + +										
Todalakopsis bremekampii	+ + + + +	+ + + + +										
Salacia leptoclada	+ 1 A +	+ + + + +										
Hymenocardia ulmoides	+ + 1 +	+ + + + +										
Dialium schlechteri	+ + + + +	+ + + + +										
Cleistanthus schlechteri	+ + 1 1 +	+ + + + +										
Socarmone delagoensis	+ + + + +	+ + + + +										
Drypetes natalensis	+ + + + +	+ + + + +										
Monodora junodi	+ 1 + + +	+ + + + +										
Leptactinia delagoensis ssp. delagoensis	+ + + + +	+ + + + +										
Brachylaena huillensis	+ + + + +	+ + + + +										
Manikara discolor	+ + + + +	+ + + + +										
Vilox amboniensis	+ + + + +	+ + + + +										
Newtonia hildebrandtii	1 1 + + 1	+ + + + +										
Combretum celastroides	+ + + + +	+ + + + +										
Microcoelia exilis	+ + + + +	+ + + + +										
Erythrophleum lasianthum	+ + + + +	+ + + + +										
Protaspargus falcatius	+ + + + +	+ + + + +										
Hyposestes aristata	+ + + + +	+ + + + +										
Sansevieria cf. metallica	+ + + + +	+ + + + +										
Boscia foetida ssp. rehmanniana	+ + + + +	+ + + + +										
Uvaria caffra	+ + + + +	+ + + + +										
Brachiaria chusqueoides	+ + + + +	+ + + + +										
Euphorbia grandidens	+ + + + +	+ + + + +										
Hippocratis delagoensis	+ + + + +	+ + + + +										
Schlechteria mitostemmatoides	+ + + + +	+ + + + +										
Tricalysia capensis	+ + + + +	+ + + + +										
SPECIES GROUP D												
Sporolachys africana				A + A A B	1	1						
Berchemia zeyheri				+ + + + +								
Cassine aethiopica				+ + + + +								
Sansevieria hyacinthoides				+ 1 + + +								
Zuziphus mucronata				1 1 1 +								
Euclea divinorum				+ + + A +								
Justicia prostrata				+ + + + +								
Dovyalis longispina				+ + + + +								
Schotia capitata				+ + + + +								
Sideroxylon inerme				+ + + + +								
Protaspargus suaveolens				+ + + + +								
Senecio viminalis				+ + + + +								
Capparis brassii				+ + + + +								
Capparis tomentosa				+ + + + +								
Carissa bispinosa				+ + B								
Euphorbia ingens				R R +								
Acacia senegal				+ + + + +								
Pappas capensis				+ + + + +								
Pavetta calophylla				+ + + + +								
Schotia brachypetala				+ 1 +								
Acalypha glabrata				+ + + + +								
Crossandra greenstockii				+ + + + +								
Stychnos decussata				+ + + + +								
Euclea undulata				+ + + + +								
Orthosiphon suffrutescens				+ + + + +								
Azima tetraantha				+ + + + +								
Pyrostria hystrix				+ + + + +								
Thespesia acutikoba				R R								
SPECIES GROUP E												
Panicum deustum	+ + + + +	+ + + + +	+ R +	1 + 1 1								
Monanthes caffra	+ + + + +	+ + + + +	+ R +	A + + + +								
Synaptolipsis kirkii	R R +	+ + + + +	+ + + + +	+ + + + +								
Tricalysia lanceolata	+ + + + +	+ + + + +	+ + + + +	+ + + + +								
Pythax locuples	+ + + + +	+ + + + +	R	1 +								

Table 3 cont.

COMMUNITY NUMBER	1		2		3		4		5		6		7	
	1.1	1.2	3.1	3.1.1	3.1.2	3.2	3.2.1	3.2.2	5.1	5.2	6	7	7	7
RELEVÉ No.	4 0 5 3 6	3 5 3 4	0 1 0 1 1	4 4 5 5 2 3	3 2 0 5	3 4 3 4 2 4 6 2 5 8	3 4 2 2 5 6 4	0 0 0 3 5 6	0 1 2	0 1 1	2 2 5 4 5 2	1 1 1 1		
SPECIES PER RELEVÉ	9 1 0 4 2	7 8 9 2	5 5 7 1 7	4 0 3 1 3 0	1 5 9 9	8 6 5 1 0 8 0 1 6 1	3 3 4 2 7 4 7	2 4 3 6 5 3	6 8 6	8 0 4	9 8 4 5 2 7	3 2 6 9		
	3 3 3 3 3	3 4 3 3	5 3 4 4 4	3 3 4 4 4 5	4 3 3 2	3 3 3 2 3 4 3 4 4 2	4 3 3 4 3 2 3	2 2 3 1 1 1	2 3 3	1 2 3	1 1 1 1 1 3	1 1 1 1		
	5 6 2 6 4	6 1 0 3	5 8 5 6 0	6 8 3 5 2 0	8 2 1 8	5 6 8 7 6 7 2 3 3 9	1 8 8 4 5 9 6	5 9 6 8 8 3	0 6 2	8 2 0	9 8 4 8 8 8	9 1 2 1		
SPECIES GROUP M														
Andropogon schirensis														
Tephrosia longipes ssp longipes														
Bewisia biflora														
Indigofera inhambanensis														
Ureythrum agropyroides														
Cyperus obtusiflorus														
Trachyandra cf salti														
Sporobolus congensis														
Tricicera mossambicense														
Pavonia leptocalyx														
Sporobolus subulatus														
Indigofera podophylla														
SPECIES GROUP N														
Diheteropogon amplectens														
Perotis patens														
Aristida stipitata ssp spicata														
Diospyros galeata														
Bulbostylis burchellii														
Ozoroa engleri														
Bulbostylis parviflora														
Themum pallidum														
Dicercocaryum eriocarpum														
SPECIES GROUP O														
Terminalia sericea														
Digitaria eriantha														
Eugenia mossambicensis														
Corchorus junodii														
Albertisia delagoensis														
Landolphia kirkii														
SPECIES GROUP P														
Panicum maximum														
Commelina africana														
Commelina cf erecta														
SPECIES GROUP Q														
Waltheria indica														
Sporobolus pyramidalis														
Eragrostis ciliaris														
Monochma debile														
Indigofera sp														
SPECIES GROUP R														
Acacia borleae														
Koehia virgata														
Eragrostis plana														
Ocimum sp														
SPECIES GROUP S														
Nidorella auriculata														
Justicia flava														
Kyllinga enecia														
Aristida congesta														
SPECIES GROUP T														
Imperata cylindrica														
Eragrostis lappula														
Dactyloctenium geminatum														
Acacia nilotica														
Panicum genuflexum														
Nidorella anomala														
Chloris gayana														
Ischaemum fasciculatum														
Sporobolus virginicus														
Andropogon hulleensis														
Sorghastrum stipoides														
Hydrocotyle bonariensis														
Phragmites australis														
Helichrysum cf longense														
Vahlia capensis														
Cyperus sphaerospermus														
SPECIES GROUP U														
Eragrostis heteromera														
Agathisanthemum bojeri														
Epilobium galepinum														
Justicia betonica														
SPECIES GROUP V														
Oxalis cf semiloba														
Nymphaea nouchali														
Ceratophyllum demersum														
Cyperus distans														
Digitaria didactyla														
Chamaecrista sp.														
Echinochloa pyramidalis														
Cyperus denudatus														
Pycnosia nitida														
Nesipia oleracea														
Ludwigia cf stolonifera														
SPECIES GROUP W														
Cyperus natalensis														
Eragrostis inamoena														
Sesbania biapinosa														

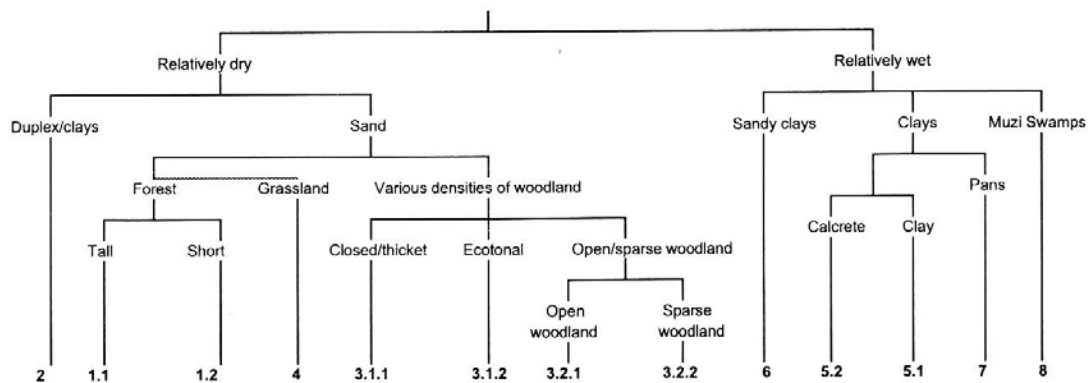


Figure 2: Dendrogram illustrating the habitat relationships of the different plant communities. Community numbers correspond with descriptions in the text. Grassland community 4 is always associated with the margin of Sand Forest. It is hypothesised that these grassland zones around Sand Forest are the 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 *Psyrax 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-Themeda 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 *Monanthataxis caffra* have a high constancy in this commu-

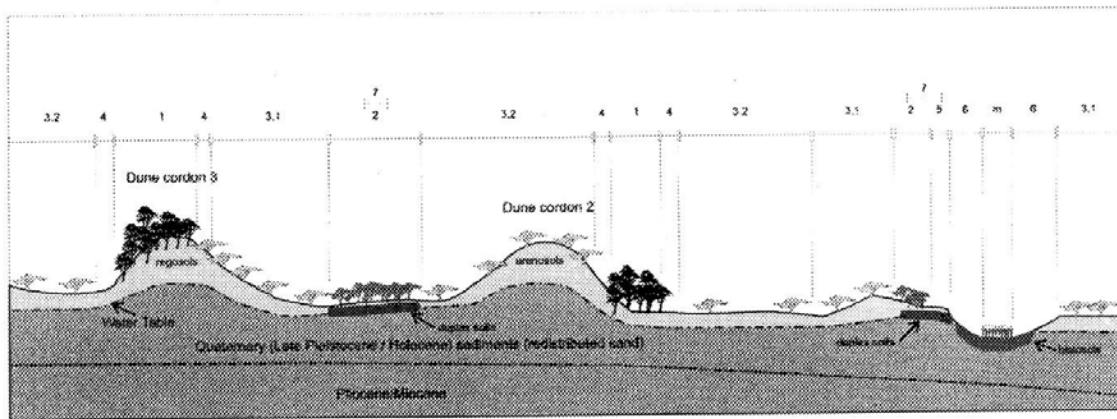


Figure 3: Schematic representation of the distribution of the different plant communities in the Tembe Elephant Park and surrounding areas. Dotted lines indicate overlapping distributions. Community numbers correspond with descriptions in the text. m = Muzi Swamp

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 myrtilifolia*, *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 albostratus*. 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: Maputaland Centre endemic or near-endemic plant species (according to Van Wyk 1996), and the plant communities with which they are associated

Endemic/near-endemic taxon	Family	Plant community number									
		1.1	1.2	2	3.1	3.2	4	5	6	7	
<i>Acacia kraussiana</i>	Mimosaceae	XX									
<i>Acridocarpus natalitius</i> var. <i>linearifolius</i>	Malpighiaceae					X					
<i>Albertisia delagoensis</i>	Menispermaceae				XX	XX					
<i>Aloe marlothii</i> subsp. <i>orientalis</i>	Asphodelaceae					XX					
<i>Aloe parvibracteata</i>	Asphodelaceae					X					
<i>Ancylanthos monteiri</i>	Rubiaceae		X		X						
<i>Aneilema arenicola</i>	Commelinaceae	X	X								
<i>Aspidoglossum delagoense</i>	Asclepiadaceae									X	
<i>Barleria prionitis</i> subsp. <i>delagoensis</i>	Acanthaceae	X	X								
<i>Bonatea lamprophylla</i>	Orchidaceae	X									
<i>Brachychnoa fragilis</i>	Poaceae	X	X		X						
<i>Brachychnoa schiemaniana</i>	Poaceae	X	X								
<i>Canthium setiflorum</i> subsp. <i>setiflorum</i>	Rubiaceae				X						
<i>Cassipourea mossambicensis</i>	Rhizophoraceae	X	XX								
<i>Cissampelos hirta</i>	Menispermaceae				XX		X				
<i>Cleome borensis</i>	Capparaceae		X		X	X	X				
<i>Coffea racemosa</i>	Rubiaceae	XX			X						
<i>Combretum celastroides</i> subsp. <i>orientale</i>	Combretaceae	XX	XX								
<i>Combretum mkuzense</i>	Combretaceae		X								
<i>Corchorus junodii</i>	Tiliaceae				X	XXX					
<i>Crassula maputensis</i>	Crassulaceae	X	X								
<i>Crinum acaule</i>	Amaryllidaceae					X					
<i>Crossandra fruticulosa</i>	Acanthaceae			X							
<i>Crotalaria monteiri</i> var. <i>monteiri</i>	Fabaceae				X	XX	X				
<i>Croton steenkampianus</i>	Euphorbiaceae	XX									
<i>Dialium schlechteri</i>	Caesalpinaceae	XXX	XXX		XX	X					
<i>Diospyros inhacaensis</i>	Ebenaceae			X	X						
<i>Dovyalis longispina</i>	Flacourtiaceae			XXX	X						
<i>Encephalartos ferox</i>	Zamiaceae	X	X								
<i>Eragrostis moggii</i> var. <i>moggii</i>	Poaceae		X	X	X						
<i>Erythrophleum lasianthum</i>	Fabaceae	XX	XX								
<i>Erythroxyllum delagoense</i>	Erythroxylaceae			XX	XX						
<i>Eugenia mossambicensis</i>	Myrtaceae				X	XXX	X				
<i>Galpinia transvaalica</i>	Lythraceae			X							
<i>Gardenia cornuta</i>	Rubiaceae			X							
<i>Grewia microthyrsa</i>	Tiliaceae	X	XXX	X	X	X					
<i>Haplocoelum gallense</i>	Sapindaceae	XXX	X								
<i>Helichrysum adenocarpum</i> subsp. <i>ammophilum</i>	Asteraceae									X	
<i>Helichrysum silvaticum</i>	Asteraceae				X	X					
<i>Helichrysum tongense</i>	Asteraceae									XX	
<i>Hippocratea delagoensis</i>	Celastraceae	X	X		X						
<i>Hyperacanthus microphyllus</i>	Rubiaceae	XX	XXX								
<i>Indigofera delagoensis</i>	Fabaceae				X	X					
<i>Indigofera inhambanensis</i>	Fabaceae					XX	XXX			X	
<i>Indigofera podophylla</i>	Fabaceae						XX				
<i>Kalanchoe neglecta</i>	Crassulaceae			X							
<i>Lagynias lasiantha</i>	Rubiaceae	X									
<i>Lepidium suluense</i>	Brassicaceae									X	
<i>Maerua nervosa</i>	Capparaceae			X							
<i>Maytenus markwardii</i>	Celastraceae				X	XX					
<i>Memecylon sousae</i>	Melastomataceae		X								
<i>Ochna barbosae</i>	Ochnaceae		X								
<i>Oxyanthus latifolius</i>	Rubiaceae		XX								
<i>Oxygonum robustum</i>	Polygonaceae					XX	X				
<i>Ozoroa engleri</i>	Anacardiaceae				X	XXX	XX				
<i>Parinari capensis</i> subsp. <i>incohata</i>	Chrysobalanaceae					XX					
<i>Pavetta catophylla</i>	Rubiaceae	X		XX							
<i>Pavetta gerstnerii</i>	Rubiaceae	X	X								
<i>Pavetta</i> sp. nov.	Rubiaceae				X	XX					
<i>Pelargonium tongaense</i>	Geraniaceae			X							
<i>Phylanthus</i> sp. nov.	Euphorbiaceae	X	XX								

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							
<i>Rhus kwazuluana</i>	Anacardiaceae					x					
<i>Salacia kraussii</i>	Celastraceae					xxx	x				
<i>Sanseveria coccinea</i>	Liliaceae				x						
<i>Schotie capitata</i>	Fabaceae			xxx							
<i>Sclerochiton apiculatus</i>	Acanthaceae		x								
<i>Secamone delagoensis</i>	Asclepiadaceae	xxx	xxx	xxx	x						
<i>Striga junodii</i>	Scrophulariaceae								x		
<i>Strophanthus gerrardii</i>	Apocynaceae	x									
<i>Strophanthus luteolus</i>	Apocynaceae	xx	x								
<i>Tarenna junodii</i>	Rubiaceae		x		xx						
<i>Thespesia acutiloba</i>	Malvaceae			x							
<i>Todallipsis bremekampii</i>	Rutaceae	xxx	xxx								
<i>Tricalysia delagoensis</i>	Rubiaceae	x	x	x							
<i>Tricalysia junodii</i> var. <i>junodii</i>	Rubiaceae			xx							
<i>Tricliceras 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			
<i>Warburgia salutaris</i>	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					
TOTAL											
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 dystric 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 revouilii*. 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 cathartica* (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-Themeda 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 amplexens* 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 amplexens*, *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 dystic 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 *Bewisia 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 amplexens*, *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-Dalium schlechteri* inland forest.

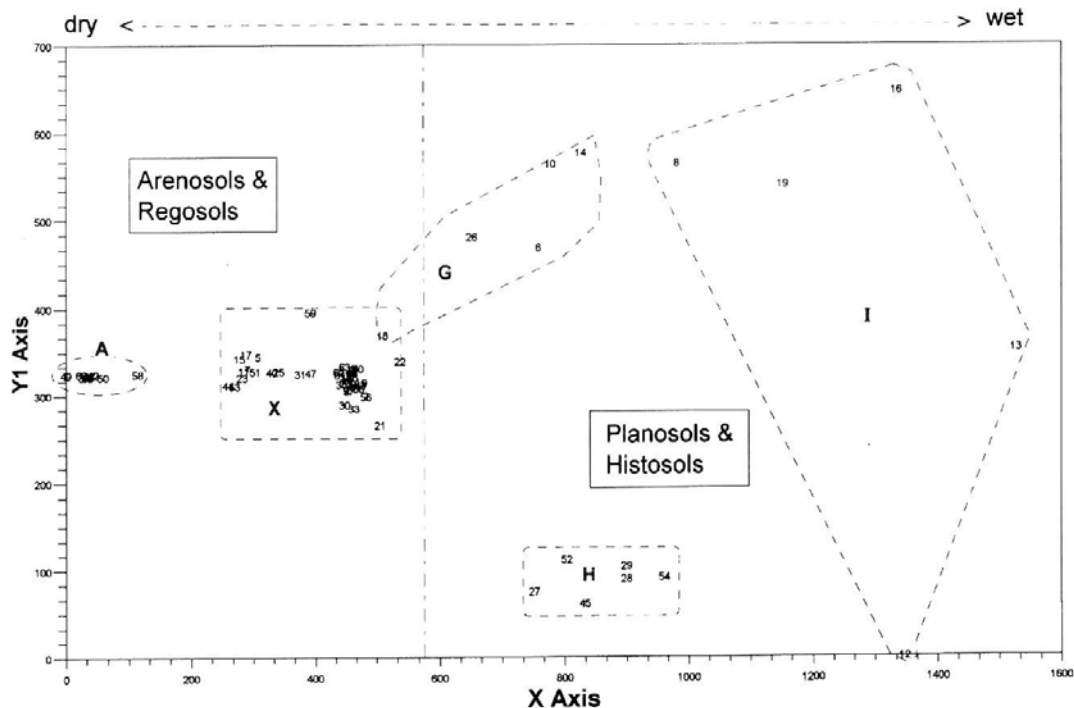


Figure 4: Ordination (X and Y1) of the relevés from the Tembe Elephant Park and surrounding areas. A, *Drypetes arguta-Uvaria lucida* subsp. *virens* Sand Forest of deep sandy areas (dry sands). X, *Spirostachys africana-Berchemia zeyheri* closed woodland on duplex soils (clays); *Andropogon schirensis-Tephrosia longipes* subsp. *longipes* grassland associated with Sand Forest; *Strychnos madagascariensis-Combretum molle* woodland of deep sandy areas. 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* aquatic vegetation of standing water in marshes and pans

However, the latter inland forest type contains many coastal dune forest species and is obviously more closely associated with coastal dune forest whilst containing a few Sand Forest elements. The open to sparse woodlands described in this study do have similarities with the *Themeda-Salacietum* M. Myre (1964) woody grasslands of Myre (1964) and Matthews *et al.* (1999). The typical woodland communities, as described in the present study, are limited in distribution and in variety in Sileza Nature Reserve (Matthews *et al.* 1999).

The Muzi Swamp communities described in this study are also rather similar to the Sileza Nature Reserve's *Ischaemum fasciculatum-Eragrostis inamoena* hygrophilous grasslands and specifically to the *Monocymbium ceresiiforme-Eragrostis lappula* grassland of areas not regularly inundated with water (pan edges). However, in TEP, which has drier conditions with much deeper water table levels, these communities are limited, and species compositions differ accordingly.

Major determinants of plant communities

A simple situation exists in the MC with the important determinants being the interconnected effects of water table

(moisture), soil type and topography, upon which fire and vegetation dynamics have been superimposed. Casual observations and comparison with other studies (notably Myre 1964, 1971, Lubbe 1996, Matthews *et al.* 1999) have nevertheless shown that the plant communities (and thus associated environmental factors) of the present study extend over most of the Maputaland Coastal Plain. In the case of TEP, which lies in a drier and topographically more elevated part of the Maputaland Coastal Plain, water table level is not a leading factor, although soil moisture plays an important role. In the case of Sand Forest associated with the ancient dune cordons and driest soils, it is suggested that historic plant dynamics could be a major determinant of the present day Sand Forest patches.

Regular fires are a natural phenomenon in these areas, although today most fires are anthropogenic. As a result of humans, fires are more regular (sometimes more than once a year) and are now taking place at times of year when the vegetation would not naturally, on a regular basis, be exposed to fire. In many managed areas, current fire frequency and intensities are lower than in the past, resulting in increased woody biomass in these areas (Van Wilgen and Scholes 1997). There can be no doubt that fire is an important natural ecological factor in these communities. In the

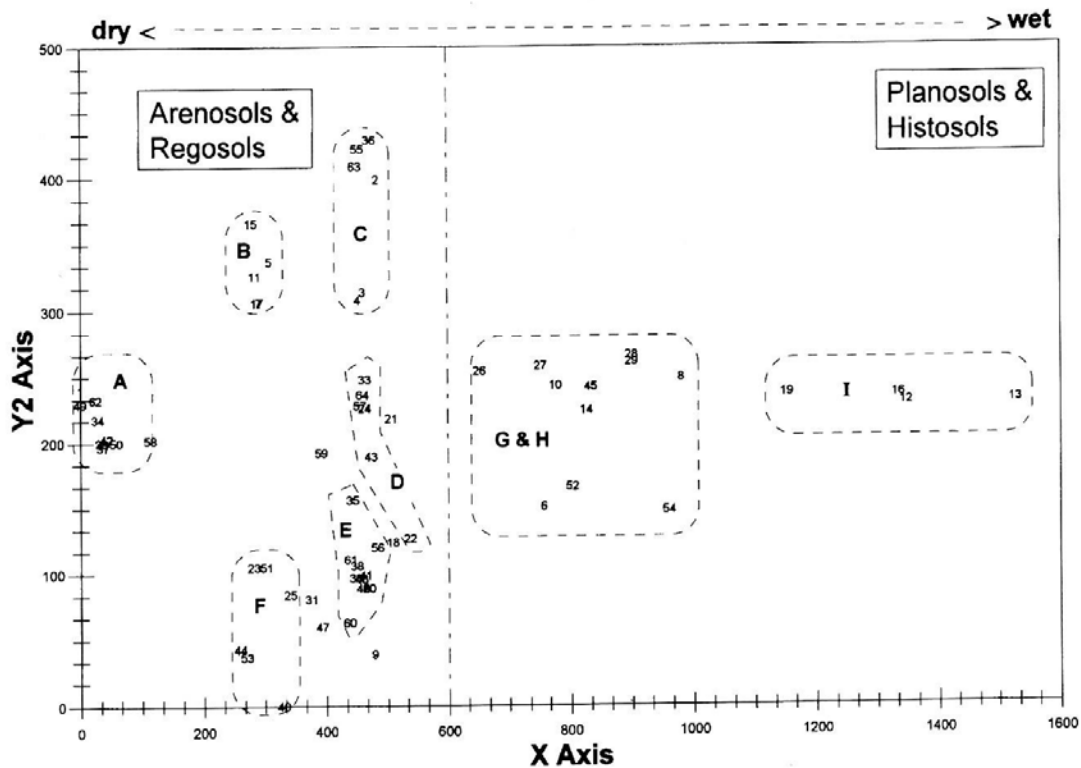


Figure 5: Ordination (X and Y2) of the relevés from the Tembe Elephant Park and surrounding areas. A, *Drypetes arguta-Uvaria lucida* subsp. *virens* Sand Forest of deep sandy areas (dry sands). B, *Spirostachys africana-Berchemia zeyheri* closed woodland on duplex soils (clays). C, *Andropogon schirensis-Tephrosia 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-*

cariensis-Combretum molle woodland. Most of the *Salacia kraussii-Themedra 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 twinspot (*Hypargos margaritatus*) and Woodward's batis (*Batis fratrum*) 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 maughamii*, *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 northeast. 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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CHAPTER 6

POSSIBLE ALLELOPATHIC INTERFERENCE IN SAND FOREST:
A PRELIMINARY STUDY

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Possible allelopathic interference in Sand Forest: a preliminary study*

Abstract

Sand Forest is a rare, species-rich tropical dry forest type mainly restricted to ancient coastal sand dunes in Maputaland. Forest patches are typically sharply delineated by a narrow (about 2–4 m wide) zone of bare or sparsely vegetated sand, followed by grassland and then woodland, which is the prevailing vegetation type in the region. We propose the hypothesis that Sand Forest may have allelopathic effects on its environment, hence the characteristic zonation of the surrounding vegetation. Data of exploratory germination trials utilising wheat and lettuce as bioassay plants, as well as inorganic and organic soil analyses, are presented to test this hypothesis. Sand Forest soil shows an inhibitory effect on the emergence and growth of wheat and lettuce; wheat being more sensitive than lettuce. Inhibition decreases progressively from Sand Forest through grassland to woodland. The inhibitory principle(s) can be mobilised (leached out) from soil by water. Certain, as yet unidentified, organic compounds present in Sand Forest soil occur in lesser quantity at the edge of the Sand Forest, but are apparently absent in the grassland and woodland soils.

Introduction

Floristically the Forest Biome in southern Africa may be classified into three broad forest types (Low & Rebelo 1996), namely Afromontane Forest, from temperate, mainly high altitude inland regions; Coastal Forest, from the subtropical/tropical eastern seaboard; and Sand Forest, a rare, tropical, dry forest type from the southern parts of the Mozambican Coastal Plain. Of these three forest types, Sand Forest is the least studied and poorest known. It is, however, of considerable biological and conservation interest because of its very restricted occurrence, rich biodiversity and presumed relictual, yet relatively recent, evolutionary status.

Sand Forest (Moll 1977; Moll & White 1978; Moll, 1980), also known as *Licuat*i Forest in Mozambique (Myre 1964; Myre 1971), is more or less confined to the broad coastal plain between St Lucia in northern KwaZulu-Natal, South Africa, and Maputo in southern Mozambique—a region known as Maputaland. Forest stands occur as isolated patches mainly associated with

* Findings are preliminary as the experimental design was not statistically robust.

ancient north-south trending inland sand dunes (Matthews *et al.* 2001). Some of these dune cordons, which can be traced for long distances along the inland margin of the coastal zone, mark stillstands during marine regressions (Botha 1997). The oldest ones are probably Pliocene (± 3 Ma BP) whereas the youngest are probably Late Pleistocene (30 000–10 000 BP) (Davis 1976; Hobday 1976; Botha 1997; Wright 1997).

Maputaland is recognised as a globally important region of plant diversity and endemism, referred to as the Maputaland Centre [MC] (Van Wyk 1994; Van Wyk 1996). In the MC high levels of endemism (especially neo-endemics) are spread across virtually the whole taxonomic spectrum, involving both plants and animals. A significant number of these endemics/near-endemics are associated with Sand Forest, making this perhaps the most remarkable plant community in the MC (Van Wyk 1996; Matthews *et al.* 2001).

An outstanding feature of Sand Forest is its very sharp edges, in most cases delineated by narrow (about 2–4 m wide) zones of bare to sparsely vegetated sand (Matthews *et al.* 2001). In Maputaland these zones of white sand are unique to Sand Forest and particularly noticeable from the air, even in satellite images. In most cases the sparsely vegetated zones are followed by grassy areas; these have a general appearance reminiscent of early successional (disturbed) vegetation due to the presence of pioneering plant species such as the grass *Perotis patens* Gand. (Matthews *et al.* 2001). Hitherto the bare to sparsely vegetated zones were generally assumed to have been caused by the trampling effect of game and cattle, with no special ecological significance attached to the phenomenon. This assumption is based on the fact that Sand Forest is a very dense (almost impenetrable) vegetation type, hence larger mammals are forced to walk around the edges.

In this paper we propose, for the first time, the hypothesis that the bare zones around Sand Forest are the result of an inhibitory effect induced by allelochemicals originating from the forest. Allelopathy is any direct or indirect beneficial or harmful effect of one plant species (including microorganisms) on the other through release of chemical compounds (allelochemicals) into the environment (Rice 1984). A plant may interfere with the growth of its neighbours directly through resource competition or chemical inhibition, or indirectly if it harbours or attracts organisms such as herbivores or pathogens that affect neighbours (Harper 1977; Fuerst & Putnam 1983; Weidenhamer 1996). Plant-plant interference (Rice 1984) may involve not only competition for water, light and nutrients, but also allelopathic phenomena that release toxic organic compounds into the environment. Under appropriate conditions, these chemicals are released in sufficient quantities to affect the growth and development of individuals of the same or other species (Seigler

1996). These substances are released into the environment through leaching of living plants, root exudates, volatilisation, residue decomposition and microbial activity (Muller 1969).

Proving that bioactive compounds (or their derivatives) exist in nature (Fuerst & Putnam 1983) and/or enter the environment (rhizosphere) to affect other organisms (Nilsson 1994), is exceedingly difficult, but it is well supported experimentally in studies performed under controlled conditions (Weidenhamer *et al.* 1989; Weston 1996). Such experiments have established that a large number of plants have the potential to inhibit seed germination and the growth of other plants through the action of allelochemicals. Here we present field observations and provisional experimental results carried out to test for potential allelopathic activity of Sand Forest soil. Although inconclusive in several respects, it is hoped that the new ideas raised may stimulate debate and further research.

Material and methods

This study comprises two components, namely various germination trials, and an investigation into the soil chemistry of selected sites. Fieldwork was conducted in the southern portion of the Tembe Elephant Park, northern KwaZulu-Natal. Tembe Elephant Park lies in the southern part of the Mozambican Coastal Plain and contains large representative samples of well-developed Sand Forest. In the study area the sparsely vegetated border zone of a *Drypetes arguta-Uvaria lucida* Sand Forest (Myre 1971) community on deep sandy soil is followed by *Andropogon schirensis-Tephrosia longipes* grassland (Myre 1971) that intergrade into various woodland communities. Samples of surface soil (not deeper than 200 mm) were collected from four different sites, along a transect from Sand Forest to woodland, as well as an additional site which once carried Sand Forest; these are described in more detail below.

Site 1: Sand Forest, sample taken in the Sand Forest approximately 10 m in from the edge of the sand forest border;

Site 2: Sparsely vegetated border zone directly adjacent to the Sand Forest, sample taken approximately 2 m outside the Sand Forest edge;

Site 3: Grassland directly bordering and associated with Sand Forest, but well away from the sparsely vegetated zone, sample taken about 15 m from the Sand Forest edge;

Site 4: Woodland, sample taken from a representative area of woodland, which is the prevailing vegetation type in the areas between Sand Forest;

Site 5: Sand Forest patch which was totally destroyed by a devastating crown fire approximately

one year before. The area was still essentially devoid of vegetation.

All plant species present at Sites 1 to 4 (in a radius of approximately 10 m) were recorded, and an estimate of cover-abundance noted for each species (Table 1). These four soil samples formed the basis for most of the seed germination trials as well as some of the soil analyses. Soils at all the sample sites consist of dystrophic regosols. They are well leached (dystrophic) and relatively acidic [pH (H₂O) approximately 5.5–6].

Germination trials

Germination trials were conducted in pots in a greenhouse at the Department of Botany, University of Pretoria, Pretoria, under prevailing temperature and light conditions and begun on the 11 March 1997. We investigated the emergence and subsequent growth behaviour of lettuce (*Lactuca sativa* cv. Great Lakes) and wheat (*Triticum aestivum* cv. Inia) to test for possible soil-inhibitory effects. Soil samples were collected five days prior to the start of the trials.

In Trial 1 ten seeds were planted per pot, with five replicates for each soil sample, and in Trial 2 one seed was planted per pot, with 20 replicates for each soil sample. This was done for soil samples from Sites 1 to 4 and for both seed cultivars. Rainwater was used to water the pots. Excess water was collected in the base of each pot, and re-used in the watering of the same pot; this ensured that any compounds that could be leached from the soil would be returned to the same pot. Water collected in the base also prevented the soil from drying out. After 12 days the percentage emergence (percentage of total number of seeds planted that emerged above ground) was calculated based on seedlings present per pot. After 20 days the seedlings were carefully removed from the pots, the roots cleaned in water, the above and below ground parts separated and lengths measured. These parts were then dried to a constant dry mass in an oven (for 40 hrs) and weighed to obtain their mass. All these were done separately for the different trials and seed cultivars. Results are shown in Figures 1 & 2.

Table 1 Plant species composition, with cover-abundance percentages for each species, at the four primary soil-sampling sites in Tembe Elephant Park, northern KwaZulu-Natal.

Taxon	Cover (%)			
	Sand Forest (Site 1)	Sand Forest edge (Site 2)	Grassland (Site 3)	Woodland (Site 4)
<i>Drypetes arguta</i>	1–5			
<i>Croton pseudopulchellus</i>	1–5	rare		
<i>Psydrax fragrantissima</i>	1–5			
<i>Landolphia kirkii</i>	1–5			<1
<i>Cyperus albostratus</i>	1–5			
<i>Hymenocardia ulmoides</i>	<1			rare
<i>Manilkara discolor</i>	<1			
<i>Brachylaena huillensis</i>	<1			
<i>Tricalysia capensis</i>	<1			
<i>Pteleopsis myrtifolia</i>	<1			
<i>Cola greenwayi</i>	<1			
<i>Grewia microthyrsa</i>	<1			
<i>Hippocratea delagoensis</i>	<1			
<i>Uvaria lucida</i> subsp. <i>virens</i>	<1			
<i>Oplismenus hirtellus</i>	<1			
<i>Panicum deustum</i>	<1.			
<i>Tricalysia junodii</i>	rare			
<i>Phyllanthus</i> sp. nov	rare			
<i>Perotis patens</i>		50	<1	
<i>Indigofera podophylla</i>		<1	<1	
<i>Psydrax locuples</i>		rare		<1
<i>Andropogon schirensis</i>			5–12	
<i>Aristida stipitata</i> subsp. <i>spicata</i>			1–5	
<i>Digitaria natalensis</i>			1–5	
<i>Urelytrum agropyroides</i>			<1	
<i>Schizachyrium sanguineum</i>			<1	
<i>Pavonia leptocalyx</i>			<1	
<i>Panicum maximum</i>				25–50
<i>Strychnos spinosa</i>				1–5
<i>Euclea natalensis</i>				1–5
<i>Trichilia emetica</i>				1–5
<i>Tabernaemontana elegans</i>				1–5
<i>Bridelia cathartica</i>				<1
<i>Azelia quanzensis</i>				<1
<i>Canthium setiflorum</i>				<1
<i>Ochna barbosa</i>				<1
<i>Justica flava</i>				<1
<i>Asparagus</i> sp.				<1
<i>Cleistanthus schlechteri</i>				rare

In Trial 3 freshly prepared rainwater leachate (solution) from the Sand Forest soil sample (Site 1) were used in a series of germination treatments involving woodland soil (Site 4) and burned Sand Forest soil (Site 5). Five seeds of each of the two seed cultivars were planted per pot, with five replicates per treatment. The different treatments were as follows: (a) woodland soil watered with rainwater throughout the trial (control); (b) woodland soil watered with leachate from Sand Forest soil throughout the trial; (c) woodland soil watered with rainwater until the first emergence, thereafter watered with Sand Forest soil leachate; (d) burned Sand Forest soil watered with rainwater throughout the trial. Results are shown in Fig. 3.

In Trial 4 only soil from Sand Forest (Site 1) was used. The soil was first baked at 150°C for two hours. Five seeds were planted per pot, with five replicates for each seed cultivar. Rainwater was used to water the pots.

Soil analyses

A sub-sample of each of the soils from Sites 1 to 4 was subjected to soil analyses. In a first phase study, soil samples were analysed by means of X-ray fluorescent spectroscopy (Table 2). In a second phase study, soil samples from Sites 1 to 4 were supplemented by two additional soil samples representative of each biotype from sites elsewhere in Tembe Elephant Park (Table 3). Three soil samples per biotype were used to gain some understanding of the variation in soil chemistry within types. Soil samples were dried at 110 °C, homogenised, and split using a cone quartering method. One sub-sample from each sample was leached with distilled water using a mechanical shaker with an eccentric motion. Selected elements and physico-chemical characteristics were determined by conventional wet chemical methods and atomic absorption spectroscopy. One sub-sample from each type was leached with methanol, and a trace of the organic compounds present obtained on a gas chromatograph [GC] coupled to a mass spectrometer [MS]. No attempt was made to identify the organic compounds since this was considered essentially an exploratory investigation.

Table 2 Phase one soil analysis of the four principal soil types used in the germination trials

Component (ppm)	Soil sampling site			
	Sand Forest (Site 1)	Sand Forest edge (Site 2)	Grassland (Site 3)	Woodland (Site 4)
Density (g/ml)	1.34	1.43	1.43	1.42
Acidity	0.78	1.14	1.12	0.15
Total cations	2.36	1.65	1.64	4.66
pH (KCL)	3.61	3.91	3.88	5.09
Organic carbon (%)	38	0	0	0
C:N ratio	14.1	-	11.2	12.1
NIRS clay (%)	16	13	12	9
P	3	2	6	5
K	143	43	83	164
Ca	109	33	25	583
Mg	82	28	22	144
Acid sat.	33	69	68	3
Zn	0.6	0.3	0.3	1
Mn	12	4	3	5
C total	0.788	0.417	0.369	0.601
C organic	0.733	0.349	0.309	0.515
C/CO ₃	0.055	0.068	0.06	0.086
B ppm	81	89	78	122
SiO ₂	96.23	96.23	95.4	94.77
TiO ₂	0.21	0.21	0.17	0.22
Al ₂ O ₃	2.1	2.1	1.76	2.12
Fe ₂ O ₃	0.8	0.8	0.64	0.98
MnO	<0.02	<0.02	<0.02	0.02
MgO	<0.02	<0.02	<0.02	0.03
CaO	0.02	0.02	0.02	0.12
Na ₂ O	0.06	0.06	0.06	0.21
K ₂ O	0.52	0.52	0.58	0.69
P ₂ O ₅	0.03	<0.02	<0.02	<0.02
Cr ₂ O ₃	<0.01	<0.01	<0.01	0.01
L.O.I.	1.03	1.03	0.95	1.66
<i>TOTAL</i>	100.84	100.84	99.44	100.54
Ba	137	114	124	139
Cr	23	20	18	108
Cu	15	15	15	14
Ga	<5	<5	<5	<5
Hf	<5	6	5	6
Mo	<2	<2	<2	3
Nb	4	4	4	4
Ni	4	4	5	6
Pb	12	12	12	13
Rb	28	24	24	26
Sc	4	5	3	5
Sr	24	18	19	30
Ta	<5	<5	<5	<5
Th	<5	<5	<5	<5
U	3	<2	3	3
V	16	15	14	17
W	<5	<5	<5	6
Y	<5	<5	<5	<5
Zn	5	5	5	7
Zr	150	150	131	176

Results and discussion

Germination trials

The emergence recorded in Trials 1 and 2 is depicted in Fig. 1. In all trials both lettuce and wheat seed showed a very low percentage emergence in Sand Forest soil (as low as 0–5%). Wheat showed a percent emergence lower than lettuce in all trials including those using the Sand Forest leachate. Wheat also showed an increased percentage emergence gradient from Sand Forest to woodland. In the case of lettuce, however, no clear gradient was observed in any of the trials: it only showed low emergence in all the Sand Forest soil trials. It would appear that some attribute of the Sand Forest soil is inhibiting emergence. No plant emergence was recorded in the baked Sand Forest soil, suggesting that the factor contributing to the inhibition of growth (germination) is present even after prolonged exposure to high temperature.

Figures 2 & 3 depict the total dry mass of the belowground and aboveground parts of the seedlings in trials 1 to 3. Because of the extremely small mass of the individual plant parts per pot, these had to be combined to make weighing practical. Hence no statistical analyses could be applied to these data sets of plant mass. We nevertheless did a single factor ANOVA analysis of the length measurements of the plant parts per pot, which gives an indication of the variability of the data (Figs 2B & 3). In nearly all the trials in which seed cultivars were exposed to the Sand Forest soil or leachate, the plants had the lowest mean dry mass (plant growth was inhibited or suppressed by some attribute of these soils). In Trial 2 (Fig. 2A), however, wheat planted in Sand Forest soil did not have the lowest dry mass. This can be explained by the fact that there was only one plant to be weighed; clearly not a sufficient sample. However, in the same trial lettuce planted in Sand Forest soil provided a sufficient sample and yielded the second lowest mean dry mass. In all the trials (except for the one with wheat noted above) there were distinct gradients along the soil sample transect from low to high mean dry mass. Greatest suppression of growth occurred in the Sand Forest soils, with the inhibition gradually decreasing with increasing distance from this biotype. Woodland soil always yielded the highest mean dry biomass.

Results of the trials with soil from the old burnt Sand Forest compared well with those from the woodland trials. It is possible that the inhibiting factor/compound in the old Sand Forest soil had been reduced to approximately the same levels as that found in woodland soil. This may be due to either leaching as a result of greater infiltration of rainwater (these areas were totally denuded of vegetation for about a year) or natural degradation in the soil, or a combination of both.

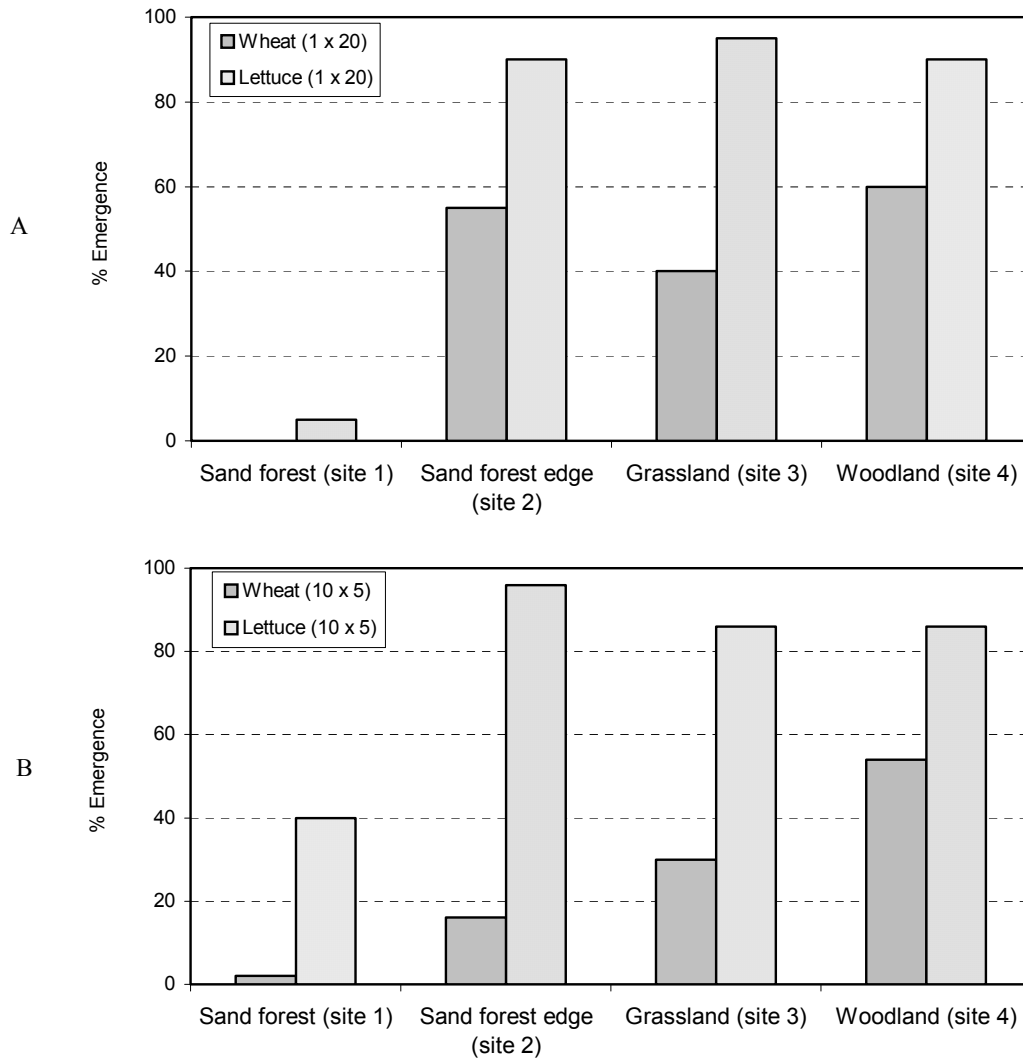


Figure 1 Percentage emergence of wheat and lettuce in soil samples from four different habitats. A: ten seeds per pot; five repetitions per species; watered with rainwater. B: one seed per pot; twenty repetitions per species; watered with rainwater.

The Sand Forest soil leachate trials also showed a distinct gradient. Treatments using Sand Forest leachate throughout the duration of the trial yielded the lowest mean dry mass. These results indicate that the compound/factor that suppresses growth can be mobilised by water moving through the soil, and is thus being leached. Results of the burnt Sand Forest soil trials support this deduction.

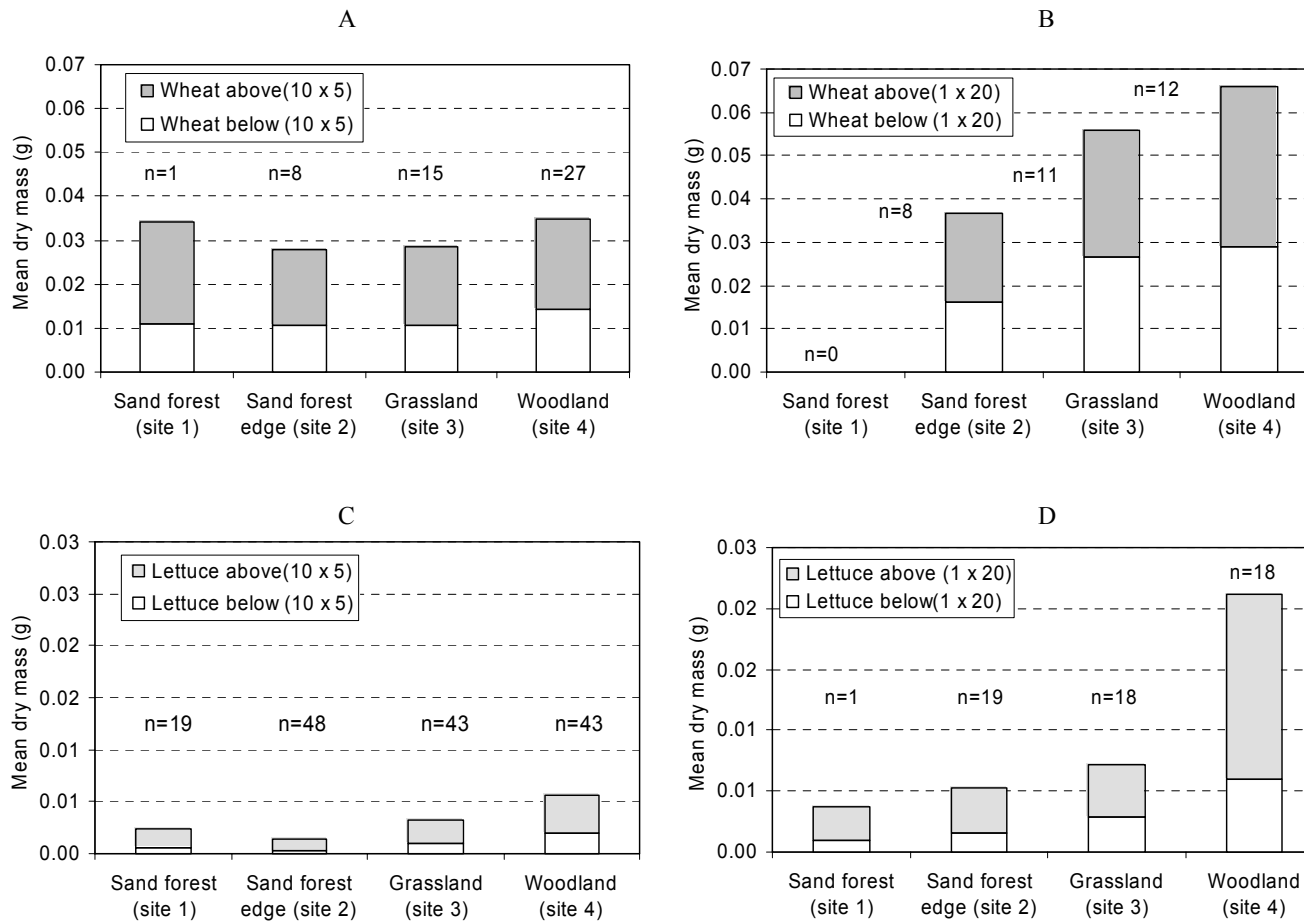


Figure 2 Mean dry mass (g) of the above and below ground parts of wheat and lettuce plants that emerged in soil samples from four different habitats. A&C: ten seeds per pot; five repetitions per species; watered with rainwater. B&D: one seed per pot; 20 repetitions per species; watered with rainwater. Single factor ANOVA analysis of the length measurements of the plant parts per pot (see text) in B indicates significant differences between treatments (Wheat, above: $P=0.05$, P -value 1.47^{-5} ; below: $P=0.05$, P -value 5.63^{-6} . Lettuce, above: $P=0.0$, P -value 4.31^{-28} ; below: $P=0.05$, P -value 1.93^{-13}).

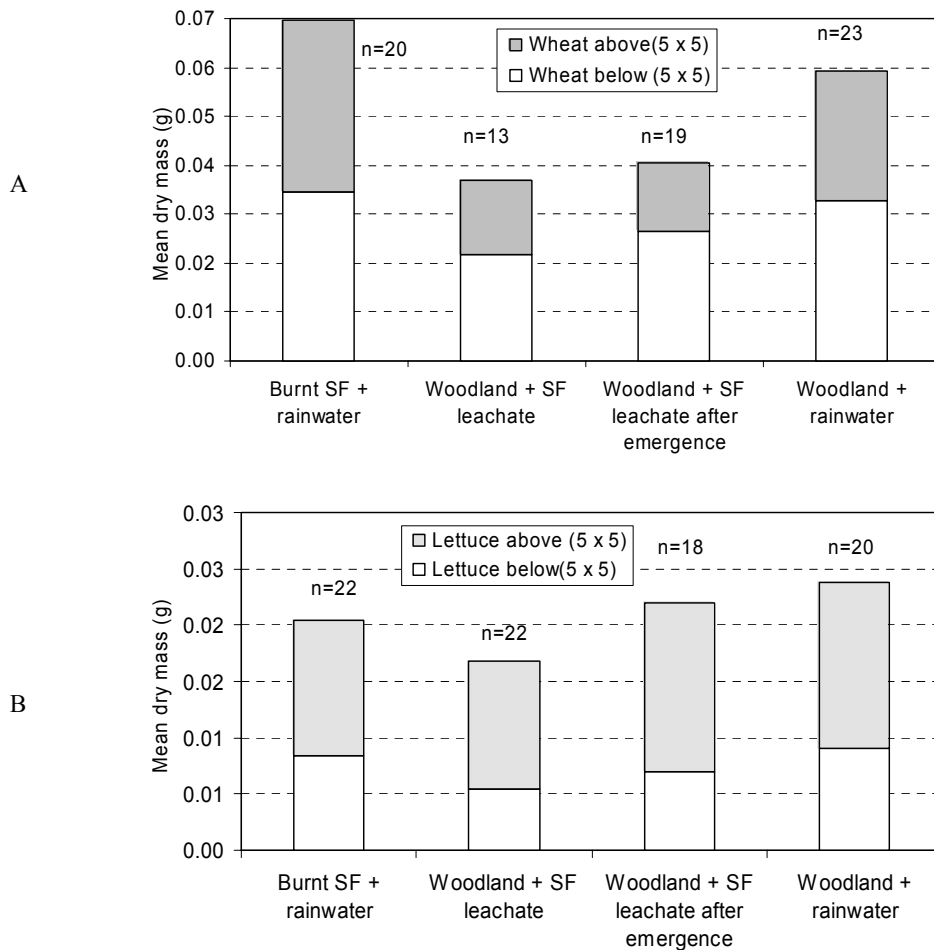


Figure 3 Mean dry mass (g) of the above and below ground parts of wheat (A) and lettuce (B) plants that emerged from soils subjected to different treatments (five seeds per pot; five repetitions per species). Treatments (from left to right): (a) old burned Sand Forest soil, watered with Sand Forest leachate; (b) woodland soil, watered with Sand Forest leachate; (c) woodland soil, watered with rainwater prior to plant emergence, thereafter with Sand Forest leachate; (d) woodland soil, watered with rainwater. Single factor ANOVA analysis of the length measurements of the plant parts per pot (see text) indicates significant differences between treatments (Wheat, above: $P=0.05$, P -value 0.0034; below: $P=0.05$, P -value 0.031. Lettuce, above: $P=0.05$, P -value 0.168; below: $P=0.05$, P -value 0.0088).

In Trial 1, where ten seeds were used per pot, the influence of competition (Weidenhamer Richaedson & Fisher 1989; Thijs Shann & Weidenhamer 1994; Weidenhamer 1996) for resources by the different emerging plants could come to the fore. However, results from this trial were almost identical to those of the other trials, except that the plants were smaller. This may be a possible indication of competition for resources, compounded by the effect of the hypothesised growth-suppressing compound. In this case intraspecific competition is considered to have

complemented the suppression of growth. Water and light were not limiting in this case, with the result that competition may well have involved macro and/or micro-nutrients. The primary objective of an allelopathic species is to eliminate other species (Seigler 1996). This means that allelopathy mainly manifests at the interspecific level, whereas resource competition occurs both at inter- and intraspecific levels.

Soil analyses

Results of the first phase soil study (Table 2) show the dominant oxide in all the samples to be silica, indicating that the coversands in the study area consist mainly of quartz sand. Lesser quantities of aluminium, manganese, calcium, sodium and potassium are indicative of the mineral suite associated with resistates, for instance feldspars. The trace element analyses show that boron, barium, chromium, hafnium, niobium, nickel, lead, rubidium, scandium, titanium, iron, strontium, uranium, vanadium, zinc and zircon are present in noticeable concentrations. The rare earth elements, plus the presence of uranium, zircon and titanium is indicative of a heavy mineral suite similar to that found in the present-day coastal dune cordon along the Maputaland Coast. Typical minerals would include zircon (accounting for the presence of uranium, zirconium and hafnium) and ilmenite (titanium and iron). These minerals are stable oxides and silicates with the result that the metals should not be available for uptake by plants and animals. The high boron concentration evident in all the samples is ascribed to the presence of tourmaline, a boron-containing stable complex silicate mineral. Since the potential for these elements to have toxic effects on plants may be high, it was considered necessary to investigate the bio-availability of some of the elements in a second phase analyses. Boron, molybdenum, calcium, copper, sodium and vanadium in particular were investigated due to their potential positive/negative effects on plant growth.

Inorganic analyses

Inorganic analyses of the soil samples (Table 3) indicate that calcium, copper, molybdenum, sodium and vanadium are present in low concentrations in all the samples. Boron is present in concentrations at approximately the lower detection limit for the instrumentation (0.5 ppm), with the exception of one sub-sample from the Sand Forest where the boron concentration was slightly higher (1.5 ppm). Aluminium values were relatively high, although no marked difference in concentrations can be seen between the different biotypes. Acidity of the distilled water extract as well as the conductivity, however, show marked differences between Sand Forest soils and those from the other three biotypes. Sand Forest soils give rise to a leachate that is more acidic, and contains more dissolved solids. The pH of the Sand Forest edge, grassland and woodland soils

ranged from 5.5–6.4, while that of the Sand Forest itself ranged from 3.8–5.8. The conductivity, a measure of the total amount of dissolved solids in solution, ranged from 15.4–22.6 mS/m in the case of the Sand Forest leachate, while the values for all the other sites ranged from 6.6–12.9 mS/m. From these results it is clear that the Sand Forest leachate contains a compound or compounds that render the soil more acidic. Basic inorganic soil chemistry is, however, essentially similar for soils from all four the sites, as indicated in Table 1.

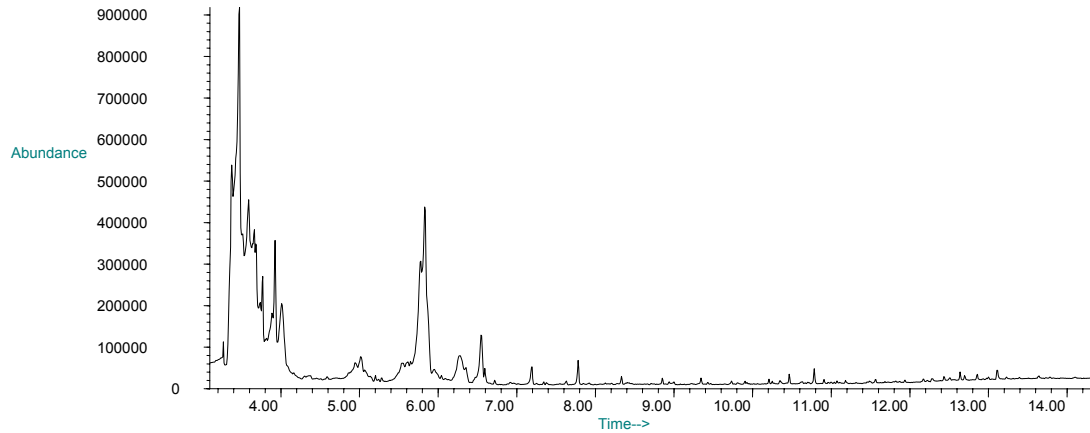
Table 3 Phase two selected inorganic soil analysis of soils from four different biotypes: Sand Forest, Sand Forest edge (border zone), grassland and woodland. In addition to the sample used in the germination trials, two more soil samples for each biotype from different localities (1, 2 & 3) were analysed to gain some understanding of the variation in soil chemistry within the biotypes.

Component (ppm)	Soil sampling site											
	Sand Forest			Sand Forest edge			Grassland			Woodland		
	1	2	3	1	2	3	1	2	3	1	2	3
pH (KCL)	3.8	3.9	5.8	5.7	5.7	5.6	5.5	6	6	6.4	6.3	6.3
Conductivity	15.4	20.2	22.6	5.7	8.2	8	7.4	6.4	5.6	12.9	8.2	8.3
Al	1.18	1.61	0.46	2.01	1.7	1.15	2.42	1	1.97	1.44	0.88	3.29
B	1.5	0.7	0.7	0.5	0.5	0.4	0.5	0.7	0.7	0.6	0.4	0.6
Ca	2	3	23	2	3	3	2	2	2	10	7	8
Cu	0	0.03	0.01	0	0.01	0	0	0	0	0.01	0	0
Mo	0	0	0	0	0	0	0	0	0	0	0	0
Na	6	8	8	6	7	6	7	6	6	6	5	6
V	0	0	0	0	0.01	0.01	0.01	0.01	0.01	0.01	0	0.01

Organic analyses

Methanol leachates produced for analysis were colourless, except for the Sand Forest sample, which had a yellow colour (perhaps indicative of plant phenolics). GC-MS traces of the organic compounds showed compositional differences between the leachates from the different biotypes. The traces for woodland and grassland habitats were virtually identical, both in terms of the compounds present as well as relative abundance. Most of the compounds in the leachates from these biotypes moved very rapidly through the column. In the sample from the edge of the Sand Forest there is a small decrease in the relative abundance of the most prominent compound noted in the first two types, while there are small increases in compounds with slightly retarded rates of movement. The sample from the Sand Forest shows the continuation of the trend, with a major increase in slow-moving compounds and concomitant decrease in fast-moving compounds.

Sample wl



Sample gl

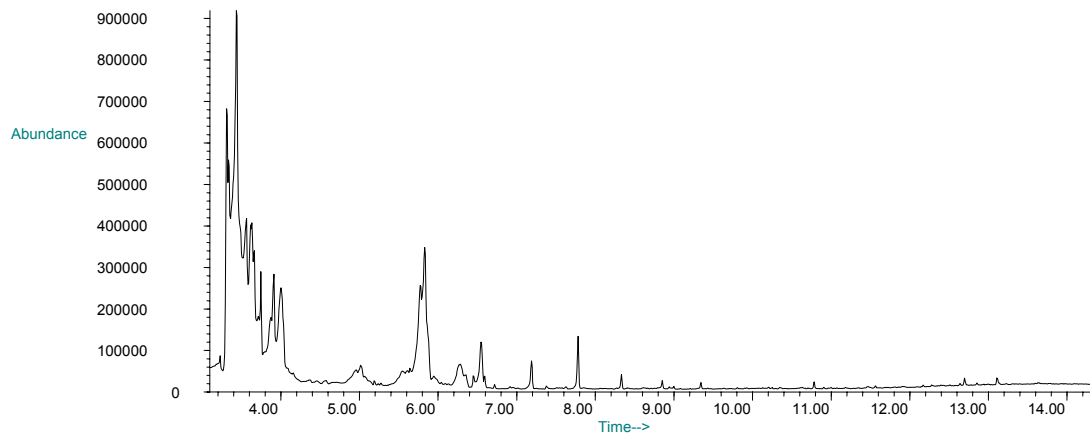
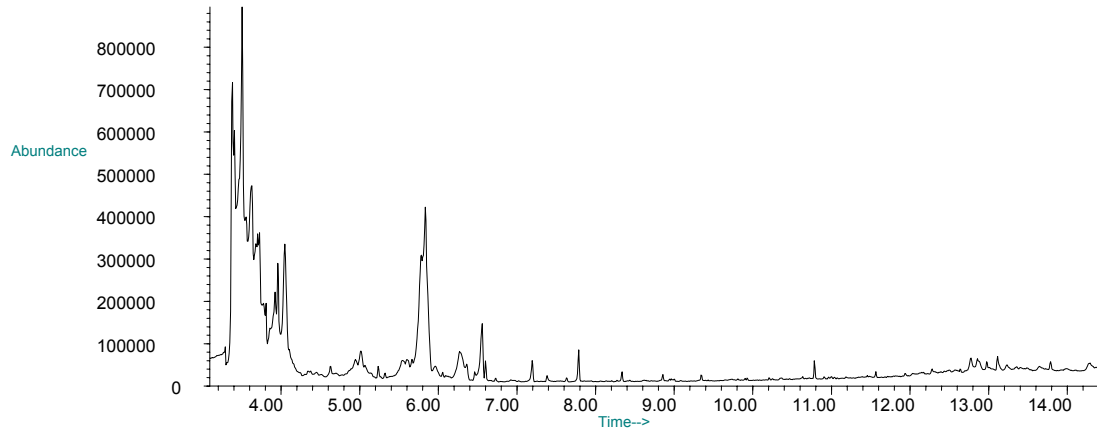


Figure 4 GC-MS traces of organic compounds (methanol leachates) in the four principal soil types used in the germination trials, namely woodland (wl) and grassland (gl). Note increase in slow-moving compounds and concomitant decrease in fast moving ones in soil samples from the Sand Forest edge and Sand Forest.

Sample sfe



Sample sf

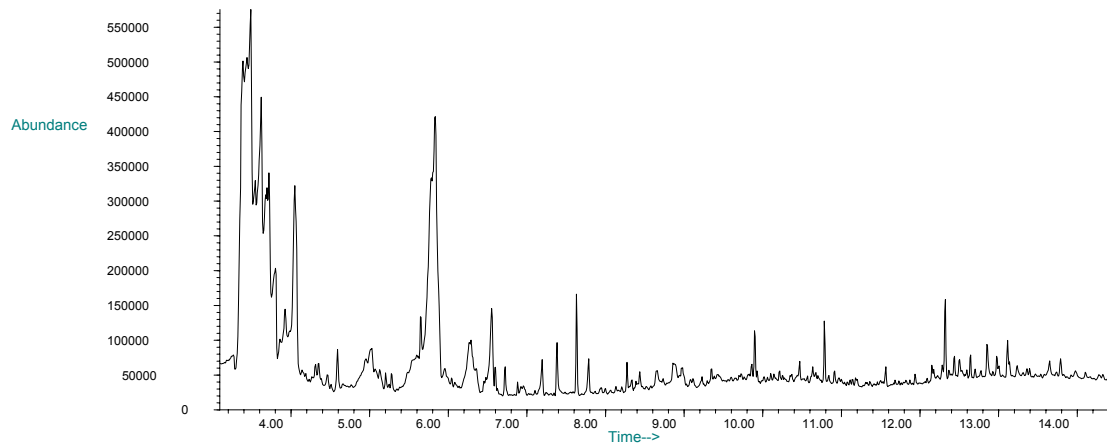


Figure 4 (Continued.) GC-MS traces of organic compounds (methanol leachates) in the four principal soil types used in the germination trials, namely Sand Forest edge (sfe) and Sand Forest (sf). Note increase in slow-moving compounds and concomitant decrease in fast moving ones in soil samples from the Sand Forest edge and Sand Forest.

Potential benefits of allelopathy to Sand Forest

Assuming that the inhibitory effects displayed by Sand Forest soils in the germination trials also operate under natural conditions, what is the potential benefit of allelopathic properties to Sand Forest? Which would be the target species inhibited by the allelochemicals? It is speculated that in the case of Sand Forest the target species are likely to be found among non-Sand Forest specialist, although there may well be Sand Forest species that are also affected. However, as Sand Forest is floristically so distinctive, the bulk of the species of this community, at least in the recruiting phase, must somehow cope with this inhibition. That woodland species are particularly sensitive to the inhibitory compound(s) are perhaps suggested by the nearly total lack of transition of woodland to Sand Forest. Whereas Sand Forest species are to be found in woodland (as isolated outliers), woodland species (again as outliers) are very rarely seen in typical stands of Sand Forest, especially in the drier inland parts of Maputaland. In the wetter more coastal forms of Sand Forest (for example *Artabotrys monteiroae-Dialium schlechteri* Forest (Matthews, Van Wyk & Van Rooyen 1999), some woodland species have been recorded—again very few, but nevertheless more than what is present in the drier Sand Forest patches. This difference could be due to the higher rainfall which would manifest in higher infiltration, leaching and microbial decomposition, thus resulting in more rapid removal of the active inhibitory compounds.

Sand Forest is an unusual forest type in the sense that it is found under relatively low rainfall (average ~600 mm/annum)—conditions not normally associated with major forest development. In the drier inland parts of Maputaland, such as in Tembe Elephant Park, no development of new Sand Forest patches is evident, nor is there any evidence of regeneration following the occasional complete destruction by fire of existing patches. Hence, at least in the latter parts, Sand Forest appears to be a relict vegetation type, having probably evolved in response to aridification over a considerable period of time from perhaps a Coastal Forest type that covered the dune cordons during former wetter climatic conditions. Sand Forest therefore has to directly compete with woodland species and communities well adapted to arid and fire conditions. By evolving allelopathic properties, Sand Forest may well have attained an advantage in a habitat/biozone that it would otherwise not be able to compete in.

Furthermore, Sand Forest is extremely sensitive to fire; it does not regenerate after being burned. Yet, natural woodland and grassland fires are of frequent occurrence throughout Maputaland. The bare or sparsely vegetated zones surrounding Sand Forest undoubtedly also serve as an effective natural fire break. In this regard striking parallelisms seem to exist between the

pattern of Sand Forest distribution in Maputaland and that of Florida Scrub in the United States of America, a dense, fire-sensitive vegetation type that occurs as isolated islands throughout the more common fire-adapted Florida Sandhill vegetation (Williamson, Richardson & Fisher 1992; Fischer *et al.* 1994; Weidenhamer 1996).

Is Sand Forest allelopathic?

For proof of an allelopathic interference, the following criteria, modelled after Koch's postulates in microbiology, should ideally be met (Fuerst & Putnam 1983): (a) identify and quantify specific symptoms of interference; (b) isolate, identify, and synthesize the toxin, characterising its biological activity through bioassays; (c) simulate the interference by providing the toxin as it would be provided in nature; and (d) quantify the amount of toxin released to the environment and taken up by the target plant.

As the present study was exploratory in purpose and approach, these criteria are far from being satisfied. On the other hand, owing to the complexities of allelopathic interactions, apparently no cases of unambiguous proof of allelopathy in the field, according to the criteria proposed above, has yet been reported. However, while conclusive proof of chemical interference may not be attainable, the challenge of obtaining strong supportive evidence for chemical interference remains (Weidenhamer 1996). Our field observations and the results of germination trials and soil analyses strongly suggest that some type of allelopathic interference is taking place in and around Sand Forest. Furthermore, in the case of Sand Forest, we suspect that plant phenolics (reviewed by Inderjit 1996) may well be implicated as allelochemicals.

Acknowledgements

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CHAPTER 7

VEGETATION-ELEPHANT INTERACTION IN TEMBE ELEPHANT PARK

MANUSCRIPT

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The comparative use of woody species in different habitats by elephants in Tembe Elephant Park, Maputaland, northern KwaZulu-Natal

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Abstract

The use of woody species by elephants in different vegetation types in Tembe Elephant Park was investigated using a modified Point-Centred-Quarter sampling design. Samples were located in seven different vegetation types and the intensity of utilization of individuals of different plant species was measured by estimating the proportion of the canopy volume that had been removed by elephants. A classification of species into utilization categories was produced which enabled assessment of the importance of different species to elephants, and also of the potential impact of elephants on different tree species. Ninety of the 137 plant species encountered in the study were utilized. Thirteen species were selected for, 32 were used at random, 35 were avoided and at least 9 were rejected totally. Selection at the plant family level also occurred. Seventy five percent of the diet was made up by seven plant species and 90% by 13 species. Because the staple diet was made up by relatively abundant species, rarer species which are highly preferred may be threatened. Species were utilized with different intensities in different habitats. Those that were selected for in one type were also usually heavily utilized in other types but with different intensities. The number of species that were utilized in any habitat was proportional to the number found in that vegetation type. The results suggest that elephants could have serious negative impact on the diversity of Sand Forest. The need for monitoring and further study in this regard is indicated.

Introduction

Management of elephant populations requires a thorough understanding of their impact on plant populations. The first step in developing this understanding is to establish the intensity of utilisation of individuals of different plant species. To date no data on the use of plants by elephants have been collected for Tembe Elephant Park [TEP]. The studies available on food

selection by elephants in other localities are not helpful in enabling prediction of the use of plants in Tembe Elephant Park as no general principles emerge from these studies. A sampling strategy, that provided relatively comprehensive data quickly and effectively, was used. An adaptation of the Point-Centred-Quarter (PCQ) technique (Cottam & Curtis 1956) that reduced the number of measurements required was used to establish utilization of woody species in different plant communities (vegetation types). These data were used to construct a classification of woody species in terms of their abundance, importance in the elephant diet, and the potential effect of feeding on the demographics of the species. Results are compared to those from other localities. The primary aim of this paper is to detail the vegetation types and species selected for by elephant based on utilization levels and to make predictions about which vegetation communities and woody species are most vulnerable to extirpation and/or transformation, in Tembe Elephant Park.

Study area

Tembe Elephant Park is 30 013 ha in extent and located in Maputaland, northern KwaZulu-Natal (Figure 1). The stratigraphy consists of a multi-layered sequence of aeolian sand deposits of marine origin, which forms north-south trending dune ridges (SACS 1980). Elevation ranges from about 50 m to 129 m above sea level. The soils of the study area developed from the relative homogeneous, grey, siliceous, aeolian sands and are highly leached (dystrophic) and relatively acidic (Watkeys *et al.* 1993). In the depressions between the ridges, duplex soils consisting of a clay layer occurring in depressions in the sands, that in the wet season, form pans. The only permanent surface water in the reserve for most years is the Muzi swamp, in the east of the reserve. This flows north into Mozambique. The region has a warm to hot, humid sub-tropical climate with hot summers and cool to warm winters (Schultze 1982). Temperatures range from 4° C to 45° C with a mean of 23.6° C. Rain is received throughout the year with a summer peak. Total annual rainfall at Sihangwana varies from 245 mm to 2 105 mm with a mean of 716 mm. Average humidity's are relatively high even in the drier inland parts of the region.

For Figure 1; Vegetation map of Tembe Elephant Park showing place names and road network see Chapter 5.

Tembe Elephant Park is located within the Maputaland Centre of Endemism. More than 2 500 plant species occur in the centre, which includes 230 endemics and near-endemic plant species

and/or infraspecific taxa (Van Wyk 1994). Eighty-four Maputaland Centre endemic plant taxa have been recorded for the study area (Matthews *et al.* 2003). According to the revised vegetation map of South Africa, Tembe Elephant Park falls into the *Subhumid Lowveld Bushveld* (Granger 1996) of the Savanna Biome. Moll & White (1978) distinguish four vegetation zones in Tembe Elephant Park i.e. Pallid-sand Bushveld, Sand Forest, the Muzi Swamp and Palmveld. Matthews *et al.* (2004) recognises eight physiognomic units with different species composition (Fig 1). Based on these the following types were differentiated in this study:

1. *Sand Forest*. This type occurs as a forest – grassland mosaic with many small open grassland patches scattered in the forest matrix. Prominent species are *Drypetes arguta*, *Cola greenwayi*, *Uvaria lucida* and large specimens of *Newtonia hildebrandtii*. Sand Forest is rich in plant species with many endemics. (Sand Forest covers about 15% of Tembe Elephant Park).
2. *Thicket on sand*. Prominent species are *Acacia burkei*, *Grewia caffra*, *Zanthoxylum capense* and *Vepris lanceolata*. In places, this habitat can become very dense. (This thicket covers about 10% of Tembe Elephant Park).
3. *Closed Woodland/Thicket on clays*. Prominent species are *Spirostachys africana*, *Coddia rudis*, *Ziziphus mucronata*, *Schotia brachypetala* and the geophyte *Sansevieria hyacinthoides*. This habitat is characterised by large termitaria on which bushclumps occur. (This type covers about 5% of Tembe Elephant Park).
4. *Closed woodland on Sand*. This type is a slightly more open form of Thicket. (This type covers about 10% of Tembe Elephant Park).
5. *Open Woodland*. Prominent species are *Strychnos madagascariensis*, *Albizia adianthifolia*, *Albizia versicolor*, *Acacia burkei*, *Terminalia sericea*, *Combretum molle*, and the grasses *Panicum maximum* and *Andropogon gayanus*. Two forms can be recognised; one in which *Albizia adianthifolia* is abundant (OW/A), and one where it is less abundant (OW). (This type covers about 35% of Tembe Elephant Park: OW - 20%, OW/A - 15%).
6. *Sparse Woodland*. Prominent species are the grasses *Themeda triandra*, *Pogonarthria squarrosa*, *Trachypogon spicatus*. The shrubs and trees are represented by *Strychnos madagascariensis*, *Terminalia sericea* and many geoxylic suffrutices such as *Dichapetalum*

cymosum, *Parinari capensis* subsp. *incohata*. (This type covers about 10% of Tembe Elephant Park)

7. Different *Grassland / Wooded Grassland* types. (This type covers about 10% of Tembe Elephant Park).
8. *Wetlands*. The most important of the wetlands is the Muzi swamp, in the east of the reserve It is covered by reeds through most of its length with only a few places having open water. The other wetlands are perennial pans on duplex soils where depressions have formed and been filled by rainwater. (Wetlands covers about 5% of Tembe Elephant Park).

The area was proclaimed a reserve in 1983 and the south, west and eastern borders were fenced with a game proof and electric fence. In 1989 the northern border with Mozambique was fenced. When Tembe Elephant Park was proclaimed many of the large types of mammal were absent or at very low numbers. Nine types of animal, White Rhinoceros (35), Black Rhinoceros (21), Burchell's Zebra (100), Impala (800), Eland (80), Waterbuck (100), Kudu (unknown), Blue Wildebeest (50) and Giraffe (50) were re-established, and the existing populations of Buffalo (50), Nyala (200), Bushbuck (unknown) Reedbuck (250), Warthog (unknown), was boosted by reintroduction. Numbers in brackets are the population estimates during the study (Matthews 1994).

Elephants have been recorded in the region more or less continuously since 1840 (Harris 1852; Baldwin 1895; Bulpin 1966). No accurate estimate of numbers has been obtained to date because accurate counts are not possible in the Closed Woodlands and Sand Forests. In 1940 around 40 elephants were thought to be resident in the region. Since then the estimate has ranged between 30 and 85. The current estimate is around 155-185 individuals (Matthews 2004). The sex ratio is biased towards bachelor bulls. Ostrosky (1989) estimated a male to female ratio of 1.5: 1.

Local opinion maintains that a more or less stable breeding group has probably been resident in the region of Tembe Elephant Park for a long time. The limits to their home range are thought to have been the Muzi swamps in the south-east and the Rio Maputo floodplains some 28 km to the north-west in Mozambique. This area would have included all of the northern and most of the central sections of the current Tembe Elephant Park area. Crude densities are therefore probably higher than prior to fencing.

Methods

Data Collection

Food selection has been studied in elephants using a wide range of techniques. The direct methods include observation of feeding (Napier-Bax & Sheldrick 1963; Jarman 1971; Guy 1976; Kalermera 1989; Paley & Kerley 1998), gut content analysis (Buss 1961), and faecal analysis (Ward 1982). Indirect methods include counting of the frequencies of use on individuals of different plant species (Coetzee *et al.* 1979) and estimates of the intensity of use on individuals of different plant species sampled in transects and quadrats (Van Wyk & Fairall 1969; Anderson & Walker 1974; Penzhorn *et al.* 1974; Jachmann & Bell 1985; Okula & Sise 1986; Viljoen 1989; Stuart-Hill 1992).

The objectives of this study were to determine the intensity of use of different species in different vegetation / habitat types. A secondary objective (not reported on in this paper) was to determine the spatial distribution of utilisation. Because plotless sampling methods are usually less time consuming than plot-based techniques (Walker 1970), the Point-Centre-Quarter (PCQ) Method (Cottam & Curtis 1956) was selected as an appropriate strategy, but this was modified so that the sample sizes required for accurate estimates of density of each species and the intensity of utilisation could be reduced by reducing the sampling bias towards individuals in the smaller height classes. This was achieved by recording distances to the nearest individual in five different height categories (<0.5 m, 0.5–3 m, >3–5 m, >5–8 m, >8 m) in each quarter.

Sample sites were distributed in a stratified random manner throughout the study area, in the seven vegetation/habitat types (i) Sand Forest, (ii) Thicket on sand, (iii) Thicket on clay, (iv) Closed Woodland on sand. The Open Woodland on sand was subdivided into two strata on the basis of the density of *Albizia adianthifolia* giving (v) Open Woodland with low densities of *A. adianthifolia* and (vi) Open Woodland with high densities of *A. adianthifolia*, and (vii) Sparse Woodland on sand. Sampling sites were more or less equally distributed in the seven vegetation types based on the Tembe Elephant Park road network (a pilot survey revealed no association of utilisation of trees by elephant with the roads). Forty-five sampling sites were consequently distributed at random distances along the road network. At each site, six PCQ points were located along a line that ran at an approximately right angle to the road. Three points were located on each side of the road, with the first suitably away in from the road to ensure that individuals were included in each quarter without having to cross the road. At each point

distances to the nearest individual in the five height categories were measured in each quarter. Five to nine sites were sampled in each vegetation type, giving from 30 to 54 PCQ points at which five sets of distances were measured (five height classes) in each habitat type. This gave a sample of 150 to 270 PCQ points and 600 to 1080 distance measurements in each stratum. The PCQ method usually requires samples larger than 250 PCQ recordings for estimating the densities of species in a particular vegetation type (Heyting 1968). Because both the variation in distance measurements and the variation in relative abundance were decreased by subsampling in the five height categories in different vegetation types, the sample size was considered adequate to obtain the estimates of density required. The number of individuals utilised by elephants at each PCQ point ranged from one to 16 individuals, with a mean of seven. This was considered adequate to obtain estimates of the frequency of utilisation of the different species.

For each individual plant, the species was identified and the height estimated. Canopy reduction by elephant (or other cause) was estimated using Walker's (1976) method for estimating the percentage of the canopy volume removed using eight classes, 0, from 1–10% of the canopy removed, >10–25%, >25–50%, >50–75%, >75–90%, >90–99% and 100%. Where no individual occurred in a particular height category in a particular quarter, a cut-off distance or the next nearest individual in one of the other quarters was used. If no fourth individual could be found nearby, a pseudo-species with a cut-off distance of half the distance between the sample points (10–100 m) was introduced. Sampling was carried out from January to October 1995.

Calculations

Several methods have been used to assess the intensity of use of various plant species by elephant. The simplest index used is the percentage of individual's utilized (Coetzee *et al.* 1979). The proportion of the canopy removed from various species was used by Anderson & Walker (1974). The relative proportion of mouthfuls ingested was used by Guy (1976). Preference indices of various forms that express the proportion that a species makes up in the diet, as a fraction of the proportion that it makes up in the habitat, have been used in several studies on feeding in elephants (Petrides 1975, Guy 1976, Ishwaran 1983, Viljoen 1989). Similarly they have been used in studies on food selection in a wide range of types of animals (Manly *et al.* 1993). The use of preference indices of this form has also been widely criticized by many authors e.g. Lechowicz 1982, Owen-Smith & Cooper 1987, Manly *et al.* 1993 and Schooley 1994. For these reasons three different types of indices were calculated in this study (i) The Forage Ratio, (ii) Manly's Alpha and (iii) Ivlev's Electivity Index (Krebs 1989). The three

different indices produced almost identical results. In only a very few instances where the value of the index lay on the threshold separating neutral use and slight avoidance, the electivity index indicated slight avoidance whilst the other two indicated neutral use.

The purpose of using preference ratios in this study is twofold: (i) to establish which species might be impacted by elephant feeding, (ii) to establish how both the absolute and relative abundance of a particular species in different habitats influenced the degree of selection. An index was therefore required which would allow comparisons between vegetation types.

Direct comparison of the value of Manly's Alpha index in different habitats is cumbersome because the threshold value between preference and avoidance is different for each habitat. The Electivity Index and Forage Ratio are much more easily compared, but the biological meaning of the Electivity Index is not easily interpretable. Manly's Alpha index allows test of significance for differences in preference in the different habitats (Manly 1974). The form of the ratios result in the value of all three indices, but particularly the Forage Ratio being influenced by the relative abundance of the different species. However, relative abundance also influences preference in real terms because a preferred species may be utilized more heavily where there is less interference from other food sources. The fact that there was agreement between the Forage Ratio and Manly's Alpha index suggests that the differences in the absolute value were more likely a consequence of real changes in selection rather than an artifact of the way that the forage ratio is calculated. Because preference is influenced by relative abundance, in environments where the relative abundance is changing, (such as in environments where elephants have been recently confined) the preference shown for different species can also be expected to change. For this reason any classification of trees in terms of their preference in Tembe Elephant Park at this time should be regarded as preliminary.

This logic resulted in our selection of the Forage Ratio as the index used to construct the classification and determine the influence of composition on use, with the following considerations taken into account. In theory, when the proportion that a species makes up in the diet is the same as its relative abundance, the Forage (Preference) Ratio is equal to 1. However, when utilisation rates are low (number of all species utilised / number of all species available < about 0.3), and where diversity is high, and the number of any one species in the sample low, small (about 10%) changes in the proportion of a particular species utilised, result in large changes to the preference ratio (Fig 2). Because of the effort required to obtain adequate samples in diverse vegetation, sample sizes are almost always low (number of any particular species

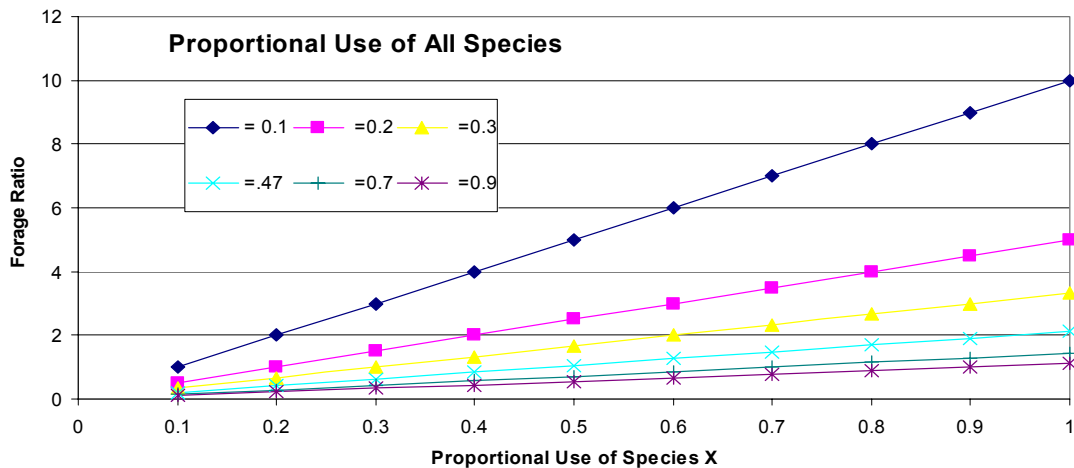


Figure 2. The relationship between the proportion of a particular species utilized and the forage ratio at different proportions of all species utilized.

(species X) available is low), so random, slight changes in the number of utilized individuals in the sample for any particular species result in large changes to the value of the Forage Ratio. The proportion of individuals utilised in this study was 47% (of individuals > 0.5 m height). Fig 2 shows that for the curve where the ratio of the number of all species utilised / the number of all species available is equal to 0.47, a 5% change in the ratio of the number of the particular species (Spp. X) utilised / number of the particular species (Spp X) available, changes the Forage Ratio value by 0.1. In this study the proportions utilized in different habitats varied between 24% and 62%. For the curve where the ratio is 0.24, a 5% change in the ratio results in a change in the Forage Ratio of 0.3 and at 0.62 a change of 0.1. A 10% leeway seems acceptable in deciding on whether the species is selected for or not. This effectively gives 90% confidence intervals. Boundaries for the worst case were used and the following range was applied. Neutral or random use was assumed where the Forage Ratio fell in the range 0.7–1.3, selection where the ratio was greater than 1.3, and rejection in the range $>0 < 0.7$, and total rejection where no use was observed. Samples of less than three individuals, although listed, were treated with caution in the analysis.

To determine the importance of any species to elephant and at the same time establish what impact elephants might have on any particular species, the values for three parameters were used. These are the volume utilized from each species, the degree of selection (preference) shown for different species (assumed to be a reflection of the nutritional status), and the density of each species. If one examines the combinations of selection and density that together result in

a particular intensity of use (in terms of the volumes of material removed) only certain combinations are logically possible. For example, if the volumes removed are categorized as high, moderate, low, or trace, the preference ratios as selected for, neutral use, rejection, and total rejection, and the densities as high, moderate, low, rare, 52 combinations which result in either high, moderate, low or trace volumes removed are possible. However of these only twelve are logical. For example, high volumes removed cannot be obtained from a combination of strong rejection and low densities. Thus species which make up a high proportion of the diet (high volumes removed) may (i) have high to low abundance and be lightly to strongly selected for, or (ii) have high abundance and be used at random (neutral selection). Species, which make up a moderate proportion of the diet may (iii) have low abundance and be selected for, (iv) have moderate abundance and be randomly utilized. Species, which make up a low proportion of the diet may (v) have low to rare abundance and be selected for, (vi) have low densities and be neutrally used, (vii) have low to moderate densities and be rejected. Species, which have trace volumes in the diet, may (viii) be rare and selected for, (ix) be rare and neutrally used, (x) have moderate to low densities and be rejected. Totally rejected species add two further categories, depending on whether they have moderate to high, or low to rare abundance.

The species which are the principle food sources which comprise the elephant's staple diet, and which supports them, come from categories (i) to (v). In terms of the impact on the populations of any particular species, those that are most likely to decline in both relative and absolute abundance are those species that are relatively rare and strongly selected for. Those species which are totally rejected or which have moderate to high abundance and are rejected will increase in relative abundance and are likely to increase in absolute abundance as well if any competitive advantages of the selected for species are removed. Thus species that fall into categories (i) to (vi) and in (viii) are those most likely to decline. Those in categories (vii), (ix), (xi), and (xii) are those most likely to increase in abundance. In evaluating the classification it is important to bear in mind that it is a loose classification, since any particular species may be allocated to a different group in different communities and could be allocated to a different group entirely as relative abundances change over time. The purpose of the classification is to indicate (i) which woody species elephants depend on as their staple diet, and (ii) which species might be threatened in terms of extirpation and therefore of concern to conservation managers at this particular point in time.

Densities were calculated for individuals in each height category separately following the method outlined by Mueller-Dombois & Ellenberg (1974).

Results and discussion

Selection for and intensity of utilisation of different woody species

Overall use

In this study 4 913 individual woody plants were sampled. No utilization was recorded in the <0.5 m height class. Of the 3 773 individuals over 0.5 m in height, 1 766 or 47% were utilised.

Of the 200 tree and shrub species occurring in Tembe Elephant Park (Tembe Herbarium Collection Records) 137 were encountered in this study. Of these 90 (66%) were utilised, and 61 (45%) had more than 10% of the canopy removed.

Douglas-Hamilton (1972) reports 134 out of 650 plant species utilized in Lake Manyara National Park, Uganda (21%); Jachmann & Bell (1985) report 35 out of 41 tree species (85%) used in *Brachystegia* Woodland in Kasungu National Park, Malawi.

The AHC (all habitats combined) column of Table 1 gives the Preference Ratios for each species in all vegetation types combined. It is immediately apparent that some species are utilized much more intensively than others. There are 13 species (10%) that are selected for (17 species {14%} if samples with <3 individuals are included). Thirty-two species (24%) (or 38 {30%} including species with <3 individuals), are neutrally utilized. Thirty five species (28%) are rejected, and nine (7%) (or 35 {28%} including species of <3 individuals) are totally rejected. There are undoubtedly some species amongst the 24 species which have samples of less than three and for which no utilization was recorded which are neutrally used or rejected.

Jachmann & Bell (1985) report 13 out of 35 species (37%) as being selected for and 22 out of 35 (63%) non-selected for. (The proportions in this study for PR values >1 are 34 out of 91 utilized species, which is also 37%).

There are relatively few species that have large volumes removed. Fifty percent of the total canopy volume removed, is made up by three species: *Albizia adianthifolia* (22.25%), *Terminalia sericea* (16.21%) and *Albizia versicolor* (10.83%). The next 25% of the total canopy volume removed, is made up by four species: *Acacia burkei* (8.95%), *Sclerocarya birrea* subsp.

caffra (7.43%), *Dialium schlechteri* (4.97%) and *Strychnos madagascariensis* (3.75%). The next 15 % is made up by six species; *Combretum molle* (3.6%), *Azelia quanzensis* (3.17%), *Acacia robusta* subsp. *clavigera* (2.97%), *Trichilia emetica* (2.36%), *Spirostachys africana* (2.0%), *Hymenocardia ulmoides* (1.45%).

A comparison of Anderson & Walker's (1974) utilisation data measured as the proportion of the canopy volume removed, and Guy's (1976) data measured as the number of mouthfuls ingested, both from the Sengwa Wildlife Research Area, Zimbabwe, indicates that the two indices (Forage (and total canopy volume removed) are related. For those species common to the two studies, mouthfuls = 0.25 * canopy volume; $r^2 = 0.85$. It may therefore be assumed that the volume removed can be used as a measure of the importance of a species in the diet. Thus 90% of the contribution to the diet by trees is made up by 13 species. The other 75 species make up the remaining 10%.

Mohosho (1997) calculated that 10 % of the winter diet was made up by monocotyledons (grass and unidentified monocotyledons). Bowland & Yeaton (1997) in the Natal Lion Park, South Africa, recorded an average 45% of the diet consisted of grass. This amount however ranged between 12% and 74% depending on the season, with the highest amount used in autumn and the lowest in late winter. The summer utilization of grasses in Tembe Elephant Park is slightly higher than the winter values (Mohosho 1997), so it is likely that the proportion of the diet made up by monocotyledons over the year is higher, probably around 15–20%.

De Boer *et al.* (2000), working in the Maputo Elephant Reserve (MER) some 70 km NE of Tembe Elephant Park recorded 31.1% of the diet is made up by grass and unidentified monocotyledons. The Maputo Elephant Reserve has much more open grassland than Tembe Elephant Park, so the proportion is probably a lot less in Tembe Elephant Park. From this can be seen that the Tembe Elephant Park and Maputo Elephant Reserve elephant diet is bias towards dicotyledons.

Trends in which a few species make up the bulk of the diet have been reported from other areas. In Murchison Falls National Park, Buss (1961) reports that, $\pm 90\%$ of the diet is made up by grass. The data Table 1, presented by Buss (1961) shows that three species make up 72% of the contribution to the diet by woody plants. The next four woody species contribute 7%. From Guy's (1976) data a rough estimate of the percentage contribution can be calculated, which yields about a 50% contribution by three species, an additional 14% by the next four woody species,

and the next ten species add a further 18%. Paley & Kerley's (1998) data show that grass and forbs made up 45% of the winter diet of elephants in Addo. Of the trees (succulents and shrubs) six species made up 53% of the diet. Of the woody species encountered in Bowland & Yeaton's (1997) study in the Natal Lion Park, five woody species made up 75% of the diet and 19 species made up 90%.

In the study by De Boer *et al.* (2000) in the Maputo Elephant Reserve, five species only make up 25% of the diet of woody plants. Ten species make up 46% of the diet, 20 species make up 68%, and 30 species 83% of the diet. The biases inherent in determining dietary composition from faecal analysis are thought to account for this disparity.

The only study on food selection in elephants where species composition is sufficiently similar to make comparisons with Tembe Elephant Park is the study by De Boer *et al.* (2000). There was a 15% overlap in the species recorded for this study and that by De Boer *et al.* (2000), [23 species in common]. Of the 17 preferred species in this study, two (*Sclerocarya birrea* and *Terminalia sericea*) were recorded as preferred in Maputo Elephant Reserve. Of the remaining species in common, which are preferred in Tembe Elephant Park, three (*Afzelia quanzensis*, *Albizia adianthifolia*, *Euphorbia tirrucalli*) are used at random, and four (*Albizia versicolor*, *Phyllanthus reticulatus*, *Strychnos madagascariensis*, *Syzygium cordatum*) are rejected in Maputo Elephant Reserve. Of the species that are neutrally used in Tembe Elephant Park, four (*Acacia karroo*, *Balanites maughamii*, *Commiphora neglecta*, *Dialium schlechteri*) are also used at random in Maputo Elephant Reserve. One (*Ziziphus mucronata*) is preferred in Maputo Elephant Reserve and two (*Acacia burkei*, *Mimusops caffra*) avoided. Of the species avoided in Tembe Elephant Park, three (*Phyllanthus reticulatus*, *Xylothea kraussiana*, *Zanthoxylum capense*) were also avoided in Maputo Elephant Reserve, four (*Dichrostachys cinerea*, *Euclea natalensis*, *Grewia caffra*, *Vangueria infausta*) were neutrally used. None that were avoided in Tembe Elephant Park were preferred in Maputo Elephant Reserve. Similarly none of the species preferred in Maputo Elephant Reserve were rejected in Tembe Elephant Park.

Selection appears to occur at the family level as well as the species level. Based on selectivity indices calculated as the proportion of individuals in a family that are utilized, as a ratio of the proportion of individuals in a family available, of the 40 families recorded, ten are selected for, eight neutrally used, nineteen rejected, and three totally rejected. The families Anacardiaceae (1.7; 3/4; where the figures are the Preference Ratio, the Number of Species Used in the Family / Number of Species in the Family recorded in TEP), Combretaceae (1.7; 4/5), Mimosaceae (1.4;

8/11), Myrtaceae (1.8; 1/2), Meliaceae (2.4; 2/3), Bignoniaceae (2.8; 1/1), Clusiaceae (1.6; 1/1), Lythraceae (1.9; 1/1), and Vitaceae (2.8; 1/1) are selected for (Tables 2 and 3). The Euphorbiaceae (0.8; 14/19), Caesalpiniaceae (1.1; 3/5), Loganiaceae (1.0; 3/4), Rhamnaceae (1.2; 2/2), Sapotaceae (1.1; 3/4), Balanitaceae (0.7; 1/1), Capparaceae (1.1; 1/2) and Meastomataceae (0.9; 1/1), are neutrally selected for. The Annonaceae (0.2; 3/3), Asteraceae (0.2; 1/2), Ebenaceae (0.2; 2/5), Rutaceae (0.2; 4/6), Malvaceae (0; 1/1), Rhizophoraceae (0; 1/1), are moderately to strongly ejected. The Ochnaceae (0; 0/3), Sapindaceae (0; 0/3) and Verbenaceae (0; 0/3) are totally rejected.

Within and between habitat differences in species use

In each of the habitats some species are selected for (7–32 species; 10–38% of the species present, excluding those less than 0.5m in height), some neutrally used (5–17 species; 6–26% of the species present), some rejected (1–11 species; 3–17% of the species present), and some are not used at all (13–38 species; 37–49% of the species present) (Tables 1 & 2).

Of the list of the forage species (those that were utilized in any vegetation type), a relatively small proportion of the individuals of any particular species (between 25% and 67%, excluding samples with less than three individuals) were utilized in a particular vegetation type. In general, the more species in the vegetation type, the more species were used (a linear regression of number of species utilized (y) against number of species in the vegetation type (x) yields $y = 0.617x - 2.451$; $r^2 = 0.93$). The proportion of species utilized in the different vegetation types, distinguished for this study, however, appears to be relatively constant, with mostly just over a half the available species being utilized, (with a range between 50% and 65%), and around a third being relatively well utilized (>10% canopy volume removed). Thus Sand Forest has the most species used followed by Thicket on clay, Closed Woodland, Open Woodland (with high *Albizia adianthifolia* densities), Thicket on sand, Open Woodland and Sparse Woodland. About two thirds of the plant families present in any one vegetation type were utilized, again with the number of families utilized being higher where the number of families was higher, and lower in the types with fewer Families. Sand Forest and Thicket have the greatest number of families utilized, followed by Open Woodland, Open Woodland (with high *Albizia adianthifolia* densities), Thicket, Closed Woodland and Sparse Woodland (Table 2).

Unlike the number of species utilised the volume removed from each vegetation type is not related to any of the number of species, the number of species utilised or the density in the

vegetation type (Table 2). Rather it is related to the abundance of large preferred trees which are used in proportion to their abundance or which are selected for. Thus those vegetation types with high abundance of species from Utilisation Classes (i)–(vi) and (viii), are most heavily utilised in terms of the volumes removed. Open Woodland (with high *Albizia adianthifolia* densities) and Open Woodland are most heavily utilised. Thicket on Clay, Thicket and Closed Woodland are utilised with moderate intensity, and Sand Forest and Sparse Woodland, least intensively (Tables 2 and 3). The only comparable data from the literature appears to be Anderson & Walker's (1974) statement that in the Sengwa Wildlife Research Area, Zimbabwe, those types with the highest abundance of favoured species were most heavily utilised. The implication of this for the management of elephants is that the staple diet species (Utilization classes (i), (ii) and (iii)) comes from these habitats. Much of the diversity of interest to conservation occurs in a single vegetation type such as Sand Forest. The rare selected for species in Utilization classes (viii) play no part in influencing the survival or fecundity of elephants, and are therefore likely to be impacted on negatively

There are 32 species selected for ($PR > 1.3$) in Sand Forest, 15 in Thicket on sand, 22 in Thicket on Clay, 20 in Closed Woodland, 11 in Open Woodland, seven in Open Woodland (with high *Albizia adianthifolia* densities), and ten in Sparse Woodland (Table 1). The numbers of species selected for in any one habitat, as with the total number of species utilized, follows the trend in numbers of species present in each habitat type ($y = 0.37x - 6.1$; $r^2 = 0.5$, where y is the number of species selected for in the habitat type and x is the number present).

It is apparent in Table 1 (preference indices) that many of the forage species are selected for with more or less equal intensity in each of the vegetation types, whilst some species are selected for more intensively, and others less intensively in a particular vegetation type compared to others. In general where a species is strongly selected for, it is selected for in all types, though with varying intensities, which range from neutral use to strong selection. These species all occur in Utilization classes (ii), (iii), (v) – *Albizia adianthifolia*, *Albizia versicolor*, *Sclerocarya birrea*, *Terminalia sericea*, *Acacia robusta*, *Azelia quanzensis*, *Trichilia emetica*, *Galpinia transvaalica*, *Garcinia livingstonei*, *Antidesma venosum*, *Manilkara discolor* and *Syzygium cordatum*. Again in general the preference ratio is higher in those types where the relative abundance of the species is lower; indicating that if a species is preferred it is actively sought after even when a large number of other species may be present. The relationship is however not apparent for all species, as some species show a wide variation in use in the different vegetation types, with the species being selected for in some types and rejected in others. These species

come from a wide range of Utilization classes and include *Acacia burkei*, *Balanites maughamii*, *Psyrdrax locuples* and *Dichrostachys cinerea*. Many of the rare species that occur in only one habitat type are moderately to strongly selected for. These include all of the species from Utilization class (viii) and *Newtonia hildebrandtii* and *Wrightia natalensis* in Sand Forest. A large proportion of the species which occur only in Thicket on Clay or in Thicket on Clay and only one or two other habitat types are selected for. These include *Manilkara discolor*, *Boscia foetida*, *Euclea divinorum*, *Cordia caffra*, *Elaeodendron transvaalensis*, *Euphorbia tirucalli*. On the other hand many of the species confined to Sand Forest are not, examples are *Manilkara discolor*, *Erythrophleum lasianthum*, *Cleistanthus schlechteri*, *Drypetes arguta*, *Tricalysia delagoense*. This suggests that perhaps the better nutritional status of clays soils may be a factor influencing selection. Only three widely dispersed species are rejected entirely. These are all from Utilization class (xi).

It has been relatively well established that species composition influences selection so it would be surprising if different habitats were not in fact utilized with different intensities. However the wide variation in the degree of selection for forage species in the different habitats suggests that there is no single factor that explains the differences in the intensity of use for many of the species discussed above. Rather different combinations of factors may be important in different situations.

Conclusions

1. The bulk of the elephants diet is made up by species which are relatively common, and which are strongly, moderately, lightly or neutrally selected for i.e. those belong to Utilisation Classes (i)–(iv). These are *Acacia burkei*, *Acacia robusta*, *Azelia quanzensis*, *Albizia adianthifolia*, *Albizia versicolor*, *Combretum molle*, *Dialium schlechteri*, *Sclerocarya birrea*, *Strychnos madagascariensis*, *Terminalia sericea* and *Trichilia emetica*.
2. It appears that the suite of species, including both relatively common and rare species, that are strongly selected for are being utilised to the extent that they may be reduced to very low levels, or possibly local extinction. The threat to each of these species depends on the demographic responses of each one to environmental conditions, including utilisation by elephants. These species which include those from Utilisation Classes (i), (iii), (v), and (viii) are *Acacia robusta*, *Azelia quanzensis*, *Albizia adianthifolia*, *Albizia versicolor*, *Antidesma venosum*, *Elaeodendron transvaalensis*, *Euphorbia tirucalli*, *Ficus stuhlmannii*, *Galpinia*

transvaalica, *Garcinia livingstonei*, *Hyperacanthus microphyllus*, *Kigelia africana*, *Manilkara discolor*, *Newtonia hildebrandtii*, *Phyllanthus reticulatus*, *Syzygium cordatum*, *Sclerocarya birrea*, *Terminalia sericea*, *Tricalysia junodii*, *Trichilia emetica*, *Warneckea sousae* and *Wrightia natalensis*.

3. More species are utilised in diverse habitats than in less diverse habitats. The proportion selected appears to be more or less constant at around 60% of the species available.
4. Those species most highly selected for are used in all habitats in which they occur, but the degree of selection (the relative preference) is different in the different habitats, and appears to be influenced, for example, by the relative abundance of other forage species.
5. Several species which are Maputaland Centre endemics with a limited distribution, and which have very little conservation status outside of Tembe Elephant Park may be threatened by elephant impact. These are *Combretum mkuzense*, *Dialium schlechteri*, *Hyperacanthus microphyllus*, *Warneckea sousae*, *Tricalysia junodii* var. *junodii* and *Wrightia natalensis*.
6. Because utilization is influenced by relative abundance, the classification presented here should be expected to change. For this reason only potential impact of elephants on any particular species can be predicted from this single survey. The accurate prediction required for the successful management of biodiversity requires that all of the factors influencing demographics be established first and thereafter monitored continuously.

Although the elephants prefer plant species from woodland habitats, evidence suggest that they are increasingly utilising Sand Forest species. Sand Forest is a unique vegetation type of limited distribution and contains many Maputaland Centre endemics species. Currently indications are that Sand Forest integrity may be threatened as a vegetation type within Tembe Elephant Park, as a result of elephant forage patterns. This is as a result of general thinning of intact forest, as well as extirpation of plant species which are a) highly selected for, b) recruits infrequently and usually in small numbers and c) species that grow slowly so that adults are not easily recruited.

Management implications: concluding remarks

The primary reasons for the proclamation of TEP was the protection of the natural elephant population of Maputaland AND the protection of Sand Forest (TEP has the greatest area of

protected Sand Forest in South Africa). This has led to a conflict of interests between Sand Forest and elephant.

Issues that need to be considered in the management around Sand Forest and elephant within TEP are:

- Expand the range of the elephant (increase surface of protected area) so as to reduce time spent in the Sand Forest zones.
- Reduce return rates of elephant to the Sand Forest areas in the western portion of the Park where most of the Sand Forest in the Park is to be found, this could potentially be done through water point management.
- Reduce direct foraging impacts on Sand Forest, which are thinning the forest as well as removing Sand Forest recruitment possibilities. Elephant and other wildlife numbers should be curtailed within TEP, especially if the range expansion possibilities cannot be achieved in the near future.
- Elephant exclusion areas, electric fencing of Sand Forest such as in done in Phinda Game Reserve.

As a rapid survey technique the approach taken in the present study appears to have worked well. Useful information on the relative use of different species and the likelihood of negative impact on their abundance from elephant feeding activity has been provided.

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Table 1.

Table showing the preference index for each species in each habitat type. The species are grouped (thick dashed line) in terms of the volume utilized and the volume available, and then in terms of selection in all habitats combined (see text). Abbreviations are: SF – Sand Forest, Th – Thicket, ThC – Thicket on Clay, CW – Closed Woodland, OW- Open Woodland, OWA – Open Woodland with high *A. adianthifolia* densities, SW – Sparse Woodland

AHC – All Habitats Combined, VPD – Volume removed/Preference/Density, CLS – Utilization Class. For the volumes removed H – High, M – Moderate, L – Low, T – Trace.

For the Preferences S – Selected (>1.3), N – Neutral Use (0.7-1.3), R – Rejected (>0 <0.7).

For the Densities Available H – High Densities, M – Moderate, L – Low, R – Rare.

* indicates samples of less than 3 individuals. # indicates those species where the All Habitats Combined data result in a classification which is different to that for most of the separate habitats.

The figures surrounded by a light dotted line indicate where the utilisation of a particular species in a particular habitat type differs substantially from the intensity of use in other habitats types.

Species	SF	Th	ThC	CW	OW	OWA	SW	AHC	VPD	CLS
<i>Albizia adianthifolia</i>	4.2	2.5*	2.4*	2*	2.1	1.5		2.1	HSL	i
<i>Albizia versicolor</i>		2.5*	2	2	1.9	1.5	1.7	1.9	HSL	i
<i>Sclerocarya birrea sub. caffra</i>	2.4	1.9	2	1.8	1.9	1.2	1.5	1.8	HSM	i
<i>Terminalia sericea</i>	4.2*	2.1	1.5	1.6	1.6	1.2	1.4	1.6	HSH	i
<hr/>										
<i>Acacia burkei</i>	1.4	1.4	1	0.9	0.6	0.7	0.7	0.8	HNH	ii
<hr/>										
<i>Acacia robusta sub. clavigera</i>	2.8	2.5*	2.1	2		0.8		1.7	MSL	iii
<i>Azelia quanzensis</i>	1.4	1.9	1.9	0.9	1.8	1.3	2*	1.4	MSL [#]	iii
<i>Trichilia emetica</i>	4.2*		1.2*	1.4	2.1		2*	2	MSL	iii
<hr/>										
<i>Combretum molle</i>	0*	1.3	1.7	1.1	1	1	1.2	1.2	MNM	iv
<i>Dialium schlechteri</i>	1.7	1.3	1.6	0.5	0.9	1	0	0.9	MNM	iv
<i>Strychnos madagascariensis</i>	2.1*	2.1	1.4	1.3	0.9	1.1	1.2	1.3	MNH [#]	iv
<hr/>										
<i>Galpinia transvaalica</i>	4.2*		2.4*					2.1	LSL	v
<i>Garcinia livingstonei</i>			2.4*	2	1.3	1	2*	1.5	LSL	v
<i>Antidesma venosum</i>			0.8	1.2	1.8	1.3		1.6	LSL	v
<i>Manilkara discolor</i>	1.8		2.4*					1	LSL*	v
<i>Newtonia hildebrandtii</i>	2.6							1.3	LSL	v
<i>Wrightia natalensis</i>	1.4							0.7	LSL	v
<i>Ficus stuhlmannii</i>					2.1*			2	LSR	v
<i>Syzygium cordatum</i>			0.8	1.2	1.8	1.6*	2*	1.4	LSR	v
<hr/>										
<i>Erythrophleum lasianthum</i>	0.7					1.6		0.9	LNL	vi
<i>Sapium integerrimum</i>	2.1*	0*		1.1	0.9	0.9		1.1	LNL	vi
<i>Ziziphus mucronata</i>		0*	1.3	2*	0.7	0.7	0*	0.9	LNL	vi
<i>Balanites maughanii</i>	0	2	0*	0*	2.1*	0.5		0.7	LNL	vi
<i>Commiphora neglecta</i>	0*	1.4	1.8	0	1.1*			0.8	LNM [#]	vi
<i>Psyrax fragrantissima</i>	1.7							0.9	LNM	vi
<i>Pteleopsis myrtifolia</i>	2.4	0.8				0*		1.1	LNM [#]	vi
<i>Spirostachys africana</i>	2.8	1.7	0.9	0.8	1.2	0.3	0.7	0.9	LNM [#]	vi
<i>Strychnos spinosa</i>	2.1*	1.2	0.5	0.6	0.9	0.8	1	0.9	LNM [#]	vi
<i>Cordia caffra</i>			2.4*	0*				1.1	LNR	vi
<hr/>										
<i>Cleistanthus schlechteri v. schlechteri</i>	0.3					1.1		0.6	LRL	vii
<i>Acacia senegal v. rostrata</i>			0.7					0.6	LRM	vii
<i>Psyrax locuples</i>	2.8	0.7	0.2	1.8	1.1*	0.8		0.8	LRM [#]	vii

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<i>Tabernaemontana elegans</i>	0.8	0.5	0	1.5	0.6	0.5		0.7	LRM [#]	vii
<i>Dichrostachys cinerea</i>	2.8	1.5	0.3	2	0.6	0.6	0	0.5	LRM [#]	vii
<i>Euclea natalensis</i>	0	0.6	0.5	0	0.1	0	0*	0.2	LRM	vii
<i>Hymenocardia ulmoides</i>	1	1				0.2	0	0.5	LRM	vii
<i>Vepris lanceolata</i>	0.7	0.3	0	0.7		0*		0.3	LRM	vii
<i>Drypetes arguta</i>	0.3	0						0.1	LRH	vii

<i>Hyperacanthus microphyllus</i>		2.5*						2	TSL*	viii
<i>Warneckea sousae</i>	1.4*							0.7	TSL*	viii
<i>Tricalysia junodii</i> var. <i>junodii</i>	2.1*							1.1	TSL*	viii
<i>Elaeodendron transvaalensis</i>			2.4*					2.1	TSR*	viii
<i>Euphorbia tirucalli</i>			2*					2.1	TSR*	viii
<i>Kigelia africana</i>				2*	2.1*			2.1	TSR*	viii
<i>Phyllanthus reticulatus</i>				2*				2.1	TSR*	viii

<i>Boscia foetida</i> sub. <i>rehmanniana</i>		1	2.4*					1.1	TNL*	ix
<i>Canthium setiflorum</i> sub. <i>setiflorum</i>		0*		1			0*	0.7	TNL*	ix
<i>Euclea divinorum</i>		0.8	1.6					1.1	TNL [#]	ix
<i>Mimusops caffra</i>	2.4			0				0.7	TNL [#]	ix
<i>Rothmannia fisheri</i> sub. <i>moramballae</i>	1.4							0.7	TNL	ix
<i>Sideroxylon inerme</i>			1					0.9	TNL	ix
<i>Tricalysia delagoensis</i>	0*			2*				1.1	TNL*	ix
<i>Drypetes natalensis</i>	1.7							0.9	TNL	ix
<i>Bridelia cathartica</i>	1.4	0*	0.8	0.9	0.9	0.5		0.8	TNM	ix
<i>Lagynias lasiantha</i>	1.4							0.7	TNM	ix
<i>Rhus guezinzi</i>	2.8	0*	0.6	1.5	0.8	0		0.8	TNM [#]	ix
<i>Acacia nilotica</i> sub. <i>kraussiana</i>	0*		0.9	1*		1.6		1.2	TNR	ix
<i>Berchemia zeyheri</i>			1.2*					1.1	TNR	ix
<i>Combretum mkuzense</i>						1		1.3	TNR	ix
<i>Ekebergia capensis</i>			2.4*	0*				1.1	TNR*	ix
<i>Schotia brachypetala</i>			1.2*	2*		0*		1.1	TNR	ix

<i>Canthium inerme</i>	0		0*	2	0*			0.7	TRL [#]	x
<i>Monodora junodii</i>	0	2.5*						0.4	TRL	x
<i>Acalypha glabrata</i>	2.1*	0*						0.5	TRL	x
<i>Acridocarpus natalitius</i> v. <i>linearifolius</i>	0*				0	0.5		0.3	TRL	x
<i>Ancylanthos monteiroi</i>		0			1.1*			0.4	TRL	x
<i>Dovyalis longispina</i>	0*		0*	1*				0.5	TRL	x
<i>Erythroxylum delagoense</i>	2.1*			0	0*	1.6*		0.6	TRL	x
<i>Grewia microthyrsa</i>		0	2.4*		0.5	0		0.5	TRL	x
<i>Margaritaria discoidea</i>		0*		1*	0*			0.4	TRL	x
<i>Maytenus senegalensis</i>		2.5*	0	0*	0.5	0*		0.3	TRL	x
<i>Ozoroa engleri</i>				0*	0.2	0.3	0	0.2	TRL	x
<i>Pavetta catophylla</i>		0*	1.2*			0*		0.4	TRL	x
<i>Phoenix reclinata</i>	0*		0.4	2*				0.5	TRL	x
<i>Ptaeroxylum obliquum</i>	0	0*	0.6	2*		0*		0.3	TRL	x
<i>Vangueria esculenta</i>	0*		0*		0	0*	2*	0.4	TRL	x
<i>Xylothea kraussiana</i>	0*	0*	0*	2*		0*		0.3	TRL	x
<i>Zanthoxylum capense</i>	0*	1.7	2.4*	0.7	0	0*		0.6	TRL	x
<i>Acacia borleae</i>			0					0	TRL	x
<i>Grewia caffra</i>	2.1	0.5	0*		0*	0		0.4	TRM [#]	x
<i>Hyphaene coriacea</i>	0.6		0	0.5	0	1.6	0.7	0.3	TRM [#]	x
<i>Salacia leptoclada</i>	0.4							0.2	TRM	x
<i>Strychnos decussata</i>	1.4	0.5	0.8		0*			0.5	TRM [#]	x
<i>Teclea gerrardii</i>	0.4	0	0*	0		0		0.1	TRM	x
<i>Todallipsia bremekampii</i>	0.6							0.3	TRM	x
<i>Tricalysia capensis</i>	0	1	1.2*	0*		0*		0.5	TRM	x
<i>Vangueria infausta</i> sub. <i>infausta</i>	0*	0.6	1.9	1	0.4	0.2	0.5	0.5	TRM [#]	x
<i>Catunaregam spinosa</i> sub. <i>spinosa</i>	1.2	0	0*	0.3	0	0	0	0.2	TRH [#]	x

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<i>Cola greenwayi</i>	0.3	0*						0.1	TRH [#]	x
<i>Brachylaena huillensis</i>	0.4	0.4	0*	0	0	0.5	0	0.1	TRH [#]	x
<i>Croton pseudopulchellus</i>	0.4	0*	0*					0.2	TRH [#]	x
<hr/>										
<i>Clausena anisata</i>	0*	0*	0*	0	0	0		0	CM	xi
<i>Coddia rudis</i>	0*	0	0	0*	0*	0*		0	CM	xi
<i>Plectroniella armata</i>	0*		0	0		0*		0	CM	xi
<hr/>										
<i>Coffea racemosa</i>			0*					0	CL*	xii
<i>Diospyros inhacaensis</i>	0*			0*				0	CL*	xii
<i>Ehretia rigida</i>		0*	0*					0	CL*	xii
<i>Euphorbia ingens</i>		0	0*	0*	0*	0*		0	CL	xii
<i>Gardenia volkensii</i>			0*				0	0	CL*	xii
<i>Haplocoelum gallense</i>	0	0*						0	CL*	xii
<i>Hyperacanthus amoenus</i>	0							0	CL*	xii
<i>Mundulia sericea</i>				0	0	0	0*	0	CL	xii
<i>Ochna arborea var. arborea</i>	0*	0*						0	CL*	xii
<i>Ochna barbosae</i>	0*					0*		0	CL	xii
<i>Ochna natalitia</i>		0*	0	0*	0*	0		0	CL	xii
<i>Oxyanthus latifolius</i>	0*							0	CL*	xii
<i>Strychnos henningsii</i>	0				0*			0	CL	xii
<i>Suregada zanzibariensis</i>	0*							0	CL*	xii
<i>Tarennia junodii</i>	0*							0	CL*	xii
<i>Vitex amboniensis</i>	0				0*	0*		0	CL	xii
<i>Acacia karroo</i>			0*					0	CR*	xii
<i>Albizia forbesii</i>		0						0	CR*	xii
<i>Casearia gladiiformis</i>				0*				0	CR*	xii
<i>Cassipourea mossambicensis</i>	0*							0	CR*	xii
<i>Combretum celastroides sub. orientale</i>	0*							0	CR*	xii
<i>Erythroxylum emarginatum</i>			0*					0	CR*	xii
<i>Euclea schimperi</i>						0*		0	CR*	xii
<i>Eugenia natalitia</i>		0*						0	CR*	xii
<i>Euphorbia grandidens</i>				0*				0	CR*	xii
<i>Lannea antiscorbutica</i>	0*							0	CR*	xii
<i>Manilkara concolor</i>				0*				0	CR*	xii
<i>Maytenus undata</i>				0*		0*		0	CR*	xii
<i>Premna mooiensis</i>						0*		0	CR*	xii
<i>Pseudobersama mossambicensis</i>	0*							0	CR*	xii
<i>Thespesia acutiloba</i>			0*					0	CR*	xii

Table 2. Numbers and ratios of species and families in the sample and the proportions utilized. Ht = height; Util. = Utilized.

Vegetation Type	Sand Forest	Thicket on sand	Thicket on clay	Closed woodland	Open Woodland	Open Woodland (<i>Albizia</i>)	Sparse Woodland
Number of Species in Sample	86	64	79	71	61	71	35
Number of Species in Sample >0.5 Ht	84	61	71	67	54	66	30
Number of Species Utilised	47	34	46	40	33	35	15
Number of Species Utilised Index >1	27	22	30	21	25	26	11
Percent of Species Utilised	54.7	53.1	58.2	56.3	54.1	49.3	42.9
Percent Species Utilised Index >1	31.4	34.4	38.0	29.6	41.0	36.6	31.4
Percent Species > 0.5 Ht. Utilised	56.0	55.7	64.8	59.7	61.1	53.0	50.0
Number Families	31	27	31	29	30	29	20
Number Families Utilised	20	18	23	18	20	18	11
Percent of Families Utilised	64.5	66.7	74.2	62.1	66.7	62.1	55.0
Densities	4726.4	2325.6	1012.6	1392.5	396.1	451.1	461.3
Volumes Utilised	5501	8095	8477	7231	18786	37347	3012

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CHAPTER 8

SAND FOREST: CHARACTERISTICS, ECOLOGY AND HYPOTHESES ON ORIGIN

8.1 Introduction

The earth is not a static place—it has always been characterized by change and it will always be so. Change is one of the most important realities in a plant community, especially on an ecological time scale. In interpreting vegetation change, a diverse set of factors is often operative (Niering 1987). Long-term vegetation changes operate at a rate which is comparable to a managers working life and on a large spatial scale which makes them difficult to observe, measure or comprehend. Consequently, slow processes are poorly understood (Stafford Smith & Pickup 1993). Traditional succession/climax concepts can often hinder rather than aid in sound vegetation management. Community development (Odum 1997) over the short to medium term (1000 years or less) is widely known as ecological succession (the ecological time scale)—an active process involving changes in both the organisms and physical environment. Changes over geological time scales (millions of years) fall under the heading of organic evolution.

Forests are difficult systems to study because the demographics that govern their long-term behaviours occur on disparate spatial and temporal scales, from square meters and weeks for germination and seedling establishment, to hectares and millennia for mortality events. Also many different processes control the structure of forest plant communities. From a variety of observations it is clear that the species richness, species composition and species dominance of plant communities are greatly affected by the availability of limiting resources (Brokaw 1985).

The modern view of forests is of a dynamic system of ever-changing mature, gap and building phases, and gap-phase species replacement/regeneration (Lawes *et al.* 2004). Thus, ‘gap dynamics’ has been a pervasive theme of the study of forests. An added complication is that gaps need not be canopy gaps. When a tree falls in the forest, the canopy hole or ‘light gap’ it creates sets in motion a chain of events known as ‘gap dynamics (gap-phase regeneration)’ which culminates in the replacement of the previous canopy tree by a new one (Hubbell & Foster 1986a). Canopy gap fill in with regrowth from three sources: seed, plants established prior to gap formation, and lateral in-growth of branches from trees on the gap periphery. In large gaps, pioneers and late secondary species, germinate from seed arriving before and after gap formation, grow rapidly and overtop the slower-growing established juveniles of primary species which survived the tree fall (Hartshorn 1978). Gap disturbances provide the principal or only means by which most forest tree species can

maintain their representation in closed canopy forests. Such seemingly simple events such as tree replacement and gap-phase regeneration are actually complex processes that are still poorly understood. Biology, chance, and history all play a role in the replacement process (Hubbell & Foster 1986b).

Three basic gap-phase regeneration guilds can be distinguished based on life history, namely mature forest trees, early pioneers and late secondary species (Hartshorn 1978; Brokaw 1985). a) Primary tree species germinate in the shade or in both sun and shade, and can persist as suppressed juveniles for some time until a gap opens. b) Early pioneers species have a different strategy for waiting for gaps to open; they frequently persist for long periods as dormant seeds in the soil. These seeds require specific gap disturbances cues to germinate. c) Late secondary species are typically shade intolerant, sun loving plants with growth (life history) similar to early pioneer species, however they often grow to much larger sizes and persist for longer periods in the canopy.

The ‘grain’ of a forest type can be categorized based on its spatial scale of forest dynamics (Everard *et al.* 1994, 1995). The spatial scale of regeneration of a species, fine grained species regenerate over a small scale (area) and seedlings and saplings of a species are found beneath or close to mature individuals, course grained species regenerate over a large area and seedlings and saplings are often rare and seldom found beneath mature individuals.

The ecology, floristics and distribution of Sand Forest in the landscape are influenced by a complex combination of biotic and abiotic factors. These would include the evolutionary history of plant species, their biology, adaptive flexibility and dispersal potential, the geology, geomorphology, soil properties, climate and its changes, and finally interaction with other plant species and animals (including man), presently and in the past (Van Wyk & Smith 2001). Under each of these, a complex of interactions and relationships exist, for example the establishment and growth of vegetation at a point in the landscape occur in response to the availability of seed (propagules) and three main resources: water, nutrients and energy (solar radiation). These resources can vary as follows: Seed may be available from local sources, or by redistribution from elsewhere, and their survival may be affected by climatic conditions and predation. Water availability depends on the soil texture, balance between infiltration and storage in the soil, and evapotranspiration. Water may be supplied directly from rainfall, but that supply can be greatly reduced or increased by the redistribution process of run-on and run-off. Nutrient availability depends on the balance between the rates of turnover in relation to the total amount of nutrients stored in the soil and vegetation, and the competitive use of these resources by other plants.

Nutrients can also be redistributed across the landscape by wind, water or animals. Solar radiation input is largely pre-determined by latitude, but it can vary locally with topographic factors such as slope, aspect, and shading.

The aim of this chapter is to consider the functioning and development, albeit largely hypothetical, of Sand Forest by taking as many of the above-mentioned biophysical factors into consideration so as to formulate some ideas on the origin and definition of Sand Forest as a community. The first part of the chapter will define Sand Forest diagnostic characters based on current information. Differences between the Afromontane, Dune Forest and Sand Forest will also be included as a means of highlighting differences. Dune Forest is important as it relates to the second part of the chapter, in which hypotheses will be proposed on Sand Forest development in which Dune Forest occupies a key position.

8.2 Sand Forest characteristics

8.2.1 What is Sand Forest?

A community is a collection of species populations that occur in the same area at the same time. The definitions are, however, different for zoologists and botanists. The largest component of an ecosystem is the plant growth and is known as the plant community. A plant community is a combination of plants that are dependent on their environment and influence one another and modify their own environment (Mueller-Dombois & Ellenberg 1974). Put simply a plant community is an assemblage of different plant species within a specific habitat and with a specific physiognomy and structure that forms an organised ecological unit in a specific area. The “climax” is a buffered and stable community, with high resilience and strong resistance to change, so it can withstand a disturbance. The climax is heterogeneous and not fixed but can change according to prevailing environmental conditions (Krebs 1985). The climax stage is self-sustainable and in equilibrium with the physical and biotic environment. Climate varies on a geological as well as an ecological time scale (~1 000 years or less) and it is therefore difficult to grasp that equilibrium can be achieved. Therefore climax is an abstract concept and the term “steady-state” (Park 1970) has been suggested to replace the term “climax communities”. Sand Forest will be characterize in light of the above explanations and definitions.

White (1983) associated southern Africa forests with 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 South Africa). Sand Forest is classified under the Tongaland-Pondoland Regional Mosaic. Sand Forest (Licuáti Forest) is also an unique inland feature of Maputaland and has been variously referred to as:- Licuáti forest (Myre 1964); Tongaland Sand Forest, Msinga bush (Moll 1968); Sand forest (Moll 1978; Moll & White 1978; Moll 1980; Taylor 1980; Ward 1981; Brooks *et al.* 1982; Cooper 1985; Felton 1999; Smith 2001; Matthews *et al.* 2003; Van Rooyen 2003); *Artabotrys monteiroae-Dialium schlechteri* Forest (Matthews *et al.* 1999); Sand Thicket and Forest (Smith 2001); Eastern Sand Forest, Western Sand Forest (Kirkwood & Midgley 1999); and Licuati Sand Forest (Mucina & Geldenhuys 2004). White's (1983) mapping was not at a scale fine enough to separate the "Sand Forests" of northern KwaZulu-Natal from other Tongaland-Pondoland forest types.

The first description of Sand Forest, under the name Licuáti Forest, was by Myre (1964). He described it from southern Mozambique as dense forest of low to average height (~5-12m). Characteristic woody species are *Balanites maughamii*, *Dialium schlechteri*, *Newtonia hildebrandtii*, *Azelia quanzensis* and *Pteleopsis myrtifolia*. Moll (1978) also describes the forest patches as very dense with numerous woody, subcanopy shrub and small tree species, with relatively few herbs. The forest patches being quite distinct. Moll (1978) lists *Balanites maughamii*, *Cleistanthus schlechteri*, *Cola greenwayi*, *Dialium schlechteri*, *Erythrophleum lasianthum*, *Hymenocardia ulmoides*, *Newtonia hildebrandtii* and *Ptaeroxylon obliquum* as the common and widespread tree species of the Sand Forest.

From phytosociological and other vegetation studies (Lubbe 1996; Kirkwood & Midgley 1999; Matthews *et al.* 1999, 2003) carried out in northern Maputaland, the following species are considered characteristic of Sand Forest: *Balanites maughamii*, *Cola greenwayi*, *Croton pseudopulchellus*, *Dialium schlechteri*, *Drypetes arguta*, *Hymenocardia ulmoides*, *Hyperacanthus microphyllus*, *Monodora junodii*, *Ochna barbosa*, *Ptaeroxylon obliquum*, *Pteleopsis myrtifolia*, *Strychnos henningsii*, *Todallioopsis bremekampii*, *Uvaria lucida* and the sedge *Cyperus albostrigatus*. Some species are distinctive to Sand Forest while being not that constant in their presence. Examples include *Newtonia hildebrandtii*, *Croton steenkampianus*, *Cleistanthus schlechteri*, *Erythrophleum lasianthum* and *Combretum celastroides*. All the preceding species can be referred to as "floristic elements" of Sand Forest.

Sand Forest are dense with a lack of forbs and small shrubs in the understory, and has distinct boundaries. Canopies in this forest type can be low (approximately 5m) to high (approximately

15m). Sand Forest has a conspicuous complement of semi-deciduous to deciduous species, a feature unique for southern African forests. Sand Forest is associated with sandy soils, which in many cases are old dunes systems. Moisture levels in these sandy soils are lower than that of the neighbouring grassland and woodlands (Unpublished neutron probe data). Rainfall in areas with Sand Forest varies from 600 to 800 mm per annum and the occurrence of mist is not uncommon. Leaf attributes are generally fairly similar to all forests, for example, Sand Forest leaves are generally evergreen (although many species in Sand Forest tend to be drought-deciduous), mesophyllous; lacking in spines; with entire margins; and non-compound (Midgley *et al.* 1995).

Moll & White (1978) considered many typical Sand Forest species (e.g. *Balanites maughamii*, *Cleistanthus schlechteri* and *Newtonia hildebrandtii*) to be Zanzibar-Inhambane linking species (the Zanzibar-Inhambane Region is the coastal phytochorion extending from southern Mozambique to East Africa). This phytochorion, together with the Tongaland-Pondoland Region, form White's (1983) Indian Ocean Belt. There are also some outlier areas where plant species which can be referred to as Sand Forest floristic elements can be found outside typical Sand Forest. Other types of dry forest under fairly similar environmental conditions as in Sand Forest, include the sandveld communities of the Pafuri area, Kruger National Park (Van Rooyen *et al.* 1981) and in the Gonarezhou National Park, Zimbabwe (P. Goodman pers. comm.).

Midgley *et al.* (1997) recognised two major forest complexes: Afromontane types associated with temperate environments, and Indian Ocean types associated with subtropical climates. The Indian Ocean forest types include Sand Forest and Dune Forests.

8.2.1.1 Distribution

Sand Forest is limited to the drier inland areas in northern KwaZulu-Natal and southern Mozambique (Maputaland). The currently known distribution of Sand Forest is from False Bay in the Greater St Lucia Wetland Park to Maputo Bay. From work done by Tinley (1971) in southern Mozambique, he referred to semi-deciduous forest with characteristic species as listed for Sand Forest, although in the northern areas (north of Maputo Bay) he noted a slight floristic change. He mapped the distribution of this dry forest type as a narrow zone up to Quissico (± 100 km south of Inhambane) Mozambique. Thus this forest type is confined to a narrow zone on the coastal plains of northern KwaZulu-Natal and southern Mozambique, from approximately False Bay up to Quissico. A narrow zone covering the approximately distance of 500 km makes this quite a limited area for this forest, especially in South Africa (zone of approximately 150 km). Cooper (1985)

estimated the total area covered by Sand Forest in South Africa at approximately 5 986 ha. Woody species similar to those that occur in Sand Forest do occur in forests north of Maputo Bay, but the species composition of these forests is different (Tinley 1971), and they are therefore not classified as Sand Forest. The increasing narrowness of the Mozambique plain to its southern end acts as a biotic filter to plant and animal dispersion and distribution.

Unlike Afromontane Forest, both Dune Forest and Sand Forest are tropical/subtropical vegetation types. Dune Forest is a relatively widespread vegetation type found along the east coast of Africa on recent (young) sand dunes. Sand Forest occurs only in Maputaland (between False Bay and Maputo Bay), and is hemmed in by the Lebombo Mountains to the west, Maputo Bay in the north, the temperate climatic conditions to the south, and the Indian Ocean to the east.

In Maputaland, where both Dune and Sand Forest occur, Dune Forest tends to inhabit the wetter habitats and younger sand dunes closer to the ocean, while Sand Forest inhabit the drier plains and ancient sand dunes further inland. Dune and Sand Forest mosaics can occur in places where Sand Forest is located closer to the coastline. At the southern most point of distribution, namely False Bay, Sand Forest and Dune Forest both occur, and seem to intermingle in places. To distinguish between the two forest types one has to look at the floristic composition. It is worth noting that one does find a few Dune Forest species in some of the driest of the Sand Forest communities, e.g. *Mimusops caffra* (form), *Acacia kraussiana* and *Isoglossa woodii*. In these dry Sand Forest communities the growth form and vegetative characteristics of the tree *Mimusops caffra* are atypical of what is to be seen in the coastal Dune Forest—perhaps an incipient species?

Afromontane Forest is a temperate vegetation type found mainly on high mountain plateaus and in protected kloofs and gullies throughout most of sub-Saharan Africa. It is mostly associated with Afromontane grassland, but in the Cape Floristic Region it is associated with Fynbos.

8.2.1.2 Species richness and endemism

Species diversity, or species richness, is a community attribute that reflects the combined influence of such processes as immigration, speciation, competition, predation and extinction (Glenn-Lewin *et al.* 1992). A frequently reported pattern has been for diversity to peak in late succession after most of the climax species have entered, and then to decrease as successional species are lost (Glenn-Lewin *et al.* 1992) but many conflicting observations have also been

made. Part of the explanation can be that change in diversity during succession depends on the environmental contribution, where more than one factor is involved. The creation of a general model of successional change in diversity is much more difficult and perhaps impossible (Glenn-Lewin 1977, 1980; Whittaker 1977).

In Sand Forest the β -diversity (the turnover of species between the different forest patches) is very high for both dominant and rare species (Van Rensburg *et al.* 2000). Therefore conserving one patch of Sand Forest will not nearly conserve all of the genetic complement of Sand Forest. Dune Forest shows a low β -diversity. The α -diversity of Sand Forest is rather similar to that of the southern African Afromontane forests (Geldenhuys 1992; Mucina & Geldenhuys 2004). Floristic richness (α -diversity) and β -diversity are probably relatively low in Afromontane forest. The southern African Afromontane plant species are noticeably very wide-ranging, with relatively very little local and regional endemism (Geldenhuys 1992). Patches of Afromontane forests throughout Africa tend to have very similar species compositions (White 1978). This perhaps explains the ability of Afromontane forest to return (re-establish itself) after destruction in the relatively short period of approximately 50–200 years, if it is adequately protected from further destruction. Also during the last glacial period, many areas that are today forest were denuded of forest. Thus in approximately 10 000 years, forest has been able to re-establish on these denuded areas (Moore *et al.* 1996).

Sand Forest does not have many fern and moss species, and those few species present, are able to withstand severe desiccation. Many epiphytes that occur in Sand Forest are lichen-like, and can withstand repeated desiccation, while the epiphytic orchids are often xerophytic with, for example, bulb-like basal thickenings. There is no well-developed herbaceous or ground layer in Sand Forest. Contrary to what Kirkwood & Midgley (1996) has claimed, the absence or shortage of a conspicuous ground layer and the lower understory in Sand Forest is not due to herbivory, but could rather be ascribed to aridity compounded by allelopathic characteristics. In contrast, Afromontane Forests with its relatively high rainfall regime, and with soil moisture further supplemented by the capturing of mist, supports a rich herbaceous layer with a relatively large and diverse fern and moss flora (Mucina & Geldenhuys 2004). Epiphytes and orchids are also of frequent occurrence. Macro-fungi, associated with the thick organic layer covering the soil in Afromontane Forest, and the higher rainfall and soil moisture content, are very prolific in these forests. In comparison to Sand Forest, Dune Forest also has a relatively large diversity of ferns and mosses and a well-developed herbaceous layer (Mucina & Geldenhuys 2004).

Southern African Forests at a local and regional scale show low levels of tree endemism (White 1983; Midgley *et al.* 1997; Matthews *et al.* 2003). Similarly for the southern African forests, few tree species are rare (MacDevette *et al.* 1989), and uncommon species are generally those in ecosystems such as Sand Forests that just penetrate southern Africa from the northeast, as in the Maputaland Centre of Plant Endemism (Van Wyk 1994). Sand Forest is a rare habitat (Van Wyk 1994), which is rich in woody species (Moll & White 1978). The species composition of Sand Forest is unique and includes several rare and Maputaland Centre endemic species (Van Wyk 1994). A significant number of endemic species, which may be plants and animals, are associated with Sand Forest, and Van Wyk (1994) and Van Wyk & Smith (2001) consider this perhaps the most remarkable plant community in the Maputaland Centre. Matthews *et al.* (2003) found that of the 225 endemic plant species recorded for Maputaland (including Lebombo Mountain endemics), 33 are found in Sand Forest with 20 largely restricted to this vegetation type. This makes this one of the communities with the highest restricted plant endemic species in Maputaland. Van Rensburg (1998) also found that certain bird species were closely associated with Sand Forest and of these species, three are endemic to the Maputaland Centre. Knowing that the distribution of Sand Forest in adjacent Mozambique covers larger areas than in KwaZulu-Natal, genuine rarity of trees must still be confirmed.

8.2.1.3 Forest structure and deciduousness

Afromontane Forest is by far the tallest of the three forest types, with trees up to 50 m in height. Dune Forest is shorter than Afromontane forest, but can be higher than Sand Forest. In Sand Forest individual specimens may reach heights of 20 m, which in most cases are old individuals of *Newtonia hildebrandtii*.

Two physiognomic or structural types of Sand Forest occur (Matthews *et al.* 2003). One fits the basic physiognomic definition of forest, while the other can be better described as a thicket (short 5–6 m high dense vegetation). These structural differences are also reflected in the floristics of the two types. Thus, what is usually described as Sand Forest actually comprises (includes) two vegetation types, namely Tall Sand Forest and Short Sand Forest (thicket), which differ in terms of both floristic and structural attributes (Matthews *et al.* 2003). As the single name ‘Sand Forest’ cannot be used at two different levels of classification, it is proposed that the term ‘Licuáti’ (the original name used by Myre 1964) be used in the future to refer to all types of Sand Forest, with ‘Tall Licuáti Forest’ or ‘Tall Sand Forest’ and ‘Licuáti Thicket’ or ‘Sand Thicket’ the two components (Izidine 2004).

Most plant species in the three main southern Africa forest types are evergreen, although some deciduous species do occur in each type of forest, with Sand Forest having the largest proportion of deciduous species. Some of the dominant species in Sand Forest are sometimes semi-deciduous, resulting in the forest appearing deciduous at times, although this is for a very short period, e.g. a month or two (Matthews, unpublished phenological data). Species playing a role here are *Combretum celastroides*, *Pteleopsis myrtifolia*, *Croton steenkampianus* and *Dialium schlechteri*. Many Sand Forest trees sometimes, drop their leaves and become dormant when it is very dry. So-called, drought-deciduous trees furthermore exacerbate this effect of deciduousness e.g. *Hymenocardia ulmoides*. Drought-deciduousness is much better developed in Sand Forest than in either Dune or Afromontane forest. The proportion of deciduous species increases where the mean annual precipitation is lower (Meadows 1985). It is mainly the presence of drought-deciduous species that has led to Sand Forest being referred to as deciduous vegetation.

In comparison with associated woodland matrix (Matthews *et al.* 2003), species of the Sand Forest are definitely the more evergreen of the two vegetation types. In winter, the woodland communities become more open, while Sand Forest remains closed and green. This suggests that Sand Forest is closer to being evergreen than totally deciduous.

Wood decomposition tends to be much slower in Sand Forest than in either of the other two forest types (Afromontane and Dune Forest). The abundance of such long-lasting hardwood in Sand Forest is probably conducive to the high insect diversity found there. It may also increase the risk of fire penetrating the forests resulting in relatively hot fires. The soils of the woodlands surrounding Sand Forest are indistinguishable from that underlying Sand Forest itself.

8.2.1.4 Dispersal and fruit types

Establishment from seed is a two-step process: dispersal and germination. Effectiveness of seed dispersal is dependent on five main factors: seed production, vector of seed transport, timing of seed release or removal and fate of dispersed seeds (Glenn-Lewin *et al.* 1992). Experimental or observational studies of dispersal are concerned usually with primary dispersal, the movement of seed from the parent plant to the ground. These studies reveal that the bulk of the seed of most plant species are deposited only a short distance from the parent plant (Levin & Kerster 1974). Seed that are dispersed by birds, however, may be carried quite far, with few seed deposited near parent plants (Murray 1988). Variability in seed dispersal is enormous and is influenced by

vegetation structure and density, wind patterns, and presences of animals including bird communities and bird behaviour.

Seed germination is also a complex physiological process that, as a result of natural selection, has been modified in a variety of ways to ensure that seeds germinate when there is a high probability of seedling survival. Soil conditions also play a major role, e.g. soil moisture, light levels, temperature fluctuations, and chemicals released by plants and plant litter that can inhibit germination (Glenn-Lewin *et al.* 1992).

Life history properties of secondary plant species in tropical lowland forest include a short life cycle, high growth rate, high reproductive resource allocation, continuous and early seed production, small seed size, long seed viability and chemical protection against herbivory (Whitmore 1990) [Compare Table 2.].

There is a large bias towards edible fruit and animal dispersed propagules in all three forest types. Wind seems to become more important as a dispersal agent in coastal regions. Midgley (1993) states that Sand Forest is dominated by species with wind-dispersed seeds, whereas other Indian Ocean forests types (Midgley *et al.* 1997) are dominated by fleshy-fruited species. However, Matthews *et al.* 2003 and unpublished data by Matthews, found that plant species with fleshy fruits were the most common within Sand Forest, even when considering cover-abundance. In Sand Forest, for example, 74 out of 103 investigated taxa (70%) had fleshy fruit. Genuine wind-dispersed seeds, not just fruits with wings that in most cases would come to rest nearby parent plants (e.g. *Combretum* spp. with their winged fruits), were quite rare. The same can be said for the MC endemic plant species in Sand Forest, only two out of the thirty-three endemic species recorded had winged fruit and these were both species of the genus *Combretum*.

8.2.1.5 Rooting

Deep tap root systems have generally been associated with deep sands and arid conditions, as, for example, in the case of the species *Acacia erioloba* found on Kalahari sands. Timberlake (1980) recorded roots at a depth of 46 m. This is not the case, however, in Sand Forest, where the root systems are very shallow, with most of the roots occurring in the upper 1–1.8 m of the soil, and no records of deep tap root systems (Matthews pers. obs.). The trees in the woodlands surrounding Sand Forest also have fairly shallow root systems, as do the trees of the Dune Forest

(Matthews pers. obs.). Afromontane forest trees have deeper root systems, with the roots growing where the resources are.

8.2.1.6 Fauna

Faunal species richness and diversity is more-or-less similar in all three forest types. However, based on current knowledge, faunal species composition seems to differ. Sand Forest, for example, is rich in insect species such as butterflies and in bird species, while the mammal component is rather low (in diversity and numbers). However, the high β -diversity in the flora of Sand Forest seems to be reflected in the fauna. There seems to be no peak in any particular animal-group in Afromontane Forest and in Dune Forest. The unique faunal elements in all three of the forests are more tropical related.

Maputaland as a region has one of the highest butterfly diversities in South Africa (E. Pringle pers. comm.). Twenty five percent of the about 852 species of butterflies that occur in South Africa may be found in northern Maputaland. This is probably due to the large variety of habitats and abundance of larval food plant taxa, varying from high canopy Sand Forests to low-lying coastal areas, palmveld grasslands, as well as the area being the transition zone between tropical and more temperate regions, and thus has representatives of both.

8.2.1.7 Environment

Climate influences soil properties, nutrient recycling and vegetation growth in numerous ways but these effects are dominated in arid regions by the availability of soil water. From a biological perspective, rainfall records may be treated as events and sequences of events. An event is one or more closely spaced rainfall incidents (or soil moisture impulses), which are large enough to produce a significant vegetation response. The sequences consist of a run of events (and periods with or without rainfall) of sufficient length and magnitude that short term changes in the biological system are progressively reinforced until a new state is reached (Stafford Smith & Pickup 1993).

Rainfall and moisture

Sand Forest occurs under relatively drier conditions compared to other forest types (less than 700 mm of rain per year) and is thus classified by National Forest Classification as tropical dry forest (Von Maltitz *et al.* 2002), and where it does occur in areas of higher rainfall (greater than 700

mm), it retreats to the higher sand dunes where the sands are well-drained. This implies that if the habitat of Sand Forest stays wetter for longer (in terms of soil moisture content) than present, Sand Forest could cease to exist in those areas.

Relatively high air humidity levels can prevail in the areas where Sand Forest occurs, especially in summer. Sand Forest does experience mist, and it would seem to retain and possibly add to the soil moisture content. The high frequencies of epiphytes in Sand Forest would infer that they also benefit substantially from the mist. Marker & Russel (1984) have stated that the presence of mixed forest in low rainfall areas of the Eastern Cape can partly be ascribed to the fog and water holding capacity of deep sand to sustain forest growth. Sand Forest in Maputaland is also found on deep sand, and with the occurrence of heavy dews and low-level mist that are not uncommon, especially in winter, this could help maintain the water content of the soils. Sand Forest (specifically on the high lying areas) does appear to experience more mist than its associated vegetation type, woodland. This implies that mist may play a role in the survival and/or persistence of Sand Forest in the midst of the woodland dominated landscape. The reason may be that the mist, which is mostly of winter-occurrence, together with low soil moisture levels, may keep the transpiration rate down. In other words, mist would play the same role in winter that high air humidity plays in summer.

Dune Forest along the coast receives 1000 mm or more rain per annum (highest rainfall in the Maputaland region), and the ground water added to the soil moisture in these forests leads, in some instances, to the formation of swamp forests such as those in the Sihadla drainage of the Kosi Bay system. Being low-lying and coastal, Dune Forest experience very humid conditions and strong winds, with the seaward side being affected by salt spray. Little wind is experienced inside Dune Forest, and when wind does occur, its effect would be in the top canopy. Dune Forest is regularly exposed to salt and sand laden wind which can be very strong at times.

Temperature

Both Dune and Sand Forest lie in tropical/subtropical areas, but while Dune Forest (being part of a coastal system) experiences equitable/even temperatures throughout the year, the environment in Sand Forest can be relatively cool in winter and very hot in summer.

Afromontane Forest experiences temperate conditions in summer and temperate to cool conditions in winter. The occurrence of frost varies greatly, with some lower lying forests not experiencing any frost, while frost can be a nightly occurrence in winter in some high-altitude

localities (White 1983). Rainfall is generally 1000 mm and more per annum in Afromontane forests. Exceptions do occur, however, such as in parts of the Soutpansberg and Lebombo Mountains (Hlatikulu [Gwalaweni] Forest) where the rainfall is lower. Some Soutpansberg Forests exist, at present, also in a state of ‘suspended animation’ like Sand Forest, relying for survival on supplementation of the rain by the capturing of mist. By “suspended animation” is meant the maintenance of the existing state (vegetation community) till circumstances change to more favourable for normal dynamics or functioning to return. Unlike the situation in most Afromontane Forests, conditions in parts of the Soutpansberg are currently too dry to allow the Afromontane forests to actively establish or expand into new habitats. Many Afromontane Forests supplements their soil moisture by the capturing of mist, which is aided by the presence of mild and moisture-laden winds that improves conditions for the condensation of mist droplets. Most Afromontane Forest occurs in areas with relatively low humidity to times of high humidity (Mucina & Geldenhuys 2004).

Table 1. Approximate mean annual rainfall limits and approximate mean annual maximum, minimum temperatures and mean relative air humidity levels for the environment in which the three main forest types occur.

	<i>Sand Forest</i>	<i>Dune Forest</i>	<i>Afromontane Forest</i>
<i>Mean annual rainfall variation</i>	600–800 mm	1000–1300 mm	1000–2000 mm
<i>Mean maximum temperature</i>	~30–35 °C	~28°C	~23–25°C
<i>Mean minimum temperature</i>	~7–10 °C	~10–14 °C	~3°C
<i>Mean relative air humidity</i>	Sub humid to humid ~60–85 %	Humid ~75–90%	Sub humid – dry ~50–80%

Historic

On the Maputaland plains there would probably always have been a gradient of rainfall decreasing westwards from the ocean for some distance before increasing towards the Lebombo Mountains. The effect of the transgression and regression of the ocean in the past would therefore have been that the zones on the coastal plain suitable for Sand Forest would have shifted. Near the coast, the ground water table is currently shallow and not favourable for Sand Forest. If the sea level drops, the water table would also drop and this would result in a more favourable environment for Sand Forest, as a relatively deep water table (drier sands) are exactly the conditions that Sand Forest currently prefers.

It can be generalised that the coastal areas of Maputaland have had a reasonably stable environment compared to much of the African hinterland during the Quaternary (Tyson 1999, Adams & Faure 2000). In the last 23–5 million years BP, since the deposition of “Berea type red sands” (Pliocene Dune cordon, the remnant of the oldest ancient dune cordon deposited at the

base of the Lebombo Mountains), there were probably no major changes in the climate of the region although there would have been fluctuations related to glacial periods, the near-by Indian Ocean had a considerable impact on stabilizing the overall temperatures experienced by the region.

8.2.1.8 Substrate: soil and soil moisture

Origin and age of the Sand Forest sands and sand dunes

For at least 23 million years the Maputaland coastal areas (eastern sea board) has been exposed to a constant cycle of sea transgressions and regressions (Davis 1976; Hobday 1976; Partridge & Maud 2000). One can assume that the processes that has been operating during the past 125 000 years may well have been operating for at least the past 25 million years. The one effect that these cycles of transgressions and regressions would have had on Sand Forest and other sand-based communities is that it would have resulted in an increase or decrease in the terrestrial sand substrate available to these communities. The position of these communities is also related to climate conditions, which is directly related to distance from the coast, so these transgressions and regressions would play an important role in determining the positions of the climatically suitable zones for the different communities, and therefore the positions would have shifted during the different cycles.

Currently there are three main distinguishable dune cordons with a fourth more of a dune field (Botha *et al.* 2003), on the Maputaland coastal plains. Each of these cordons relates to a past relatively stable ocean still-stand and as such would have formed the coastline at that stage. These were not the only dune cordons formed, but they were big and stable for long enough to persist. “Dune Cordon 1”, skirts the present-day coastline. The sea-level stabilised at its present level approximately 6 500 years BP (Ramsay 1997) therefore this cordon dates back to about 10 000 years to the present (as dune formation processes are still continuing today). “Dune Cordon 2”, which is more of a dune field, is not distinct and in many ways is a complex of hummock dunes and ridges just back of the current coastline. This dune field has a range of ages of which the oldest dates back to the last glacial maximum (18 000 years ago), at which time the coastal dune cordon would have been out to sea based on the current coastal dune cordon. “Dune Cordon 3” is a reasonable prominent cordon which is distinct throughout most of Maputaland. It is very prominent around Tembe Elephant Park where it is locally known as the Sihangwana Ridge. This dune cordon dates back to 3 million to 125 000 years BP (Pliocene) and is approximately 30–40 km inland from the coast. “Dune Cordon 4”, which is the oldest, lies at the

foothills of the Lebombo Mountains along the course of the Pongola and west of the Mkuze Rivers. This is not a distinct cordon, but remnant patches of sand dunes, which in most cases are a distinct red colour and also referred to as “Berea type red sands”. This cordon dates back to the Miocene / Pliocene (~25 million) and is 50–70 km inland from the coast.

Sea levels have also fluctuated which in all cases would have resulted in dune cordon formation and removal. During the 25 to 3 million year BP period there were possibly a multitude of sea transgressions and regressions. During this period the coastline would have fluctuated between the base of the Lebombo mountain to further out to sea than the current coastline. During the 3 million to 125 000 years BP period the coastline would have been to the east of the current position of the Pongola River, notwithstanding the usual sea transgressions and regressions. Around 800 000–125 000 years BP the coastline was in approximate position between the current Muzi Swamps and inland points of the Kosi Bay system and Lake Sibaya. At approximately 117 000 years BP (Glacial Maximum) the sea level dropped to 45 meters below current ocean levels. During this period the coastal dune cordon would have been out at sea (as seen today). From around 125 000 years BP to the present day the sea has not been further inland than the current position of the Muzi Swamps. At around 18 000 years BP another Glacial Maximum was recorded and resulted in a sea level drop of ~130 m below current levels. During this period the coastal dune cordon would have been far out at sea (as seen today). The sea-level stabilised at its present level at approximately 6 500 years BP and thus the age of the current coastal dune cordon can be said to be 10 000 years to the present (Botha 1997; Maud & Botha 2000).

The sands underlying Dune and Sand Forest are of marine origin, highly leached and very poor in plant nutrients. Most of the sands of the coastal plains (inland) are wind-reworked and referred to as aeolian sand and includes the sand on which Sand Forest is found. Very little stratification takes place, with the sand generally forming an amorphous mass under relatively thin organic layers. There are inconsistencies between surface and deeper soils established ages, these discrepancies between the ages (estimated for the sand dunes by deep soil dating and by near surface soil dating) is the result of this reworking of the sands by wind. The soil top layer of the dune is much younger than the dunes themselves. The topmost layer of soil in Sand Forest is probably not much older than the soils under Dune Forest. The dune systems of Sand Forest are older than those of Dune Forest, thus following a gradient from the youngest to the oldest from the coast inland.

Soil chemistry

There are very little major differences in soil chemistry of the sands over most of the coastal flats of Maputaland (Watkeys *et al.* 1993), except in the deeper layers and between the very old Dune Cordon 4, “Berea type red sands” (Pliocene Dune cordon near the Pongola River) and the more recent cordons (3 million and younger closer to the sea). This brick red colour of the oldest cordon is apparently only obtained after ~ 1 million years (Gardner 1983). There are no differences in those parts of the soil that matters to the plants. Some of the deeper layers of the ancient sand dunes are red because of oxidation that took place. However, Sand Forest occurs on both reddish and white soils. Walker *et al.* (1981) found a similar pattern and described a chronosequence sand mass site along the coast of Queensland, Australia. Soil surfaces there vary in age from a few thousand to perhaps half a million years. Soils are sandy and are subject to relatively rapid nutrient loss through leaching, with the nutrients content of the oldest soils relatively poorer than the younger soils.

Unlike Afromontane Forest, Dune and Sand Forest are almost exclusively found on sand, in most cases in the form of sand dunes. Soils underlying Afromontane Forest tend to be clayey or limey, and may be leached and poor in nutrients, though the water holding capacity of these soils are generally much higher than in the cases of Dune and Sand Forest. The soils are secondarily leached and poor in nutrients due to the high rainfall. Stratification of the soil into definitive horizons does occur under Afromontane forest, and a thick organic layer, almost a mat, develops on top of the soil. Wood decomposition (humification) is relatively fast.

There is a tendency for Sand Forest to occupy the drier habitats in Maputaland, e.g. on the high, ancient sand dunes. This begs the question whether Woodland out competes Sand Forest in moisture areas, and whether Woodland would invade and take over the areas currently occupied by Sand Forest if it should become wetter.

Indications are that the present-day climate regime is not suitable for the establishment of Sand Forest. Sand Forest soils show hydrophobic characteristics under dry conditions, but when they get wet, have a better water-holding capacity than the surrounding Woodland soils (Fourie *et al.* 2002). Plant communities such as Sand Forest therefore seem to be able to generate their own soil moisture regime within the constraints imposed by the climate and, initially, by the physical properties of the soil. In the longer term, even soil properties can be changed because both erosion and deposition rates are closely related to the amount of plant-cover present (Stafford Smith & Pickup 1993). Sand Forest seems to ‘manipulate’ its soils thereby creating its own

habitat, not only by making the soil more suitable for itself, but also by making it less suitable for the surrounding Woodland vegetation. Low soil moisture content in Sand Forest could also have a negative effect on Sand Forest recruitment, which can be very low, effectively keeping Sand Forest from actively expanding and establishing itself. However, Sand Forest is very efficient in capturing all or most of the rainfall that penetrates the first metre of ground; so efficiently, in fact, that the soil below the root zone can be bone-dry (Matthews, unpublished neutron probe data). The ‘habit’ of Sand Forest to ‘create’ and ‘maintain’ its own habitat therefore comes with a trade-off. Although the hydrophobic character of the soils can inhibit the establishment of species from the Woodland-matrix, it also limits Sand Forest from recruiting young forest growth, thus keeping it in a state of ‘suspended animation’ instead of in a state of ‘dynamic change and growth’. This suggests that if the current climatic conditions continue indefinitely, Sand Forest will become extinct in the drier areas because it cannot recruit to any significant degree under the current environmental conditions. That Sand Forest is apparently incapable of recruiting under the current dry climatic and soil conditions seems to indicate that Sand Forest was originally established under relatively moister climatic conditions, and that the current distribution is a self-inflicted refuge.

As soil moisture plays an important role in determining whether a site is more suitable for Sand Forest or for Woodland, there are two processes that could determine which vegetation occurs on a site. Sand Forest on the higher sand dunes will probably expand under wetter climatic conditions, as more moisture in general would mean that Sand Forest could start recruiting again. The higher soil moisture (specifically) on the lower dunes, would, on the other hand, probably cause Woodland to take over and replace Sand Forest in these areas. This will happen because the dryness of the Sand Forest habitat is partly self-inflicted, something that can be demonstrated by what happens when Sand Forest is removed from a site. Prior to Sand Forest being removed, the soil moisture levels recorded for the sand forest site, are on average lower than the average levels of the surrounding vegetation-matrix (be it woodland or grassland). After the removal, the soil moisture level under the site is raised above the average for that of a Sand Forest site. (See Figure 1).

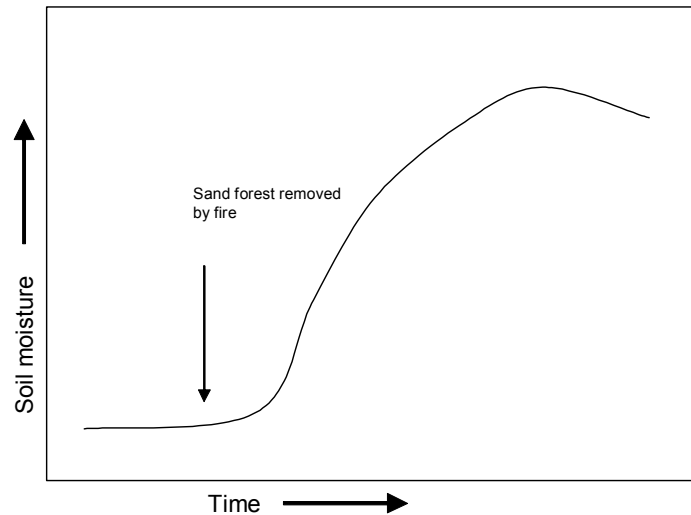


Figure 1. Schematic diagram to show the change over time of mean soil moisture content at a site before and after Sand Forest has been removed by fire (assuming mean rainfall levels). (Inferred from Matthews, unpublished neutron probe data; Fourie *et al.* 2002).

8.2.1.9 Fire

Fire is associated with all three forest types, but specifically with the vegetation which forms the matrix within which the forest are found (Bond 1997; Mucina & Geldenhuys 2004). Fire does not generally penetrate the forests deeply, but stops at the edge (Midgley *et al.* 1997). This is called an ‘edge effect’, and is especially prevalent in two of the forest types, namely Afromontane Forest and Sand Forest. The fringe flora in Afromontane Forest is especially diverse, and appears to differ considerably, in terms of floristic composition, from the core forest. The fringes of Sand Forest are less floristically diverse but also differ from the core forest. Dune Forest does not have a fringe that differs floristically much from the inner forest, but fire usually also stops at the edge (Weisser & Cooper 1993).

When fire does penetrate the core forest, the three forest types respond differently to the resulting impact. Dune Forest, which is a resilient forest type and adapted to respond relatively rapidly to severe damage or even total destruction, recovers and re-establishes itself the quickest (Matthews pers. obs.; Weisser 1979). Afromontane Forest also re-establishes itself rather quickly, but is slightly less resilient than Dune Forest. Sand Forest, on the other hand, has a very low resilience, and *does not appear* to be able to re-establish itself after severe damage by fire (Matthews *et al.* 2003).

Table 2. Summary of main distinguishing characteristics among the three principle forest types in southern Africa.

Attribute	Forest type		
	Sand Forest	Dune Forest	Afromontane Forest
1. Distribution range	x	xx	xxx
2. Species richness/area	xxx	xx	xx
3. Endemicity/area	xxx	xx	xx
4. Deciduousness	xx	x	x
5. Canopy height	xx-x	xx	xxx
6. Rooting depth	x	x	xx-xxx
7. Mean annual rainfall	x-xx	xx-xxx	xxx
8. Average temperatures	xxx-xx	xx-x	x-xx
9. Substrate-sand proportion	xxx	xxx	x-xx
10. Relative substrate age	xx	x	xx-xxx
11. Exposure to fire	xxx	xx	xx-xxx
12. Resilience	x	xxx	xx

xxx – Highest/widest/oldest/deepest; xx – moderate/average/medium; x – lowest/limited/youngest/shallow

8.2.2 Sand Forest dynamics

8.2.2.1 Succession and resilience

Preamble

The six steps of classical Clementsian succession are: nudation (creation of areas bare of plants), migration (arrival on site), ecesis (invasion of plants into new habitat, establishment on site), competition (interaction of organisms on site), re-action (modification of site) and stabilisation. A community can be viewed as a changing mosaic of patches of different sizes, ages, structures and composition. Therefore the spatial patterns are important for the understanding of community change (Glenn-Lewin *et al.* 1992). Climate is one of the most important factors determining how far succession will proceed and what type of plant growth will establish under field conditions. A community seldom reaches the ideal, equilibrium or climax stage, as it is always exposed to changes (Krebs 1985). Succession is influenced by three dimensions of disturbance: space, time and magnitude (Glenn-Lewin *et al.* 1992). A disturbance is an event that causes a significant change from the normal pattern (steady state) in an ecological system (Forman & Godron 1986).

Vegetation dynamics can be divided into seven types (Van der Maarel 1988): fluctuation, gap dynamics, patch dynamics, cyclic succession, secondary succession, primary succession and secular or long-term succession. Miles (1987) states that regardless of plant strategies, an important

determinant of the course of any succession, and the prime determinant of secondary succession, is the range of species present at the outset and migrating to the site early in succession. Gleason (1927) states, more definitely: “Succession is an extraordinary mobile phenomenon, whose processes are not to be stated as fixed laws, but only as general principles of exceedingly broad nature, and whose results need not and frequently do not ensue in any definite predictable way’ and different models have been put forward to help understand the successional process”.

Secular succession concerns long-term changes (greater than 1000 years to geological time scales) in a landscape because of long-term environmental changes, often climate. This also includes the change in the geographic distribution of species. Long-term soil changes accompany secular succession, probably as an integral process rather than as a cause or effect (Glenn-Lewin *et al.* 1992). One aspect of secular succession is the gradual change in the composition and even the structure of the climax community as a result of changes in soil conditions (Beard 1974).

Species diversity increases with time towards the mid-successional stage, where it reaches a peak because of colonisation of the available environment (Mueller-Dombois & Ellenberg 1974).

Table 3. Some general tendencies in early and late succession as it relates to Sand Forest based on Barbour *et al.* 1987.

Traits	Early stage of succession	Late stage of succession	Sand Forest traits
Biomass	Small	Large	Large
Physiognomy	Simple	Complex	Intermediate to complex
Nutrient storage	Soil	Biomass	Biomass
Role of detritus	Minor	Important	Relatively important
Mineral cycles + mineralization rate	Open (leaky), rapid rate of mineralization transfer	Closed slow rate of mineralization transfer	Closed, slow rate of mineralization transfer
Net primary production	High	Low	Low
Site quality	Extreme / xeric	Mesic / moderate	Xeric to mesic / moderate
Importance of microenvironment	Great	Moderate /dampened	moderate
Stability	Low	High	Low to high
Plant diversity	Low	High	Moderate to high
Species life histories	r (pioneer species)	K (climax species)	K (climax species)
Propogule dispersal vector	Wind	Animals	Animals / fleshy fruits
Propogule longevity	Long	Short	Short
Humification	Slow	Fast	Fast

The Initial Floristic Composition Model of Egler (1954) states that succession is determined by the species that first colonise the area and could be pioneer and climax species. This is very similar to the inhibition model of Connell & Slatyer (1977). According to Miles (1987) many studies have shown that the initial floristic composition of a site is an important factor in determining the successional development of a site.

According to the Inhibition Model (Niering 1987), the first colonizers modify the environment so that it becomes less suitable for subsequent recruitment's of both pioneer and secondary species (allelochemicals given off which inhibits germination and growth of other plants). In the inhibition model replacement occurs only when resources are released by the damage or death of previous occupants, the species composition shifts gradually and inevitably (given no further major disturbances) towards species that live longer. Simply by their life-history characteristics, long-lived species eventually dominate the ecological scene.

It seems clear that no succession, primary or secondary, ever occurs in which any single one of these models operates alone (Miles 1987). According to Odum (1997) it is generally accepted today that the ecological succession concept is a two-phased process. Early or pioneer stages tend to be random (i.e. stochastic) opportunistic species colonisation, but later stages tend to be more self-organised (i.e. deterministic).

Colonisation/secondary sites

Secondary sites are usually re-vegetated very quickly because of rapid recruitment from their seed or seedling banks, and/or clonal growth from extant plants on their peripheries (Glenn-Lewin *et al.* 1992). The order of arrival of species on a site can influence both the composition and physiognomy of the vegetation. Colonisation on primary sites is an extremely variable phenomenon, which depends greatly on seed dispersal from adjacent areas, local environmental conditions, and year to year variation in climatic conditions (Glenn-Lewin *et al.* 1992).

Vegetation acting as units or per chance groupings of species.

The different succession models relate to the succession of a particular species in particular situations, and not to vegetation types (Miles 1987). This is an unsurprising conclusion, because in succession it is the individuals and populations that change. For a vegetation to act in successional terms as a unit, and thus to permit useful generalisations about succession at a vegetation level, it would need a tightly integrated network of species, probably co-evolved and co-adapted, possessing hypothetical 'emergent' properties, and thus behaving as a vegetation gestalt. No properties of vegetation have ever been demonstrated that cannot be explained as the effects of species and of interactions of species. To quote West (1964): '...we may conclude that our present plant communities have no long history in the Quaternary, but are merely temporary aggregations under given conditions of climate, other environmental factors and historical factors'.

Lags

Studies by Vaartaja (1962) and Grime & Jeffery (1965) have shown that late-succession species maintain themselves in the presence of dominating early-succession species by having a lower metabolic rate, by repairing damages, and by fending off attacks of herbivores and soil pathogens. The late-successional species simply survive in a state of “suspended animation” until more resources are made available by the damage or death of an adjacent dominating individual. By “suspended animation” is meant the maintenance of the existing state (vegetation community) till circumstances change to more favourable for normal dynamics or functioning to return. Most geomorphic and topographic spatial patterns change very slowly and can be regarded as fixed in time (present themselves as static). Many current landscapes are the product of past climates and the processes which created these landscapes, but now many of these process are no longer active (Stafford Smith & Pickup 1993).

Indications are that the size and number of Sand Forest patches which correlate with Dune Cordon 3 (Tembe zone), approximately 50–60 km from the coast and with a mean annual rainfall of 650–700 mm, have not increased when comparing the most recent aerial photographs with the oldest available aerial photographs dating back to 1942. The Sand Forest mosaic of this zone appears to be in a state of “suspended animation”. What is apparent is that there has been a reduction in the distribution and sizes of patches in this zone. This can be attributed to harsh fires that periodically occur in the region. Sand Forest which has been impacted upon by such fires has not been able to recover back to “pristine” Sand Forest (Ostrosky pers. comm. & Matthews pers. obs.) and in most cases are reverting to woodland type communities. However, these patches still do have Sand Forest elements present, for example the more hardy species that can re-sprout and are normally large specimens such as *Cleistanthus schlechteri*. *Cleistanthus schlechteri* and skeletons of other dead hard wood species can also be seen on these sites. *Cleistanthus schlechteri* has a very hard and resistant wood that lasts for quite long after the tree has died. The possibility exists that many of the large specimens of Sand Forest elements that occur outside Sand Forest in woodlands are remnant survivors of past Sand Forest patches that are not present anymore, and therefore these species did not recruit into these woodlands.

Based on the aerial photograph comparisons, it can be seen though, that the Sand Forest patches closer to the coast, e.g. those in the areas around Sileza Nature Reserve (\pm 30 km from coast) are recruiting. Comparing the latest aerial-photos with those from 1942 do show that patches of Sand Forest are enlarging (even though just slightly) as well as the establishment of smaller Sand Forest like patches. Environmental conditions here are wetter (rainfall gradient related to distance from

coast and higher water table levels) than at the Tembe zone, soils, are very similar. This moister environment and coastal vegetation community influence does show itself in the species composition of these Sand Forest patches in that coastal elements are present which are not recorded for the Sand Forests in Tembe Elephant Park (Tembe zone).

Episodic

Sand Forest appears to be strongly episodic, recruiting only when conducive environmental conditions prevail. These periods will enhance the survival and growth of seedlings and the understory recruited plants. These episodic periods need though to be longer than one or two years for Sand Forest species to recruit.

Semi-arid woodland only rarely, perhaps every 30–50 years, experience the combination of favourable environmental conditions needed for tree regeneration (Peet 1981; Peet unpublished data; White 1985). Therefore, seedling recruitment in these areas is low and often episodic. In addition the final phase is not really a steady state phase, but rather exhibits pulses of establishment alternating with periods of declining tree seedling and sapling densities. Savannas do not represent a stable mixture of trees and grasses, but is an inherently unstable mixture which persists owing to disturbances such as fire, herbivory and fluctuating rainfall (Scholes & Walker 1993).

Time aspect

Succession is a compositional change, usually evident over a few decades to a few centuries. The change is directional, either uni- or multidirectional. Long-term change occurs over many centuries or millennia and results from equally long-term changes such as climatic change or soil development. The distinction between fluctuation and succession is arbitrary, in that a large enough fluctuation over a long enough period of time becomes succession (Bornkamm 1988). It can be said that succession involves changes in dominant or diagnostic species and new species enter the community and become diagnostic whereas fluctuations, the dominant or diagnostic species do not change and new species do not enter the community, or if they do they do not become diagnostic (Miles 1979).

If a community does exhibit some directional, cumulative, non-random change over a period of 1–500 years, it is said to be a successional community (Barbour *et al.* 1987). The time scale in primary succession may involve centuries or even thousands of years. On such a long time-scale, evolutionary changes in species adaptation and speciation cannot be ignored. Vegetation changes are relatively fast in secondary succession as it proceeds from an already established ecosystem.

The time-scale from pioneer stage to a stage of relatively equilibrium or stability can be measured in years or decades (Mueller-Dombois & Ellenberg 1974). The rate of change will be linked to the longevity of the dominant plants (Glenn-Lewin *et al.* 1992.). Secondary succession on favourable sites with ample migration can be expected to require little more than one episode of compositional sorting. In contrast, classical primary succession starting with a bare rock surface can be expected to have a long trajectory with many species coming and going during the process (Walker 1970).

Dune Forest is a dynamic and resilient vegetation type that is characterised by its proximity to the ocean and its ability to re-establish itself relatively quickly following destruction. Dune Forest associates with scrubland or grassland, and, like Afromontane Forest, exist in a state of ‘mutual replacement’ with its associated vegetation (Midgley *et al.* 1997). Succession in Dune Forest is primary (as well as secondary in cases of disturbance), with Dune Forest and its associated vegetation able to establish on bare, newly formed sand dunes, the latter process which is still active along parts of the Maputaland coast, especially in the south towards the Tugela River Mouth (Tinley 1985).

Sand Forest is less dynamic, and exists in a state of ‘suspended animation’ in which it is maintaining itself in certain habitats, and to a large extent is not actively establishing itself in new localities. It also tends not to recover after destruction, especially when severely damaged, for example, by fire. These severely damaged Sand Forest sites are usually replaced by woodland vegetation.

Afromontane Forest is a dynamic vegetation type, and exists in a state of ‘mutual replacement’ with its associated vegetation—forest can replace associated vegetation and *vice versa*. When damaged, Afromontane Forest will return to its prior state through successional processes, as discussed (Mucina & Geldenhuys 2004).

Stability and persistence

After a population is established, the ability of the population to replace individuals, as they are lost, determines whether or not it will persist. Stability can be shortly defined as the lack of change (Barbour *et al.* 1987). However, “stability” is a complex term that includes several distinct qualities (Connell & Slatyer 1977) such as resistance, resilience and persistence. Resistance is the ability of a community to remain unchanged during a period of stress. Resilience is the ability of a community to return to “normal” following a period of stress or disturbance. Persistence is the ability to remain unchanged over time. Some persistent

communities are neither resistant nor resilient, but owe their continued existence to a protected, buffered environment.

Stability will increase with succession (higher in so-called “climax communities”). Climax communities have inertia, changing slowly in the face of environmental changes and therefore are more resistant. Stability (resilience) is the ability to return to its balance point (homeostasis) following a major disturbance (fire, etc.) in this case the pre-climax communities are more resilient and climax communities are less resilient, this means that climax communities could be more fragile (the possibility of them recovering to their former state after a disturbance is not guaranteed). There is a difference to resistance to change compared to resilience to change in the face of pressures. In the case of Sand Forest it could have a low resilience to disturbance, e.g. fire, or any other impact, but be resistant to specific impacts such as fire and also be persistent as it has a buffered environment.

8.2.2.2 Allelopathy

Dissolved organic matter (DOM), which leaks out of decomposing plant material as well as from living cells, accumulates in increasing amounts and varieties in the soil. These “extrametabolites” not only power microbial food chains, but some products also act as inhibitors (antibiotics) or growth promoters (vitamins, hormones etc.) that would affect growth and species composition. Creating an increasingly biotic environment is one of the main ways the community facilitates a succession of species (Odum 1997).

A plant may interfere with the growth of its neighbours directly through resource competition or chemical inhibition, or indirectly if it harbours or attracts organisms such as herbivores or pathogens that affect neighbours (Muller 1969; Harper 1977; Fuerst & Putnam 1983; Weidenhamer 1996). Plant-plant interference (Rice 1984) may involve not only competition for water, light and nutrients, but also allelopathic phenomena that release toxic organic compounds into the environment. Under appropriate conditions, these chemicals are released in sufficient quantities to affect the growth and development of individuals of the same or other species (Seigler 1996). These substances are released into the environment through leaching from living plants, root exudates, volatilisation, residue decomposition and microbial activity (Muller 1969). The primary objective of allelopathic species, is to eliminate other species (Muller 1969). This means that allelopathy mainly occurs on an interspecific level, whereas resource competition occurs both at inter- and intraspecific levels.

In addition to the hydrophobic soils, Sand Forest also seems to produce compounds that produce an allelopathic effect. This is probably what produces the bare zone surrounding Sand Forest, an assumption that seems to be substantiated by the fact that the bare zone appears much more distinct in the driest areas—allelopathic effects being more pronounced in these poorly leached areas. Weidenhamer (1996) noted that environmental stress such as water and nutrient limitations, salinity and high plant densities enhances the production of allelochemicals in plants. Whereas the hydrophobic soils benefit neither Sand Forest nor Woodland, the allelopathic substances benefit Sand Forest because it can actively exclude competitors from the habitat, and the bare allelopathic zone can also act as a fire barrier. This allelopathic effect could give Sand Forest an advantage in an environment that is not quite optimal.

It is here proposed that in Sand Forest it is not one plant against its neighbour plant or other Sand Forest plants, but all seem to play a role in some way in producing the allelopathic property, which keeps out other competing plant communities such as the woodlands that dominate the area. In many communities, organisms interact for some time and undergo genetic modifications. This close association between species is called co-adaptation (or co-evolution) (Seigler 1996). Selection for organisms that can tolerate, detoxify, or utilise the compounds produced by other community members appears to occur widely and frequently. In natural plant communities, many of the organisms in a community will co-adapt to the release of allelopathic substances (Seigler 1996). This pulls all species together, working as a unit to produce an enhanced allelopathic effect.

Density-dependence

In natural communities the effect of toxins in the soil are intensified by factors such as low plant densities, harsh environmental conditions and nutrient stress (Weidenhamer *et al.* 1989). Thus high densities of plants would effectively result in reduced allelopathic effects and Sand Forest is an example of a vegetation type with high densities of plants. Adult plants at high densities can cope with these concentration levels of allelochemicals, but new recruiting plants must be able to deal directly with the allelochemicals which at these levels could act as toxins.

Rice (1984) has stated that quantitative and qualitative changes in allelochemicals may occur during succession. In natural communities, succession occurs with time. This allelopathic effect in Sand Forest may also be a successional attribute that changes over time, with certain species able to cope with the high concentration at maturity and other species at earlier stages of succession. This could give rise to a state when the juvenile plants of many of the larger species

(e.g. *Newtonia hildebrandtii*) in the forest are absent or scarce. The mature species established possibly when conditions were different and the allelopathic attributes were not that inhibitive to that specific species. It is recognized that pioneer species exhibit different co-adaptations and interactions than those of most climax species (Seigler 1996).

If vegetation is virtually totally removed, such as in the case of a devastating fire, the allelopathic effect can be amplified. As stated by Inderjit (1996) environmental processes, such as fire, indirectly enhance the allelochemical levels in the soil, by reducing the concentrations of the soil chelators responsible for allelochemical breakdown. It may also increase the hydrophobicity of the soil. If the density of plants has been reduced drastically and the high concentrations present are not metabolised, this could result in these allelochemicals levels being even toxic to the dominant mature species, which normally would have coped with these allelochemicals, such has been the case of Sand Forest. Only after leaching of the inhibiting agent from the soils, will species establish. In the case of Tembe Sand Forest it seems to be between 1–2 years, pending on rainfall before Woodland or Sand Forest species recruit into these major disturbed areas (Matthews pers. obs.). The chance is then that these could also be woodland elements which now can cope with these lower concentrations of the allelochemicals as well as been better adapted to the harsher environment.

8.2.2.3 Gap replacements

Vegetative propagation is an important mechanism for the persistence of species in sites subjected to periodic disturbances, such as fire and tree falls. Gap replacements is where recruitment is restricted to sites where the vegetation is totally, or partially, destroyed as a result of factors such as fire, tree fall and animal activities. It occurs not only in forest, but also in grassland, wetlands and shrublands (Glenn-Lewin *et al.* 1992). Gap dynamics provide new possibilities for establishment and re-establishment of new and/or mature species.

For species whose seeds cannot germinate under a plant canopy, recruitment of new populations is restricted to gaps or openings in the vegetation. Conditions within established vegetation prevent the germination of seeds of most species. This has been shown by studies in which seed has been sown into different types of plant communities (Cavers & Harper 1967; Peart & Foin 1985; Bakker *et al.* 1985; Peart 1989 a, b). Possible reasons for the existence of conditions not conducive for germination include: spectral composition of light, thickness of litter layer, day and night temperatures and soil-moisture levels. For lowland tropical forest in Panama,

(Brokaw 1982) estimated a turnover time of 113 years to 126 years depending on the minimum gap size that one assumed.

Gap dynamics is important and very active in Afromontane Forest, where seed banks and already established understory plants (“seedling bank”) initiates regeneration after disturbance. There is abundant evidence that many Afromontane forests are still actively establishing themselves and that the distribution of Afromontane Forest has fluctuated considerably over thousands of years (Adams & Faure 2000). During the last glaciation period (18 000–10 000 years BP), large areas were cleared of all forest types including Afromontane Forest, but what we see today, was subsequently re-colonised by the different forest types including Afromontane Forest. It is marked that many Afromontane forest species are very wide ranging, with very little regional endemism. Afromontane forest seems to be able to re-establish itself in places where it was destroyed or did not occur. In case of destruction of forest but where parts of the forest still persist, recovery of the forest can occur in a relatively short period of time, if adequately protected from subsequent disturbance. Tree-fall gaps Mean Return Intervals range between 50–200 years for most forest types, though scattered individuals trees can have much greater longevities (Runkle 1985). Disturbance regimes themselves are subject to change during succession.

Though gap replacements do occur in Dune Forest, it is of less importance than in Afromontane Forest, here the seed banks playing an important role. Dune Forest is very resilient and dynamic, explaining the ability of Dune Forest to re-establish itself very quickly after destruction or disturbance. Weisser (1979) established from aerial photos that it might take a mature *Acacia kosiensis* woodland about 25–60 years to become established on grassland and about 30–150 years to be replaced by secondary Dune Forest. A fire that occurred in a Dune Forest just north of Rocktail Bay in 1994, virtually destroyed extensive parts of the dune forest. After ten years the damaged forest has recovered and is very hard to distinguish from the surrounding un-burnt Dune Forest. Dune Forest forms part of primary succession on the bare sand of a dune that has been denuded of vegetation, or newly laid down through oceanic processes. Dune Forest therefore can be referred to as a type of ‘pioneer forest’ able to initiate and forms part of primary succession.

Gap dynamics does not appear to play a significant role in Sand Forest; indeed, it seems that gap dynamics may not nearly operate at the scale at which it operates in the other two forest types. Therefore because of this and other aspects as discussed before, Sand Forest can be regarded as

not a resilient vegetation type. There are good indications that Sand Forest does not easily recover/re-establish itself after a major impact that has damaged or destroyed the forest (Ostrosky pers. comm., Matthews pers. obs.). There is also no evidence that Sand Forest in the drier inland areas is actively expanding its boundaries and colonising new sites, this under the current climate and environmental conditions. Comparison of aerial photos of 1942 (Matthews *et al.* 2003; Izidine 2004) and the latest aerial photos (2000; a period of 58 years) show no increase in the size or number of patches. Even to the north in Mozambique, the old cut lines (roads) through the Sand Forest (in the Reserva Florestal do Licuáti) are still visible today after about 60 years. Sand Forest seems as if it exists in a state of ‘suspended animation’—maintaining itself in areas where it still exists in a pristine state. In this respect, Sand Forest differs significantly from Afromontane and Dune Forest.

Although sometimes recruitment in gaps must have taken place in Sand Forest when environmental conditions are favourable, i.e. when soil moisture and rainfall is above what we currently consider as the mean or norm. These gaps though, should not be open too neighbouring woodland/grassland communities. These gaps should also not be too large as leaching of the allelopathic soils could give woodland species a greater ability to recruit into these gaps. If these gaps are large to medium and open to neighbouring woodland communities (seed source/progule) then these woodland communities would be given a favourable chance to invade as soon as allelopathic conditions have reduced enough to allow woodland species to germinate and establish. Allelopathic conditions directly after gap creation could also be negative to many Sand Forest species recruitment (Weidenhamer *et al.* 1989; Rice 1984), because some leaching could be needed before even Sand Forest species will germinate and recruit. Only those Sand Forest species able to cope with the allelopathic conditions would survive the process that created the gap in the first place. The long term survival of the Sand Forest species could also be temporary if woodland and grassland species took hold in these disturbed areas (substantial higher grass biomass), as the woodland communities would increase the probability of fires occurring, especially if in direct contact with neighbouring woodland. This continued exposure to fire would in effect slowly remove the Sand Forest species from such sites.

Most managerial decisions are made based on short-term evidence. In southern Africa, forest types are often lumped together as ‘does not recover from severe disturbance or destruction’. The reality is, however, that Afromontane forest and Dune Forest will probably, given enough time, proper management and adequate protection from further disruptions, recover completely from severe disturbance and even total destruction. The floristic composition of these forests in some

cases would probably not be exactly or even nearly the same as it was prior to the disturbance or destruction, but the fully functional forest *system* and *dynamics* will return. The same cannot be said of Sand Forest, however. If destroyed, the Sand Forest system will probably never recover, unless the conditions, which are in favour of Sand Forest formation and/or succession, return, which is linked to climate conditions and possibly even to distance from the coast.

How is gap-fall-succession influenced by allelopathy?

Gap falls in most forest and dense vegetation has a stimulatory effect on surrounding and nearby species, largely because of increased availability of resources. According to Glenn-Lewin *et al.* (1992) the following three mechanisms increase availability of resources. Firstly, the decrease in rate of uptake and use of resources. Secondly, the increased decay and mineralization of nutrients previously held in organic matter. Thirdly, exposure of bare soil where a thick litter layer previously may have impeded seedling establishment. The specific canopy trees may also have had an influence on the species composition of the understory vegetation through their effects on the establishment, growth and mortality of herbs and seedlings of woody plants (Woods & Whittaker 1981; MaGuire & Forman 1983; Beatty 1984). Microsite differences beneath canopy species may result from variations in the quality and quantity of litter, which in turn, may affect availability of soil nutrients or result in allelopathic interactions (e.g. Gauch & Stone 1979; Beatty & Scoles 1988; Boettcher & Kalisz 1990). Therefore, depending where the gap is, its size and rainfall at the time, the recruitment taking place would depend on the recruit's ability to cope with the allelopathic effect. Under favourable conditions, Sand Forest elements could recruit under present Sand Forest canopy as well as at smallish gap-falls inside the forest. However, with large gap-falls and resulted enhanced leaching, the opposite could occur, with grassland and woodland species taking hold, especially since they are able to cope with, what for forest would be more harsher environmental conditions.

8.3. Sand Forest evolution: speculations and hypotheses

“The presence of the same form in distant places is no evidence that it was created twice, but that it can move.” Steve Jones – Almost like a whale (1999).

8.3.1 Evolution/speciation preamble

As species composition changes during succession and becomes more predictable with increased competitive sorting, we should expect genetic variation within species to become restricted and the distribution of the remaining genetic variation to be more predictable. Unfortunately, scant information currently exists on changes in genetic variation within species during succession (Gray 1987) but the data that is available is consistent with this prediction. Therefore, Sand Forest species as they occur today should be evolving very slowly, as they are long-lived species that have succeeded in becoming established. Figuratively, to change now genetically is like playing with fire, as it could mean no survival for propagules. It's got a lifetime of a big tree to replace itself, this when conditions are right; it has no need to test for new abilities to survive under current non-suitable conditions. Therefore it has time to change—slowly.

Stress (adverse environmental conditions–evolution)

Energy and other resources necessary for growth, maintenance, survival, and reproduction are usually limited. When sub-optimal conditions exist this produces stress. Stress, as defined by Parsons (1991), arises from any factor causing a potentially lasting injurious change to a biological system. Stress is a common state affecting free-living organisms and it thereby not only imposes important selection pressures on individual organisms, but also affects the development of phenotypes upon which selection acts. After Møller & Swaddle (1997), a host of potentially evolutionary important processors can be affected by sub-optimal conditions experienced by individuals. Adverse environmental conditions have been suggested to affect the level of recombination, mutation, and transposition, the additive genetic and phenotypic variation, the intensity of selection, and hence the speed of micro-evolutionary change. These include phenomena associated with the genetic variation that may give rise to evolutionary change: increased rates of recombination, mutation, and transposition, and increased additive genetic variance.

Organisms have to allocate a very large fraction of their metabolism to cope with extreme environments, and little excess energy will be available for the stable developments of phenotypes

and for reproduction. Availability of excess energy for development of stable phenotypes and reproduction will, particularly, be found under moderate sub-optimal habitats, and these may be the conditions most conducive to an evolutionary response to selection. Therefore, moderately sub-optimal environmental conditions are assumed to be permissive for gradual evolutionary change.

Distributional limits of species are important in that they reveal the conditions that prevent further range expansion (Møller & Swaddle 1997). Furthermore, peripheral populations play an important role in several theories of peripatric speciation.

Two evolutionary phenomena may be facilitated by extremely adverse environmental conditions, the destabilisation of the developmental process, and the resultant novel major deviations in phenotypes: speciation and major evolutionary innovations (Møller & Swaddle 1997). Evolutionary novelties have been shown to arise relatively rapidly (on a palaeontological time-scale) during adverse environmental conditions (Gould & Eldredge 1977; Mayr 1982).

Two modes of evolutionary change can be unified if the phenotypic response to adverse environmental conditions depends on the adversity of such conditions.

- a) Long-term changes in response to adverse environmental conditions that are gradual and energetically relatively inexpensive in terms of maintenance and repair.
- b) Short-term changes in response to severe environmental conditions that will be sudden and energetically expensive to the individual in terms of maintenance and repair. It will rely on environmentally induced unmasking of genetic variability and loss of canalisation (Hofmann 1983; Kieser 1987, 1993). [Canalisation is defined as the stabilised flow of a developmental trajectory of a genotype under different environmental conditions (Schmalhausen 1940; Waddington 1940)].

Moderate sub-optimal conditions results in moderate phenotypic changes that facilitate gradual evolutionary change, while extreme environmental conditions tend to reveal major phenotypic deviants that may give rise to major phenotypic changes as seen in connection with speciation and the evolution of major innovations.

8.3.2 Hypotheses on origin of Sand Forest

Three possible hypotheses are proposed to explain the establishment and foundation for Sand Forest.

- **H₁ : The primary hypotheses is that Sand Forest is (long term successional outcome) transformed Dune Forest.**
- **H_{1a} : A variation of the primary hypotheses is that Dune Forest is the precursor of Sand Forest, but that Sand Forest has subsequently become a separate functioning plant community on its own.**
- **H₂ : The alternative one is that Sand Forest is a self-generating forest community that is independent of Dune Forest precursors.**

Guiding principles and assumptions:

- i. The regression of the ocean stimulates the establishment of new plant communities on the Maputaland coastal plain, while transgression can wipe out plant communities on the Maputaland coastal plain.
- ii. Regressions and transgressions have been taking place since the break-up of Gondwana, at least 65 million years ago, although the last approximate 5 million years are relevant to the current coastal plains oldest dune formation (Dune Cordon 3), namely the Sihangwana Ridge.
- iii. There has been a constant transgression of the coastline for the last 125 000 years. The coast has not been further inland than the Sihangwana Ridge for the past 125 000 years.
- iv. No matter where the coastline was at any particular time, there would have been sand and coastal sand dunes, and there would have been Dune Forest like plant assemblages. These Dune Forest communities would not necessarily have had the same floristic composition that Dune Forest has today, but would have had similar functional properties.

- v. Dune Forest is strictly associated with the coastline, and as the coastline regressed, the composition of the remaining “dune” forest changed or disappeared, while the true Dune Forest moved with the coastline. If there is bare sand close to the ocean, Dune Forest could establish itself there.
- vi. Dune Forest has a relatively quick succession (Weisser 1979). The dynamics of Dune Forest are founded upon primary succession.
- vii. Sand Forest communities are “persistent” in a buffered environment.

Primary hypothesis (H₁): Sand Forest is transformed Dune Forest.

As the ocean regressed, sand dunes with their assemblages of Dune Forest elements remained behind. These “Dune” forest communities gradually changed their floristic compositions as the ocean moved away and the local climate changed. Those species that were totally dependent on the proximity of the ocean gradually disappeared from the community, while those species that could survive the drier conditions persisted. This differential extinction or elimination would have been the main niche opener in the community. These niches could now be filled in three different ways:

- i. Immigration from pre-existing, similarly dry inland habitats could have taken place;
- ii. Species that were ‘sub-ordinate’, ‘low-key’ or ‘rare’ in the primary Dune Forest assemblage, could have assumed more prominent positions where tolerances allowed; and
- iii. Speciation of species that previously occurred in the primary Dune Forest or surrounding vegetation could have taken place, making those taxa better adapted to the changed environments. This last was probably especially related to Sand Forest, as there still exists a large number of ‘aberrant’ forms of more widespread taxa in Sand Forest.

This mixture of species that would have resulted is still in existence today, and can be seen in the inland forests of Maputaland, which consist mainly of Dune Forest elements, supplemented by Sand Forest and other forest (tropical and temperate) elements. The arid elements in these ‘mixed forests’ could have moved in from the north (northern Mozambique), where the coastal plain would always have been much broader and tropical than in the south.

As the ocean pulled back further, the changed Dune Forest would have had to become increasingly drought adapted, as the resulting plains between the Lebombo Mountains in the west and the ocean in the east, would have been drier than the original Dune Forest habitat in terms of both rainfall and soil moisture (water table depth). It had to change in terms of floristic composition, but the original forest structure remained in place. It is speculated that eventually these patches of ‘left-behind’ Dune or ‘mixed’ forest, had changed enough from the primary Dune Forest (especially in terms of floristic composition and functioning) that it could be recognised as another community type, what today is called Sand Forest. It is therefore suggested that Sand Forest originated by a process of “evolutionary vegetation change” associated with environmental change in the manner described, over a very long period of time (geological time scales).

Pointers in support of hypothesis

Once Sand Forest has established itself on a sand dune, it can maintain itself in that habitat, but indications are that it cannot colonise primary or exposed dunes. Considering present-day evidence, and behaviour, it would seem that Sand Forest is not capable of colonising an isolated, (non-Sand Forest) sand dune. It also cannot very easily establish itself in woodland or grassland; and where Sand Forest does occur today, neither does it easily re-establish itself after severe destruction. This would support the view that Sand Forest is transformed Dune Forest.

The only opportunities for the establishment of forest on open dunes would always have been along the coast, and these forests would always have been Dune Forest, not Sand Forest. The current inland Sand Forest (as on the Sihangwana Ridge) one can see today must therefore have been maintaining itself for the last 125 000 years (since the last major transgression of the ocean). It is speculated therefore, that when Sand Forest is destroyed, it cannot replace itself, as Dune Forest is necessary as a precursor, and that these dunes are now too far away from the ocean for Dune Forest to establish there.

As part of soil carbon studies (Catapano 2004), charcoal layers were consistently found in more sample pits under woodland and grassland, than under Sand Forest. It follows from this that fire is very much a feature of woodland and Woody Grassland (both of these vegetation types are adapted to deal with regular fires), but not so much for Sand Forest. Woodland must have been woodland for a very long time and consistently exposed to fire. However, in the case of Sand Forest, the frequency of occurrence of charcoal and charcoal ¹⁴ C dating (Catapano 2004) supports the idea that sites with Sand Forest have been in existence for a very long time.

Catapano (2004) concludes that geochronology coupled with carbon isotope data from SOM as well as the abundance of charcoal and the apparent conservation of C:N ratios collectively indicate stable vegetation regimes since approximately 1800 BP.

Sand Forest is surrounded by fire-prone vegetation types, namely the woodland and Woody Grassland mosaic. Occasionally, when fire does penetrate Sand Forest, it is very destructive. If Sand Forest is derived from Dune Forest, all that subsequently happened was that it shrunk due to damage caused by fire. Eventually Sand Forest will become smaller and smaller due to fire impacts. It is a relict vegetation type even though it is relatively recent in geological terms (neo-endemic), because it seems to be “out of sync” with its environment. Sand Forest in the past would have covered larger areas of the Maputaland coastal plains as is the case today. In a protected sand dune island in southern Mozambique there is still a contiguous intact Sand Forest (thicket) of about 25 km long by 15 km wide covering 140 km² found in the Licuáti Forest Reserve (Izidine 2004).

Further support for the hypothesis would be to find a gradient of forest types between the ocean and the relict shoreline furthest from the ocean, with pristine Dune Forest occurring closest to the ocean, and pure Sand Forest occurring closest to the mountains on the deepest sand or highest inland dunes, as is the situation currently.

Sand Forest floristic elements are sometimes found in woodland (Matthews *et al.* 2003). One explanation for this occurrence is that these elements are relicts (and not precursors) of Sand Forest that was left behind after severe destruction by fire left the habitat open for woodland to invade. These relicts are mostly the very large hardwood trees that persist as remnants for a relatively short period of time. However, Maputaland is a dynamic region, and speciation and evolutionary processes appear to be very much active and in place. It is therefore quite feasible that some Sand Forest elements are becoming adapted to woodland conditions. Woodland elements, on the other hand, are not able to enter pristine Sand Forest, because Sand Forest is very exclusive. It competitively excludes (competitive exclusion) other vegetation types by chemical (allelopathy) and physical (hydrophobic soils) means—a buffered environment.

Origin of the woodland and other communities

The question that now arises is how the woodland matrix developed. When the ocean retreated, it left behind Dune Forest and associated vegetation. Therefore, just as in some areas Sand Forest replaced Dune Forest, in others woodland could have replaced the Dune Forest. The same may

be true for the Woody grasslands of Maputaland, which is basically woodland but occurs in areas with a high water table. As aridity increased, woodland and Woody Grassland would have been more adapted to replace the coastal dune vegetation. It appears that woodland was mainly established by immigration, as there is little evidence of local speciation and most of the woodland species have wide distribution ranges through most of the subtropical savannas of southern Africa.

Arguments for/against the hypothesis as well as alternative hypotheses (based on preceding discussion)

For the alternative hypothesis (H_2) [Sand Forest is a self-regenerating forest community that is independent of Dune Forest precursors] to be true, one would expect the following to be true:

- That Sand Forest consists of a mosaic of colonisation and of obviously different plant age classes, *typical* of most forest structures. [False]
- That there would be a uniform diversity throughout its distribution as is the case with Afromontane Forest, which has a low β -diversity. [True & False]
- There should be a good replicate of recruitment stages with a normal growth curve in Sand Forest. Gaps would be filled, and Sand Forest would recover after impacts. At least, the recovery rate should be in harmony with that of the neighbouring vegetation types. One would see both destruction and re-colonisation. Also what is destroyed in one place could be replaced in another. There should be a mutual replacement balance as would be expected of any typical forest. Woodland and Sand Forest should not out-compete each other in the long-term. [False]
- Either Sand Forest would have links to similar forest types in other parts of southern Africa, or it would be more widespread in southern Africa, not as local as it is, or it would develop from scratch from pre-existing species in the area. [False]
- Sand Forest should have dynamics similar to other forest types. [False]
- Chance should play a role in the distribution pattern of Sand Forest. It should have a random distribution where suitable habitat exists. There should be signs of Sand Forest everywhere, just as there are signs of woodland everywhere. Patches of Sand Forest should not always be Sand Forest, and patches of woodland should not always be woodland; especially as the substrate is the same for both vegetation types. [False]

- The evolutionary rate and the pressure to evolve would be low. Sand Forest taxa would have changed little from their ancestors, to keep the competitive advantage that these taxa had over the woodland ancestors. [?]
- There should be little evidence of stress in the vegetation, and many long-lived taxa should occur. [?]

The probability to form a forest *de novo* in a woodland area is lower than the probability that a drought adapted woodland develops. Mesic woodland, when it becomes dry, would become arid woodland, not arid forest. The alternative hypothesis (**H₂**) is therefore very unlikely.

For the primary hypothesis (**H₁**) [Sand Forest is transformed Dune Forest] to be true, one would expect Sand Forest to have the following characteristics:

- Sand Forest would have closer taxa links with Dune Forest than with any other vegetation types. [True & False]
- Floristic relationships would exist between Sand and Dune Forest. [True]
- Sand Forest would show very little ecological interaction with woodland. [True]
- There would be neo-endemics present in Sand Forest, because it would be a relatively stressful environment conducive of speciation. [True]
- There would be no new establishment of Sand Forest where there were no Dune Forest precursors. [?]
- One would expect Sand Forest to occur on sites where well-developed Dune Forest would have been present in the past. If the ocean regressed relatively fast, only the oldest, better-developed dunes would have supported well-developed Dune Forest. The best-developed Sand Forest would occur where the best-developed Dune Forest had occurred, and that would be where the largest and most stable dune cordons were or still currently are. [True / False]
- One would expect to find relatively less amounts of charcoal layers under Sand Forest; one would expect that in the past there should not have been woodland present on those sites. If charcoal does occur, it should be charcoal from Sand or Dune Forest species. [?]
- The break-up of Sand Forest patches would have occurred very early on, because fire is hypothesized as always been a factor on the coastal plains. [True]
- Since the establishment of Sand Forest, on the large scale, only receding (shrinkage) has taken place. It is hypothesized that if intact Sand Forest is present it can slightly expand or retract depending on the water regime, but it cannot establish a new core. It can only expand

from existing cores of Sand Forest. This slight expansion is event-driven. When it is wetter for longer periods of time, it will expand slightly, when it is drier, it will recede; when it is exposed to fire it can be removed from areas. [True - ?]

- If Sand Forest were exterminated completely, one would expect it not to return; instead the site would be taken over by the surrounding matrix vegetation (Woodland). [True]
- There would be a large β -diversity turnover. Some patches would be very diverse. Other would be less so, depending on chance events that influenced it in the past. [True]
- The endemics would be mostly related to Dune Forest taxa. [True & False]

The variation of the primary hypothesis (H_{1a}) [Dune Forest is the precursor of Sand Forest, but that Sand Forest has subsequently become a separate functioning plant community on its own] would have most of the characters described for the first hypothesis (H_1). Exceptions are that:

- There could be new establishment of Sand Forest where there were no Dune Forest precursors. [True & False]
- There would be a bias towards Dune Forest relatives, but other more tropical taxa could also be present. [True]

The strongest difference between the first (H_1) and the variation of the first hypotheses (H_{1a}) lies with floristics and the response to changing environments.

Before accepting any of the hypotheses as superior to the others, one must make provisions for climatic change and variance. The lack of recruitment one currently observes in Sand Forest may only be because it is currently a dry period (a dry cycle of ~10 years or more). Thus the lack of recruitment and successional processes could be directly linked to this. Although this would only really influence the first two hypotheses (H_1 & H_{1a}), effectively confirming which of the two is closer to the truth. If climate conditions do become more favourable and Sand Forest does start recruiting independent of Dune Forest precursors, this would definitely support the variation of the primary hypothesis (H_{1a}).

Effectively if the environment were to change in the following ways for a long enough period of time what would we expect to happen to “Sand Forest” (or what effectively was the basis for the Sand Forest vegetation community) based on the three hypotheses? :

Wetter

H₁. “Sand Forest” would diminish—prefers drier dunes but needs to be established via Dune Forest dynamics. [Stable to Negative Impact].

H_{1a}. “Sand Forest” would recruit and expand in areas where already present and further from coast and retreat from the moister zones closer to the coast. [Stable to Positive impact].

H₂. “Sand Forest” would recruit and expand in areas where already present as well as in other suitable areas. [Positive impact].

Drier

H₁. “Sand Forest” would diminish—has preference for drier sand dunes but needs to be established via Dune Forest dynamics. [Negative Impact].

H_{1a}. “Sand Forest” would recruit but not expand in areas where already present and retreat from the relative drier zones. [Stable to Negative Impact].

H₂. “Sand Forest” would retreat from unsuitable areas and expand in other suitable areas. [Stable].

Coast transgression/regression.

Transgression or regression would have differing impacts:

H₁. Regression: Sand Forest would recruit and expand in relation to the establishment of Dune Forest precursors. [Stable to Positive impact].

Transgression: would result in the retreat or removal of Sand Forest from unsuitable zones. [Negative Impact].

H_{1a}. Regression: Sand Forest would recruit, but not expand in areas where already present as well as retreating from the drier zones that would develop deeper inland. [Stable to Negative Impact].

Transgression: Sand Forest would recruit and expand in the suitable zones (to a point – only as far as the base of the Lebombo Mountains) and where already present. Sand Forest would retreat from the moister zones close to coast. [Positive impact and then stable to negative].

H₂. Regression: Sand Forest would recruit into suitable areas and retreat from unsuitable zones. [Stable].

Transgression: Sand Forest would recruit into suitable zones and retreat or be removed from unsuitable zones. [Stable to Negative Impact].

Conclusion

The bulk of the evidence supports the variation of the primary hypothesis (**H_{1a}**) [Dune Forest is the precursor of Sand Forest, but that Sand Forest has subsequently become a separate functioning plant community on its own].

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CHAPTER 9
GENERAL DISCUSSION

9.1 General discussion

The *principle hypothesis* of this thesis is that the Maputaland Centre of Plant Endemism is characterised by plant communities each being specific to a particular set of environmental variables, including a rich biodiversity with endemic and rare taxa, and exhibits a relationship with the geomorphological history of the region. The information assembled supports these hypotheses and Figure 1, presents a flow diagram of these hypothesized developmental / succession paths of Sand Forest over time. The Maputaland Centre of Plant Endemism proved to have a diversity of plant communities that are specifically related to certain environmental variables (Chapters 4 to 6). The study did not aim to determine the endemic and threatened taxa, but merely to establish how these species were linked to specific plant communities. Endemic taxa were already determined by the work of Van Wyk (1994) and Van Wyk & Smith (2001). The results of the vegetation studies highlighted two plant communities as playing an important role in the regions biodiversity namely Sand Forest and Woody Grassland. Knowledge of the vegetation and flora of the Maputaland Centre of Plant Endemism and the role that large herbivores (specifically elephant) and fire may play in the dynamics of the different vegetation communities, can help facilitate the formulation of management strategies, specifically for those habitats in the region which play an important role in conserving the regions biodiversity. Following on this is the possibility of also evaluating existing management directives for the region, be it for the conservation of important biodiversity areas, or for sustainable utilisation of the region's natural resources or for ecotourism.

The present study adopted a broad approach to the floristic classification of vegetation to address the need for sound information on the floristics patterns and diversity of the unique and rare plants and communities of the Maputaland Centre of Plant Endemism. It is aimed to provide useful botanical information that was lacking for the region. Apart from the identification of plant communities, analyses of plant-soil associations and plant-herbivore interactions were also explored. Ideas on the phytogeography, possible origins of the habitats, specifically Sand Forest of Maputaland, were presented in an attempt to explain some of the patterns of diversity, vegetation anomalies and dynamics. Various ideas are presented born from speculations on the origin and evolution of Sand Forest (Chapter 8). These ideas on Sand Forest origin and evolution were evaluated with respect to the geological and geomorphological evolution of the region.

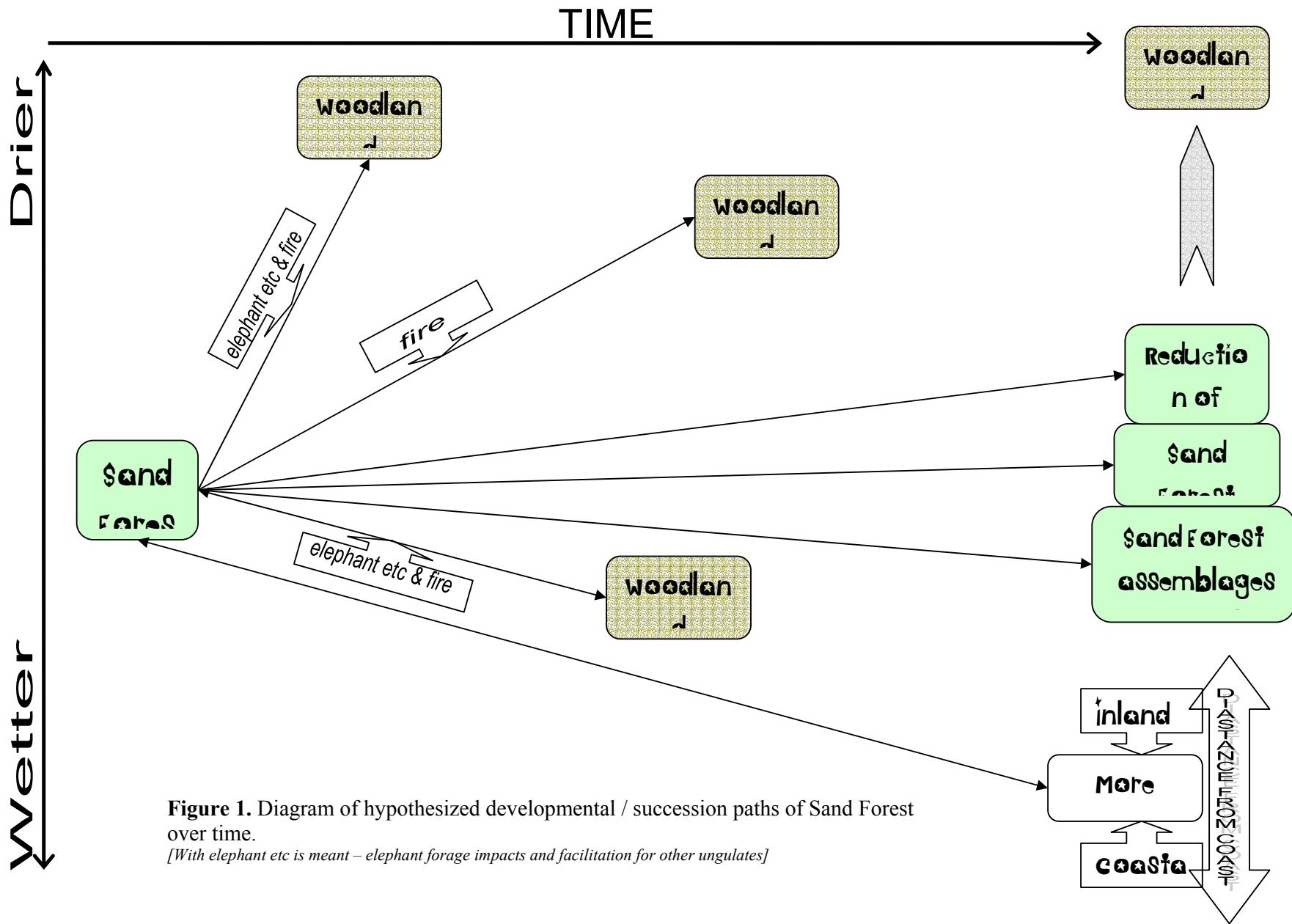


Figure 1. Diagram of hypothesized developmental / succession paths of Sand Forest over time.
[With elephant etc is meant – elephant forage impacts and facilitation for other ungulates]

Research opportunities were addressed (see section 9.3) to focus future work on gaps in knowledge, which could help in interpreting many of the outstanding issues regarding Sand Forest.

9.2 Reflecting on outcome of study

When one does a study like this, most of us would like to bring new information to the fore, this new knowledge to change current beliefs and understanding, and in so doing make science work for man in whatever small way. In a sense, this study has done that, although in future these ideas and understanding of what was thought to be might also be interrogated. Through this cross-examination, new perspectives come into being. These are the building blocks of science and future knowledge. In the following points, I would like to highlight, what for me, is new evidence and information that changes and/or challenges past beliefs or is simply new viewpoints of what possibly is.

Scientific inquiry requires investigators to challenge the validity and interpretation of evidence; hence the name research.

—Wayne G. Watson

- Two main habitats were highlighted as being very important to Maputaland's biodiversity, namely Sand Forest and Woody Grassland. Most of the emphasis of this work was placed on Sand Forest and in the case of this habitat much new information on its composition, dynamics and possible evolution has been brought to light. New insights highlight the role that the habitat type plays in the overall biodiversity to the region. The work also highlights the sensitivity of this habitat in light of the effective management of biological resources and these attributes.
- Two physiognomic or structural types of Sand Forest were distinguished (Matthews *et al.* 2003). One fits the basic physiognomic definition of forest, while the other can be better described as a thicket. These structural differences are also reflected in the floristics.
- Sand Forest seems to “manipulate” its soils thereby creating its own habitat, not only by making the soil more suitable for itself, but also by making it less suitable for the surrounding woodland vegetation (possible allelopathic characteristics). Sand Forest soils

show hydrophobic characteristics under dry conditions, but when they get sufficiently wet, have a better water-holding capacity than the surrounding woodland soils (Fourie *et al.* 2002).

- The Sand Forest mosaic of most of Maputaland appears to be in a state of “suspended animation”. By “suspended animation” is meant the maintenance of the existing state (vegetation community) till circumstances change to more favourable for normal dynamics or functioning to return. Catapano (2004) concludes that the Sand Forest assemblages must have remained stable since at least ~ 1800 BP years ago.
- In the past the coastal grasslands of Maputaland were seen as secondary in the sense of being "unnaturally" degraded forest or savanna. We contend rather that these grasslands are essentially primary in nature and the association between fire and these grasslands must be as old as the grasslands themselves.
- Some of the coastal grasslands of Maputaland also feature an abundance of geoxyllic suffrutices (resulting in the woody nature of these areas) and in many cases these plants in the past were seen as indicative of overgrazed and burnt grasslands conditions. But in actual fact this is a unique feature of a specific habitat. These dwarf woody plants can be compared with extremely stunted trees, a fact which led White (1976) to refer to them as the "underground forests of Africa".
- Kirkwood & Midgley (1996) have argued, the absence or shortage of a conspicuous ground layer and the lower understory in Sand Forest is due to herbivory. However, this study and unpublished data point towards aridity, shade, compounded by possible allelopathic characteristics. Absence of a conspicuous ground layer is the natural state in this forest type.
- Midgley (1993) states that Sand Forest is dominated by species with wind-dispersed seeds. However, Matthews *et al.* (2001) and unpublished data indicate that plant species with fleshy fruits were the most common type in Sand Forest, even when considering cover-abundance.
- We have developed a rapid survey technique for elephant impact, by using a modified Point Centre Quarter (PCQ) technique, which appears to have worked well. Useful

information on the relative use of different species and the likelihood of negative impact on their abundance from elephant feeding activity was produced.

9.3 Future research

In all studies there are gaps that become prevalent as one starts trying to interpret the results. These are important to record as it can help direct further research into the subject and related topics. From this study the following gaps and issues would help in interpreting some of the hypotheses presented. The pointers and questions put forward are in no particular order.

- Establish and compare the fauna and faunal diversity of the three principle forest types in southern Africa. More detailed studies are needed on:
 - The unique faunal element in all three of the forest types are all tropical related, but is Sand Forest's complement of tropical related animals the most pronounced?
 - Are Sand Forests and Dune Forest more closely related, faunistically?
 - What are the faunal communities and based on what resources in the three forest types?
- Sand Forest provides considerable opportunity for further research into the validity of its alleged allelopathic effects.
- Trees in Sand Forest seem to reach older ages than in woodland. Is this true and could this also be due to fire or the absence of fire?
- Research the evidence underneath Sand Forest that can reflect on the succession of that site, for example, the charcoal found in the soils underneath Sand Forest. If the hypothesis that Dune Forest is the precursor of Sand Forest, but that Sand Forest has subsequently become a separate functioning community on its own, is correct, then the charcoal under Sand Forest must be either Dune Forest or Sand Forest, but not grassland or woodland. It would, however, be reasonable to find charcoal of woodland or grassland species underlying Dune Forest, which in turn underlies Sand Forest, but if woodland or grassland charcoal were to be found under Sand Forest with no indication of Dune Forest, it could disprove the hypothesis.
- Currently Sand Forest shows a high turnover of species between the different forests patches (Van Rensburg *et al.* 2000), this applies to both dominant and rare species. More work on species turnover between patches on all taxonomic levels would be instructive.
- Does Sand Forest indeed occupy habitats more exposed to mist than woodland, and if this is the case, how does Sand Forest benefit from the exposure to mist?

- How much (i.e. what percentage of) rainfall reaches the ground following interception by the above ground parts of plants—compare between the different habitats of Maputaland.
- To what extent do the fauna collaborate floristic patterns in Maputaland?
- At what elephant population level could Sand Forest and elephant co-exist in a closed system such as Tembe Elephant Park?
- Maputaland combines a number of different and unique habitat types, from woodland to dense Sand Forest to wet coastal dune Forest. Each of these habitats contains species of invertebrates that are unique to it, perhaps one of the best researched examples being the butterflies. Based on the work of E. Pringle (pers. comm.), no less than 25% of the about 852 species of butterflies that occur in South Africa may be found in the KwaZulu-Natal part of Maputaland. Maputaland as a region has the highest biodiversity of butterflies in South Africa, and its species number is much higher than that of the Kruger National Park. Most invertebrates are very poorly known and therefore provides considerable opportunity for inventory research.
- It was considered premature to formally describe most of the syntaxa recognized during the present study. More phytosociological studies in other areas of the Maputaland Coastal plain are needed to correlate results.
- Detailed comparative studies on the ecology of the unusual Woody Grassland, in relation to conventional grassland and savanna, would be most instructive. There is a need to investigate in more detail the possible determinants and evolution of the suffruticose habit in the Woody Grassland of Maputaland.
- The taxonomic status of a *Podocarpus* species in Maputaland requires clarification.
 - Claims that pollen evidence suggests that Afromontane Forest once occurred on the coast of Maputaland (Scott *et al.* 1992) need further testing. The *Podocarpus*-pollen that people assume is indicative of temperate conditions may be misleading. *Podocarpus* species are not necessarily Afromontane Forest elements; there exist, for example, what appears to be a form of *Podocarpus falcatus* in the swamp forests of Maputaland. The presence of this *Podocarpus* is indicative of tropical conditions, as it is usually associated with the palm *Raphia australis*. The climatic history of Maputaland furthermore argues against Afromontane Forest ever occurring there.
 - Why is *Raphia australis* pollen not recorded together with *Podocarpus* pollen, currently the two species are both associated with swamp like conditions?
- Palynological analyses of boreholes and peat lands are used in inferring past environmental conditions. It would be very informative to compare the relevant existing

taxa's pollen, with pollen that is currently used in the environmental condition predictions, crucial for correct predictions.

- It is desirable to carry out a much larger number of *in situ* permeability tests, soil wet ability tests and water retention tests to confirm on a broader scale the findings presented in this study.
- Repeat the bioassays for possible allelopathic interference in Sand Forest with a more refined experimental design which is statistically robust.
- This study produced many hypothesis on the dynamics, historic development and the environmental driving forces for Sand Forest development, creating a bases for an intensive modelling exercise which could produce informative results, especially if the current climate change scenarios are applied.
- A quantitative, floristic comparison of Sand Forest on dune ridges along an east–west gradient could assist in interpreting the long term dynamics and evolution of Sand Forest.

CHAPTER 10
MANAGEMENT IMPLICATIONS

Preamble

Park management is big business, getting bigger and more complex everyday, especially with the international expectation that it will be the prime mechanism for maintaining global biological diversity Child (2004) and an integral part of the socio-economic environment in which it is embedded. Today, successful park management requires a much wider perspective than provided by conservation biology alone. If ecological reserves are to survive, each must be an example of sustainable management for all parties concerned. They cannot continue as state-managed areas of poorly executed nature conservation, but should become bridgeheads for better landuse (Child 2002). This highlights the difficult position in which park managers are placed, in most cases the absence of a clear, socially relevant and legitimate conservation philosophy.

If Conservation management agencies are to understand and manage the challenges they face, Child 2004 suggests that possible solutions lie in the way society sets about conserving and using parks and reserves. The key appears to lie not in making management more *efficient*, but in defining exactly what it aims to accomplish. Help towards achieving this effectiveness is likely to come from disciplines that are largely foreign to conservationists. This could include balancing economic issues, politics, modern business management, institutional strategies, and stakeholders' needs with the ecological and biodiversity purpose of the park. ***Thus to have a clear vision (based on stakeholder participation) and be responsible and accountable to it, this is critical to deliver on a park's mandate.***

Conservation management agencies had and have so many demands that they do not know what to focus on and as Drucker (1973) pointed out, nothing is ever accomplished unless scarce resources are concentrated on a few priorities. Because we cannot manage for something we cannot describe, we therefore need to define what exactly a park's conservation mandate should be, so that we can define the performance and accountability of public conservation management agencies.

The current vehicle that is used to develop a unified, clear vision so as to achieve a park's mandate is the Integrated Management Plan (IMP). The IMP forms the framework within which the reserve will be managed, aligned and developed in an endeavour to achieve the biodiversity

conservation, ecotourism and partnership objectives as envisaged and set by the various stakeholders during a consultative planning process.

It is important that today's research findings inform the decision-making process based on a park's clearly defined objectives (*parks mandate - IMP*). As researchers we are not to prescribe our ideas and findings as we are not party to all aspects of the conservation management decision-making—aligned to the IMP. We as researchers therefore need to state outcomes in ways which are inductive, understood and applicable by the management decision forms that are working to meet the broader goals (IMP alignment). We are to *inform the process* so that the management team who is responsible for the park mandate can be accountable to the stakeholders as per the park's vision and overall objectives. With the recommendations that follow, an effort has been made to inform the process and not to prescribe to it.

Efficient biological surveys are a fundamental requirement for the effective management of biological resources and constitute the most basic activity in the field of conservation biology (Margules & Austin 1991). Conservation priorities in Maputaland were identified after a series of reports, including definitive surveys by Bruton & Cooper (1980) and Tinley & Van Riet (1981). Both reports discuss the natural biotic riches of the region and indicate the need to safeguard these attributes. Although many surveys have been carried out, these authors have not defined or identified critical sites for biodiversity protection/conservation management. Much of the work carried out in the present study deals with this last point, although the focus was not specifically on sites but more on the habitats to which many of the biodiversity elements are closely associated. By mapping these habitats and/or being able to recognize these habitats in the field, critical and important sites for biodiversity protection/conservation can be identified and appropriate management procedures put in place.

Two main habitats were highlighted as being particularly important to Maputaland's biodiversity, namely Sand Forest and Woody Grassland (the Maputaland Centre's endemic vegetation types). Conservation of these two habitats would have the greatest impact on conservation of Maputaland's unique biodiversity. By understanding the structure and distribution of Sand Forest, Woody Grassland and related habitats, appropriate management guidelines can be put in place, both in and outside conservation areas. The very restricted occurrence of a strong tropical fauna in Maputaland provides another reason why these habitats, which the animals are associated with, should be soundly managed and conserved. Maputaland provides South Africa with a glimpse of the tropics and as such is a national asset.

The people of Maputaland have traditionally harvested natural resources, and for keeping these practices sustainable some type of quota for the harvesting of the remaining resources need to be put in place. However, the only way that this can be achieved is through mitigating impacts and this can only be done based on information gathered on biodiversity and its driving forces in the region. Results presented here would go a long way to address this last need, the information been used in reserve and area management, land-use planning, and extrapolation to other parts of Maputaland, as well as in further ecological studies. Sand Forest areas should also be promoted as a premier ecotourism destination, as it is rich in rare plants, many scarce mammals, reptiles and birds including many unknown invertebrates.

10.1 Maputaland

- As the location of the region's principal habitats is related to climate conditions, which is directly related to distance from the coast, past ocean transgressions and regressions play an important role in determining the positions of the climatically suitable zones for the different habitats. This means that in the long term (100 years and more) management of these areas will need the full range of the current habitats so as to deal with these climate changes.
- The grasslands in the region are relatively poorly conserved and managed.
- Outside the conservation areas in Maputaland, the main threats to the Sand Forest habitat are uncontrolled, such as random fires that are used in clearing areas for agriculture, uncontrolled cattle grazing, as well as selective species utilisation for traditional medicines and timber.
- Uncontrolled cattle grazing and random, uncontrolled fire affects species composition and diversity, but probably do not change the structure of the grasslands (Potgieter per com.).
- The continued afforestation of the Woody Grassland with pines, eucalypts, cashew nuts and other alien trees could, bring about a drop in the level of the water table. This could result in a dramatic increase in the woody component of the vegetation of the region.
- The planting of alien trees species over large tracts of grassland, on the other hand, not only destroys the grassland habitat but is also expected to affect the hydrology of the region negatively.

Recommendations

In the region as a whole, to achieve the maximum conservation of biodiversity of the endemic-rich flora and fauna of the Maputaland Centre (MC), specifically of the two endemic habitats of the MC, the following issues are highlighted.

- The full range of the MC habitats need to be available to deal with climate change, this through corridors or compatible landuse.
- Uncontrolled heavy cattle grazing combined with fire regimes not compatible with current ecology, need to be managed if the full spectrum of the grassland biodiversity is to be conserved and sustainably utilised.
- Continued afforestation of the coastal grasslands needs to be restricted. Afforestation effectively transforms the grasslands into commercial timber plantations, consequently changing water table levels. This will probably result in the grassland communities changing into more woodland type vegetation communities.
- These land transformations are also a major source of alien plant infestations, such as the problem plant *Chromolaena odorata*. Currently millions of Rands are spent on the eradication of this species in infested areas.
- Areas outside formal conservation areas, that have near pristine Sand Forest and coastal grasslands containing Woody Grassland, need to receive conservation attention.

10.2 Sileza Nature Reserve [SNR]

- With relatively little Woody Grassland formally conserved, the SNR, despite its small size, fulfils a crucial role in ensuring the preservation of the endemic-rich flora and fauna of the MC.
- Regular seasonal fire is an important factor in maintaining the Woody Grassland of coastal Maputaland.
- These grasslands are essentially primary in nature and not secondary in the sense of being "unnaturally" degraded forest or savanna.

Recommendations

There currently does not seem to be many pressing management issues in the Sileza Nature Reserve as the ecosystem is maintaining itself quite well under current environmental scenarios.

Sileza Nature Reserve does though fulfil a crucial role in ensuring the preservation of the endemic-rich flora and fauna of the coastal grassland and Sand Forest ecosystems.

The coastal grasslands in and around Sileza Nature Reserve have been receiving annual to bi-annual burns for quite some time already, be it natural or anthropogenic. These grasslands have a component that is unique to the MC, namely a large number of geoxylic suffrutices. The existence of these Woody Grasslands is based on water table levels and regular fires. From the vegetation work done in these grasslands, the current fire regimes, where not combined with high numbers of cattle, seems to have no detrimental effect on the biodiversity of the grasslands but is essential for their maintenance. Therefore, in the case of the management of the Sileza Nature Reserve, it is felt that annual random mosaic burns (as is currently the case) is a sound strategy if the current habitats are to be maintained in a reasonable natural state, although stocking rates of game and cattle should be kept at the lower levels. These regular fires would prevent accumulation of biomass and thus keep to minimum destructive runaway fires, which could penetrate the Sand Forest patches in Sileza Nature Reserve.

10.3 Tembe Elephant Park

- Tembe Elephant Park has the greatest area of protected Sand Forest in South Africa and thus fulfils a crucial role in ensuring the preservation of the endemic-rich flora and fauna of the MC.
- Sand Forest seems to exist in a state of ‘suspended animation’—maintaining itself in areas where it exists in a pristine state. In the management of these forest patches, any disturbance should be kept to a minimum, as disturbance would slowly erode these Sand Forest patches.
- The inclusion of Sand Forest in conservation areas, where there is an abundance of large ungulates, is no guarantee of the future persistence of this vegetation type.
- In Sand Forest, β -diversity (defined as the turnover of species between the different forest patches) is very high for both dominant and rare species (Van Rensburg *et al.* 2000). Therefore conserving one patch of Sand Forest will not nearly be adequate to conserve all of the genetic complement of Sand Forest.
- The effects of large herbivores, regular fires and the Sand Forest dynamics itself can lead to the disappearance of this vegetation type. One such threat to Sand Forest within a conservation area is highlighted in Tembe Elephant Park, where the over abundance of elephant is combined with the current fire regime.

- Under the time scale that Sands Forest dynamics seem to operate, any destructive impacts could negatively affect Sand Forest conservation within Tembe Elephant Park.
- The primary reasons for the proclamation of Tembe Elephant Park was the protection of the natural elephant population of Maputaland and the protection of Sand Forest. This has lead to a conflict of interests between Sand Forest and elephant. Although these elephants prefer plant species from woodland habitats, they are increasingly utilising Sand Forest species.
- Presently, it appears that a suite of plant species, including both relatively common and rare species, that are strongly selected for, are being utilised by the elephants to the extent that they may be reduced to very low densities, or possibly local extinction.

In Tembe Elephant Park we have a complex situation with many conflicting scenarios as well as the Park objectives at odds with the long term conservation of the current biodiversity and systems in the Park (TEP has the greatest area of protected Sand Forest in South Africa). To get a good overall balance for the future, well-focused visions for the Park and application of these visions within set time frames is going to be crucial. To paint a picture of the complex nature of the conflicting scenarios facing the managers of this park, here are some of the issues that need to be taken into consideration by management when formulating very specific management policies and practices (not the aim of the present study – IMP process):

- The long-term vision for Tembe Elephant Park is as follows (Extract from Draft Integrated Development Plan based on Proclamation agreements for Tembe Elephant Park): “The ecological integrity and cultural values of Tembe Elephant Park, in conserving the Tembe elephants, Sand Forest and associated biodiversity, is maintained and enhanced in realising sustained benefits to the people of the Tembe community through land partnerships and sustainable tourism”.
- The reserves’ conservation objectives and reason for establishment are to:
 - Protect the lives and property of the local people from damage and injury by free roaming elephant.
 - Preserve the last naturally occurring population of African elephant in KwaZulu-Natal.
 - Conserve and protect the unique Sand Forest.
 - Protect one of the largest populations of suni antelope (*Neotragus moschatus*) in southern Africa.

- Regular seasonal fires are an important part of the woodland/savanna systems in Tembe Elephant Park, yet negative impacts on Sand Forest are of concern (reserve objectives).
- The elephant population of Tembe Elephant Park is expanding and with it comes impacts on the habitat and in this case impact on Sand Forest is of concern (reserve objectives).
- Natural resource use (sustained benefits to the people of the Tembe community) from reed cutting to ad hoc access to registered inyanga's to collect medicinal plants in the Park.
- Sustainable tourism and the need for game numbers to be at a level that regular sightings of specifically "big five" animals (of which elephant is one) are at levels good for tourism.

In trying to balance the issues highlighted it will need to be done through integrated development plans in consultation with *all stakeholders*, which will need to be focused upon *agreed visions*. These agreed visions would dictate the more practical steps to be implemented to balance the issues raised. This will involve different expertise on conservation, tourism, local people needs and political. Recommendations that follow are issues that need to be considered from the point of view of balancing the biodiversity conservation objectives of the park.

In the case of Sand Forest, because it is such a sensitive habitat, any impacts need to be kept to a minimum if the long-term preservation of such forest and its associated fauna is to be achieved, thus all destructive impacts to Sand Forest need to be kept to a minimum. Issues that need to be addressed or put in place that would enhance the viability of the long-term conservation/preservation of the Sand Forest habitat are:

- It is important that the integrity of the Sand Forest edges remains intact to provide some protection against fire, so that the natural mosaic fires of Tembe can continue, as these fires are an essential part of the Tembe Elephant Park ecosystem as a whole.
- The current resource use in the Park is mainly reed harvesting, which has the least impact on the reserves biodiversity objectives, but harvesting of medicinal or any plants in the Sand Forest needs to be monitored closely and kept at sufficiently low levels.
- The most central issue is the one involving the elephant. Specifically in that the elephant of Tembe Elephant Park are a conservation objective for the Park (also KwaZulu-Natal), a tourism draw card as well as a critical part of the proposed Transfrontier initiative with Mozambique. The elephant population is growing and with it comes increased impacts on Tembe Elephant Park's different habitats of which the impacts on Sand Forest is of the most concern (Sand Forest is one of the Parks conservation objectives and part of the

reason for establishment). This is made more complex by the low recovery potential after disturbance of Sand Forest, compounded by the effects of fires penetrating the forest at these disturbed sites. Issues that need to be considered in the management around Sand Forest and elephant are:

- Expand the range of the elephant so as to reduce time spent in the Sand Forest zones. There are two ways this could be addressed, one locally and the other internationally. The local one is the Mbangweni Corridor, which would effectively link Tembe Elephant Park to the more nutritious areas of the Pongola River floodplain in Ndumo Game Reserve. The other, more long term international option, would be to reinstitute the old movement patterns of the elephant through the proposed Transfrontier initiative with Mozambique. This would be by the removal of the northern border fence with Mozambique.
- Reduce return rates of elephant to the Sand Forest areas in the western portion of the Park where most of the Sand Forest in the Park is to be found, this could potentially be done through water point management. There should be no water points kept artificially filled in the western part of the Park, especially during dry periods.
- Reduce direct foraging impacts on Sand Forest, which are thinning the forest as well as removing Sand Forest recruitment possibilities. Elephant numbers and other wildlife numbers should be curtailed within the limited area of Tembe Elephant Park, especially if the range expansion possibilities cannot be achieved in the near future. In the future it might even be necessary to create elephant exclusion areas (fencing or by other effective methods) around Sand Forest patches if pristine intact forest and its associated fauna, (the suni antelope is a conservation objective for the Park) are to be conserved.

CHAPTER 11
CONCLUSIONS

11.1 Maputaland environment and general ecology

- The geological history of Maputaland suggests that the current ecosystems in the region are most probably of recent derivation. The region was last inundated by the ocean approximately 3–1.8 million years BP ago. In fact, many endemic plant taxa comply with the concept of neo-endemics (young taxa). The MC comprises a unique environment in Africa in that it is geologically young with biological evolution, notably speciation, being actively driven.

11.2 Plant-soil characteristics

- The dominant oxide in the soil samples is silica, indicating that the cover sands in the study area consist mainly of quartz sand.
- The trace element analyses show that boron, barium, chromium, hafnium, niobium, nickel, lead, rubidium, scandium, titanium, iron, strontium, uranium, vanadium, zinc and zircon are present in noticeable concentrations.
- Inorganic analyses of soil samples indicate that calcium, copper, molybdenum, sodium and vanadium are present in low concentrations in all the samples.
- The high boron concentration evident in soil samples is ascribed to the presence of tourmaline, a boron-containing stable complex silicate mineral.
- Aluminium values are relatively high, although no marked difference in concentrations can be seen between the different biotypes studied.
- The traces of the organic compounds obtained by gas chromatography for woodland and grassland habitats were virtually identical, both in terms of the compounds present as well as relative abundance. The Sand Forest leachate, however, contains a compound or compounds that render the soil more acidic and contains more dissolved solids.
- From preliminary germination trials in soils of different vegetation types, it would appear that some attribute of the Sand Forest soil is inhibiting emergence and growth. The greatest suppression of growth occurred in the Sand Forest soils.
- Preliminary results indicate that the compound/factor that possibly suppresses growth can be mobilised by water moving through the soil, and is thus being leached.
- Changes in field-saturated permeability of the soils, were found to differ by an order of

magnitude and are likely that differences in unsaturated hydraulic conductivity, which would be closely linked to the water retention characteristics of the soil, might be even more pronounced.

- In Tembe Elephant Park, Sand Forest, and the burning of this vegetation which may occur frequently, does appear to have significant impacts on the hydraulic characteristics of the near-surface soil.

11.3 Phytosociology

- A straightforward situation exists in the phytosociology of the MC, with the important determinants for the vegetation communities in the region as a whole being the interconnected effects of water table (moisture), soil type and topography, upon which fire and vegetation dynamics have been superimposed.
- Dynamics of water in the landscape tend to show a strong relationship with the structure of the plant community at the first physiognomic level.
- Casual observations and comparison with other studies (notably Myre 1964, 1971; Lubbe 1996; Matthews *et al.* 1999; Gaugris 2004) have shown that the plant communities (and thus associated environmental factors) of the present study extend over most of the Maputaland coastal plain.
- The results of the ordination not only confirm the vegetation classification, but also give an indication of floristic and associated habitat gradients.

11.4 Tembe Elephant Park [TEP]

11.4.1 Plant communities

- In the case of Tembe Elephant Park, which lies in a drier and topographically higher part of the Maputaland coastal plain, the water table level is not a leading factor, although soil moisture plays an important role in plant communities' delineation.
- Eight ecological-interpretable plant communities have been distinguished and described for Tembe Elephant Park.
- 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.
- In the case of Sand Forest associated with the ancient dune cordons and driest soils, it is suggested that historic plant dynamics, in relation to the coastal plain geomorphology development, could be a major determinant of the present day Sand Forest patches.
- Sand Forest was found to occur in a mosaic with dry woodland and thicket.
- Fire is seen as an important natural ecological factor in the most of the plant communities except in Sand Forest.
- From casual observations and comparison with other areas it was noted that many of the “negatively” fire-impacted Sand Forest patches and margins do not regenerate at all. This leads to the assumption that the extent of Sand Forest is decreasing as a result of fire.
- Indications are that the impacts of large herbivores, such as elephant, which in the past were not closely associated with Sand Forest, in combination with fire, could speed up the changes taking place in Sand Forest and other communities. Under the time scales, that Sand Forest dynamics seems to operate, these added impacts could negatively effect Sand Forest conservation within Tembe Elephant Park.

11.4.2 Floristics

- Eighty-four endemic/near-endemic vascular plant taxa of the Maputaland Centre were recorded in Tembe Elephant Park, but the actual number present is expected to be slightly higher due to incomplete sampling.
- Most endemics plant taxa 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 madagascariensis-Combretum molle* Woodland.
- Another community relatively rich in number of endemic plant taxa is the *Spirostachys africana-Berchemia zeyheri* Closed Woodland on clay, where 20 endemic plant taxa have been recorded. This is a restricted community, in terms of size and distribution, in Tembe Elephant Park but many of the endemics have 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 communities.

11.4.3 Large herbivore (elephant) impacts

- The modified Point Centred Quarter (PCQ) approach used as a rapid survey technique worked well. Useful information on the relative use of different plant species and the likelihood of negative impacts on their abundance from elephant feeding activity, has been provided.
- It was found that the bulk of the elephant diet is made up by species which are relatively common, and which are strongly, moderately, lightly or neutrally selected for. These are *Acacia burkei*, *Acacia robusta*, *Azelia quanzensis*, *Albizia adianthifolia*, *Albizia versicolor*, *Combretum molle*, *Dialium schlechteri*, *Sclerocarya birrea*, *Strychnos madagascariensis*, *Terminalia sericea* and *Trichilia emetica*.
- It appears that the suite of species, including both relatively common and rare species, that are strongly selected for are being utilised to the extent that they may be reduced to very low levels, or possibly local extinction. These species include *Acacia robusta*, *Azelia quanzensis*, *Albizia adianthifolia*, *Albizia versicolor*, *Antidesma venosum*, *Elaeodendron transvaalense*, *Euphorbia tirucalli*, *Ficus stuhlmannii*, *Galpinia transvaalica*, *Garcinia livingstonei*, *Hyperacanthus microphyllus*, *Kigelia africana*, *Manilkara discolor*, *Newtonia hildebrandtii*, *Phyllanthus reticulatus*, *Syzygium cordatum*, *Sclerocarya birrea*, *Terminalia sericea*, *Tricalysia junodii*, *Trichilia emetica*, *Warneckea sousae* and *Wrightia natalensis*.
- Several plant species which are Maputaland endemics or near-endemics with a limited distribution, may be threatened by elephant impact within Tembe Elephant park. These include *Combretum mkuzense*, *Dialium schlechteri*, *Hyperacanthus microphyllus*, *Warneckea sousae*, *Tricalysia junodii* var. *junodii* and *Wrightia natalensis*.
- It was found that more plant species are utilised in floristically diverse habitats than in less diverse habitats.
- The proportion of selected for plant species appears to be more or less constant at around 60% of the species available.
- The study showed that those plant species most highly selected for are used in all habitats in which they occur, but the degree of selection is different in the different habitats, and appears to be influenced by the relative abundance of other forage species and other unknown factors.
- Indications are that Sand Forest, a unique vegetation type, of limited distribution and area conserved, may be threatened as a type because of general thinning, as well as direct impacts on particular plant species.

- Because utilization is influenced by relative abundance, the plant species utilization classification presented here should be expected to change. For this reason only potential impacts by elephants on any particular species can be predicted from this survey.
- Tembe Elephant Park currently does not embody prime elephant habitat – owing to limited nutritional resilient habitats and surface water being limited within Park.

11.5 Sileza Nature Reserve and surrounds

11.5.1 Plant communities

- Dynamics of water in the landscape, in this case the water table, show a strong relationship with structure and composition of the major communities.
- Twelve ecologically interpretable plant communities were distinguished and described in Sileza Nature Reserve.
- All the proposed communities are easily distinguishable in the field on the basis of growth form, general species composition and diagnostic species.
- Evidence suggests that fire is an essential factor in maintaining the Woody Grasslands of coastal Maputaland. In fact, the association between fire and these grasslands must be as old as the grasslands themselves.
- It is hypothesised that a drop in water table over the long term would be conducive towards the creation of habitats more suitable for the development of woodland, thicket and even forest.
- From aerial photo comparison it was found that the forests and woodlands of the study area turned out to be stable features—all being strictly confined to the same sites over at least the past 50 years, although size and floristic composition might have changed.

11.5.2 Floristics

- Thirty-five endemic/near-endemic plant taxa of the Maputaland Centre were recorded in Sileza Nature Reserve, but the actual number present is expected to be slightly higher due to incomplete sampling.
- Most endemics were associated with only two of the five major plant communities, with 14 taxa associated with *Artabotrys monteiroae-Dialium schlechteri* Forest (Sand Forest) and 21 with the *Themeda-Salacietum* Woody Grassland.
- The observed low species diversity and paucity of regional endemics in hygrophilous grassland communities is a common phenomenon throughout southern Africa.

- Maputaland Centre 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).
- It was found that the Maputaland Centre endemics are well represented in both grassland and Sand Forest, with the latter, on a regional basis, being perhaps the single richest community in MC in terms of plant taxa endemics.

11.6 Woody Grassland

- Despite White's (1976) statement that relatively few suffruticose species are confined to the Tongaland-Pondoland Regional Mosaic, this study found that plants species with this growth-form are abundant in the study area where they are almost exclusively confined to the *Themeda-Salacietum* Woody Grassland.
- The present study confirms the observation that geoxylic suffrutices are prevalent in areas of sandy soil and relatively low relief. However, doubt is cast on the validity of White's claim that seasonally waterlogged soil is the primary determinant for the presence of this growth-form. In the study area the distribution of geoxylic suffrutices rather reflects the depth of the water-table, being most abundant in sites where it is high, yet still below 1.8 m. These sites comprise mainly those relatively high-lying, well-drained areas such as dune crests and slopes, the surface soils of which are never waterlogged.
- Geoxylic suffrutices are noticeably absent from inter-dune depressions, the only areas that are clearly seasonally waterlogged.
- Many plant species are endemic to these Woody grasslands, but also several appear to have developed an obligate geoxylic suffruticose habit. It is hypothesised that this signifies a long evolutionary history for this particular vegetation type in the region.
- It is hypothesised that these grasslands are essentially primary in nature and not secondary in the sense of being "unnaturally" degraded forest or savanna.

11.7 Sand Forest (“Licuáti” Forest)

- This study highlighted that Sand Forest is a unique forest type and differs from all other forest types recognised for southern Africa.
- Sand Forest was found confined to a narrow zone on the coastal plains of northern KwaZulu-Natal and southern Mozambique, from approximately False Bay up to

Quissico. This makes Sand Forest quite a limited distributed forest type, especially in South Africa.

- Plant species with fleshy fruits are the most common to be found within Sand Forest, even when considering cover-abundance, and seeds/fruit are therefore chiefly animal dispersed.
- Wind-dispersed seeds, not just fruits with wings, were found to be rare in Sand Forest.
- Evidence suggests that Sand Forest has very shallow root systems, with most of the roots occurring in the upper 1–1.8 m of the soil. There are no records of deep tap root systems.

11.8 Sand Forest structure

- Sand Forests were found to be dense with no well-developed herbaceous or ground layer, with distinct boundaries.
- Indications are that drought-deciduousness is much better developed in Sand Forest than in either Dune or Afromontane Forest.
- Two physiognomic and structural types of Sand Forest were found to occur. One fits the basic physiognomic definition of forest (tall Sand Forest), while the other can be described as a thicket (short Sand Forest).
- Tall Sand Forest and Short Sand Forest (structurally more correctly referred to as thicket) differ in terms of both floristic and structural attributes.

11.9 Environment

- Sand Forest is associated with the relatively drier sandy soils, which in many cases are old dunes systems further inland in the drier northern KwaZulu-Natal and southern Mozambique areas of the greater Maputaland.
- Evidence suggest that Sand Forest occurs under relatively drier conditions compared to other forest types (less than 700 mm of rain per year) and is thus referred to as tropical dry forest, and where it does occur in areas of higher rainfall (greater than 700 mm), it retreats to the higher sand dunes where the sands are well-drained.
- Indications are that Sand Forest is very efficient in capturing all or most of the rainfall that penetrates the first metre of ground.
- Sand Forests in Maputaland are found in areas periodically experiencing heavy dews and low-level mists, especially in winter. This could effectively increase the precipitation and

play a role in the survival and/or persistence of Sand Forest in the midst of the woodland dominated landscape.

- Sand Forest soils were found to show hydrophobic characteristics under dry conditions, but when they get sufficiently wet, have a better water-holding capacity than the surrounding woodland soils.

11.10 Dynamics

- Field observations and the results of germination trials and soil analyses strongly suggest that some type of allelopathic interference is taking place in and around Sand Forest.
- Preliminary findings suggest that Sand Forest competitively excludes other vegetation types via chemical (allelopathy) and physical (hydrophobic soils) means — a buffered environment.
- It is hypothesised that in Sand Forest all plants seem to play a role in some way in producing the allelopathic property, keeping out other competing plant communities (e.g. woodlands).
- Evidence suggest that the absence or shortage of a ground layer and the lower understory in Sand Forest is not due to herbivory, but could rather be ascribed to aridity compounded by allelopathic characteristics.
- Evidence suggests that Sand Forest seems as if it exists in a state of ‘suspended animation’—maintaining itself in areas where it exists in a pristine state. This characteristic is one in which Sand Forest differs significantly from Afromontane and Dune Forest. Indications are that the present-day climate regime is not suitable for the establishment and expansion of Sand Forest. Indications are that the size and number of Sand Forest patches which correlate with Dune cordon 3 approximately 50–60 km from the coast and with a mean annual rainfall of 650–700 mm, have not increased. Catapano (2004) concludes that in these areas there have been stable vegetation regimes since at least ~ 1800 years BP ago.
- It is suggested that Sand Forest was originally established under relatively moister climatic conditions.
- It is put forward that if the current climatic conditions continue indefinitely, Sand Forest will become extinct in the drier areas because it cannot recruit to any significant degree under the current environmental conditions.
- It is suggested that Sand Forest in the past would have covered larger areas of the Maputaland coastal plains as what is the case today.

- It is hypothesised that the effect of the transgression and regression of the ocean in the past would therefore have been that the zones on the coastal plain suitable for Sand Forest would have shifted plus possibly been more wide-ranging (depending on climate conditions).
- Gap dynamics does not appear to play a significant role in Sand Forest; indeed, it seems that gap dynamics may not nearly operate at the scale at which it operates in the other two forest types. Under favourable conditions, Sand Forest elements could recruit under present Sand Forest canopy as well as in smallish gap-falls inside the forest. However, with large gap-falls the opposite could occur, with grassland and woodland species taking hold.
- Evidence was found that indicate that severely damaged Sand Forest sites (for example by fire or mammals such as elephant and man) are usually replaced by woodland vegetation.
- Indications are that many of the large specimens of Sand Forest elements that occur outside Sand Forest in woodlands are remnants or survivors of past Sand Forest patches that are not present anymore.
- Information suggests that Sand Forest is not a resilient vegetation type.

11.11 Endemicity and floristics

- Sand Forest is a forest type rich in endemic plant taxa (neo-endemics). These Sand forests rich in neo-endemic species are centred in an area south of Maputo–Quissico (Mozambique) to just north of St Lucia.
- Of the 230 endemic or near-endemic plant species recorded for Maputaland, 33 are found in Sand Forest with 20 largely confined to this vegetation type. This makes Sand Forest one of the communities with the highest number of restricted-range plant endemics in Maputaland.
- It was found that Sand Forest does not have many fern and moss species, and those few species present, are able to withstand severe desiccation.
- Informal observations showed that a large proportion of epiphytes that occur in Sand Forest are lichens (not sampled), and can withstand repeated desiccation, while the epiphytic orchids are often xerophytic.

11.12 Fire

- Sand Forest occurs in the midst of fire-prone habitats, namely the woodland and a Woody Grassland mosaic.
- It is suggested that the bare or sparsely vegetated zones (low fuel load) surrounding Sand Forest contribute to lower fire frequencies and intensities thus serve as effective natural firebreaks.
- Indications are that destructive fires which occur periodically are slowly reducing the extent of Sand Forest.

11.13 Sand Forest evolutionary history

- The bulk of the evidence supports the variation of the primary hypothesis that *Dune Forest is the precursor of Sand Forest, but that Sand Forest has subsequently become a separate functioning plant community on its own.*

11.14 Management

- Management recommendations are made for Maputaland in general, as well as more specific ones for Tembe Elephant Park and Sileza Nature Reserve.
- It is highlighted that the some of the more important outcomes of this study to be considered in management plans should be:
 - Biodiversity value of Sand Forest and Woody Grassland
 - Regional connectivity (ecological and geomorphological) of the different vegetation communities
 - Sand Forest sensitivity to impact
 - Fire
 - Woody Grassland require regular seasonal fires
 - Elephant and other large herbivore forage effects
 - Human resource use in sensitive habitats and this on the limited distributed plant species
 - Effect of alien invasive plants in sensitive habitats

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ANNEXURES

Annexure 1. Vegetation induced variability of hydraulic characteristics of aeolian sand.

Annexure 2. Testing generalities in the shape of patch occupancy frequency distributions.

Annexure 3. Table showing the volumes removed by elephant, preference index and densities per ha for each woody species in each habitat type in Tembe Elephant Park.

ANNEXURE 1

Fourie, A.B., Matthews, W.S. & Hattingh, R.P. 2002. Vegetation induced variability of hydraulic characteristics of Aeolian sand. Proc. 3rd International Conference on Unsaturated Soils, Recife, Brazil, March 2002, Vol.1, pp. 411–415.

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Vegetation induced variability of hydraulic characteristics of an aeolian sand

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ABSTRACT: There is a growing tendency to derive certain hydraulic characteristics of a soil, such as the water retention curve and saturated hydraulic conductivity, using empirical correlations with the particle size distribution. Useful as these relationships may be, the importance of other factors is recognised as influencing these empirical correlations, eg compaction density. This paper presents results that highlight another, somewhat neglected factor that may have a profound influence on the hydraulic characteristics of an aeolian sand. This is the impact of organic secretions or exudes produced by certain vegetation as a counter to the encroachment of other species. Based on field measurements presented in the paper, it appears as though these organic materials may significantly alter the water repellency of the sand, its water retention characteristics and its hydraulic conductivity. Although the findings should be considered preliminary at this stage, it highlights an area that requires further study.

1. INTRODUCTION

The Tembe Elephant Park in northern Kwazulu-Natal province of South Africa, in addition to having an extremely valuable elephant population, forms a central part of the IUCN International center of plant diversity. Southern Mozambique and the northern part of KwaZulu-Natal are recognised as a Centre of Plant Endemism, namely the Maputaland Centre [MC]. Sand Forest, also known as Licuati Forest in Mozambique, is more or less confined to the broad coastal plain between St Lucia in northern KwaZulu-Natal, South Africa, and Maputo in southern Mozambique—a region known as Maputaland. Forest stands occur as isolated patches mainly associated with ancient north-south trending inland sand dunes. A significant number of the endemics/near-endemics are associated with Sand Forest areas, making this perhaps the most remarkable plant community in the MC .

Field observations have shown that after extensive bushfires have occurred in these forests, the forest vegetation does not re-establish, but rather encroachment of grassland and woodland species takes place and the sand forest retreats. An extensive study was carried out using a neutron probe instrument to

measure profiles of water content with depth over a period of over a year at a number of locations within the Park. Sites included healthy sand forest, recently burned forest, grassland and the indigenous woodland habitats. Although the soil conditions are extremely homogeneous in terms of particle size distribution across the study area, being aeolian in origin, the neutron probe profiles at some time after a particular rainfall event were very different.

2. CHARACTERISTICS OF SITE

The area is 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. A noticeable feature of the sand forest in Tembe is its very sharp boundaries, which in most cases is defined by narrow zones of sparse vegetated to bare sand areas directly adjacent to the sand forest. These zones of bare sand are in most cases followed by grassland communities, with a general appearance reminiscent of pioneer areas. These strips bordering the sand forests were thought to be due to the trampling effect of game and were the subject of an investigation by Mathews et al (2001).

The continuing loss of valuable sand forest areas, particularly their inability to re-establish after bush fires, led to the above investigation, one of the aims of which was to investigate the potential of allelopathic interference amongst competing plant species somehow contributing to the loss of sand forest. A plant may interfere directly with the growth of its neighbours through either resource competition or chemical inhibition. This may take the form of what is known as allelopathic phenomena, whereby a plant may release toxic organic compounds into the environment. Under appropriate conditions, these chemicals are released in sufficient quantities to affect the growth and development of individuals of the same or other species. The substances are released into the environment through leaching of living plants, root exudates, volatilisation, residue decomposition and microbial activity.

It is not this potential allelopathic effect that is important in this study, but how these organic compounds may affect the hydraulic characteristics of a sand. Coupled with the effect of these organic compounds is how they alter (and thus further affect the hydraulic properties of a sand) upon burning. In the work by Mathews et al (2001), samples of sand from various locations were leached with methanol and a trace of the organic compounds present in the leachate obtained on a gas chromatograph. The most striking feature was that there were organic compounds (unidentified) present in the sand forest samples that were present in lesser quantities at the edge of the sand forest and not present at all in the grassland or woodland species. This observation should be borne in mind when considering the permeability and field moisture profiles described later in the paper.

A further complication that seems to arise at Tembe is that bush fires appear to alter the dynamics of the competition between various plant species. Current thinking is that the fires may alter the allelopathic organic compounds, thus changing the ability of one species to resist invasion by another species. Evidence of the effects that bush fires can have on soil characteristics is described below.

3. EVIDENCE FOR CHANGES IN PROPERTIES DUE TO WILDFIRES

In the fields of soil science and agriculture, the concepts of soil water repellency and the effect this may have on hydraulic characteristics is well-

documented, eg Doerr et al (2000). It is generally associated with coarse-textured, sandy soils and as shown by De Bano (1991) is most likely to develop in soils with less than 10% clay content.

De Bano et al (1970) and Savage (1974) proposed a mechanism in which heated hydrophobic organic substances in the ground litter and topsoil volatilise during burning and a proportion may travel downward into the soil, following a temperature gradient until they condense in a concentrated form, often forming a coating to the soil grains. This movement is easier in permeable, sandy soils. Aside from redistributing and concentrating these hydrophobic substances in the soil, Savage et al (1972) suggested that the heat generated during a fire improved the bonding of these substances to soil particles. It is also interesting to note that the extreme heat generated at the ground surface tends to destroy these substances, with the consequence that water repellent soil may be concentrated at some (usually relatively shallow) depth below the surface (Doerr et al, 2000). This was clearly shown by Scott and van Wyk (1990) who found that under unburnt pine plantations water repellent soils were very infrequent, although they did occur at all depths. In areas where high fuel load fires had taken place, strongly repellent soils were developed below the surface to depths of up to 15cm.

Changes to a soil which make it water repellent are also likely to alter other characteristics of the soil. Dekker and Ritsema (1994) found that an increase in the water repellency of a sandy soil decreased the water retention capacity of the soil, as would be expected.

4. SOME PROPERTIES OF THE TEMBE SAND

The cover sands of the Maputaland region are mainly aeolian in origin and consist of thin veneers of sandy topsoil. X-ray diffraction tests showed the percentage of silica oxide was not less than 94% in the samples tested, indicating that these cover soils consist mainly of sand. A typical grading curve is shown in Figure 1 and very little variation from this curve was obtained. The upper metre, if not more, can be assumed to be extremely similar across the four sites discussed later in the paper, at least as regards particle size distribution.

4.1 *In-situ permeabilities*

Tests were carried out at six different locations within the southern area of the reserve to determine the in-situ permeability of the aeolian sand and obtain some indication of its variability. The sites were chosen to provide a complete spread of the vegetation zones at Tembe and thus included sand forests and neighbouring grassland and woodland habitats as well as a relatively newly burnt section of sand forest. The tests were carried out using a Guelph permeameter (Reynolds and Elrick, 1985) and two tests at different depths were carried out at each location tested.

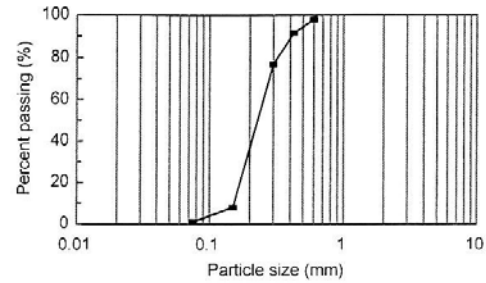
Table 1. Hydraulic conductivity measurements at Tembe

Site	Depth (cm)	Hydraulic conductivity (cm/sec)
Grassland	30	10^{-2}
	50	2×10^{-2}
Forest edge	20	7×10^{-3}
	50	3×10^{-2}
Sand forest	20	10^{-3}
	50	5×10^{-3}
Deep sand forest	26	3×10^{-3}
	51	5×10^{-3}
Woodland	20	10^{-3}
	48	10^{-2}
Burnt forest	20	4×10^{-3}
	59	10^{-2}

The results are summarized in Table 1 and the value given for permeability is effectively the field-saturated value. Given the extremely homogeneous nature of the sand, the variation in permeability is very pronounced. In particular, the grassland and woodland areas had noticeably higher permeabilities than did the sand forest. The recently burnt forest area also tended to have higher permeabilities than the unburnt forest soils. Of note at this site is the high permeability at a depth of 59cm, which is discussed later in terms of wettability tests.

Although there clearly seems to be significant differences in the measured permeabilities, with Figure 1. Typical particle size distribution curve for aeolian sand at Tembe

variations of one order of magnitude over short distances, one needs to be mindful of the inherent difficulties of carrying out permeability tests



accurately.

Further testing to determine whether the noted variation is statistically significant or not will be carried out in the near future and at present it is only possible to remark on the apparent variation, which appears to correlate with differences in prevailing vegetation. Although speculative at this time, it may be that if a sand forest area experiences a particularly high fuel-load fire, the organic material produced by the sand forest vegetation (as part of its allelopathic tendencies) is either volatilised or fluidised and migrates vertically downwards into the sand, re-condensing at some lower depth to form a particularly hydrophobic layer. This removal of the hydrophobic organic material could explain the increase in permeability that is evident for the newly burnt forest as well as the area on the edge of the forest. More permeable soil may mean that establishment of new sand forest vegetation is more difficult and hence it is out-competed by the grassland vegetation, which then successfully encroaches into newly burnt areas. As indicated above, this is still speculative and a great deal more field testing is necessary.

Further evidence of the significant differences in hydraulic characteristics between adjacent areas that are similar except for the prevailing vegetation type is given in the following section which describes the measured profiles of soil moisture during one month of the rainy season at Tembe.

5 PROFILES OF WATER CONTENT MEASURED IN-SITU

The reported profiles of moisture content were obtained using a nuclear density probe, with the vertical access tubes installed some three months prior to the period for which results are reported here. The

calibration of the instrument was checked by measuring the water content of constant-volume samples recovered during excavation for the access tubes and comparing these measurements with the instrument readings.

The two months preceding the time during which the reported measurements were taken were very dry, with a total of only 19mm rainfall. Rainfall during the month studied (October, which is the start of the rainy season) prior to the 22nd of the month totalled only 2½mm. On the 22nd and 23rd there was 22 and 32mm respectively, with very little further rain until the 30th.

The measured profiles of water content are shown in Figure 2, in terms of volumetric water content versus depth below ground surface. Although almost daily results were available, results are only shown for five particular days in order to highlight differences in response at the various sites. Results are shown for a site that was deep within a sand forest, a nearby recently burnt forest area (which had been subjected to a ‘deep’ burn), a grassland area adjacent to the sand forest and a woodland area.

At the start of the month (ie after the dry winter period) the profiles are relatively uniform, with water contents of only about 2 to 3%. These remained virtually unchanged until the start of the heavy rain on the 22nd of the month. These profiles can thus be considered to be the effective equilibrium profiles and, as shown later, are consistent with the form of the water retention curve reported later in the paper. The first set of readings obtained after the start of the rain was on the 24th of the month and there are striking differences in the response of the various sites to what was the same rainfall event. Firstly, penetration of water into the sand forest soil seemed to occur to a greater depth during the two days after the start of the rain than in the other profiles. It also appeared to get wetter, with values in excess of 12% being reached at 60cm depth. In the woodland area on the other hand, the water content did not rise above 10% and increases in water content were confined to a horizon above a depth of about 70cm, with virtually no penetration of water occurring below this depth. At first glance this appears to be contradicting the measured field permeabilities, since the woodland values were typically about an order of magnitude higher than the

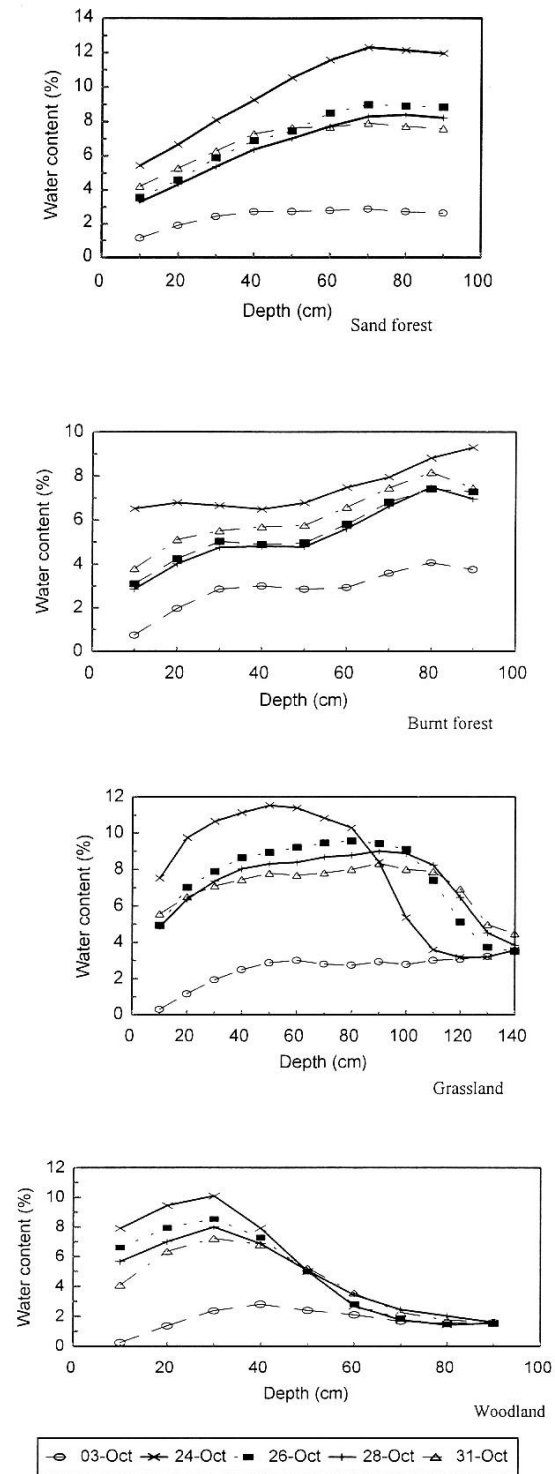


Figure 2. Profiles of water content at four sites in Tembe

forest soil values and one may therefore expect the water to penetrate to greater depth in the woodland

area than in the forest area. However, the rate of precipitation was significantly less than the infiltration capacity of any of the soils, at about 2×10^{-4} cm/sec if averaged over the 24 hour period. This means that the rainfall was able to enter the soil without saturating it and percolation occurred under partially saturated conditions. The unsaturated coefficient of hydraulic conductivity, which is a function of water content, would have controlled the rate of percolation into the soil profiles. The effects of hydrophobicity could become particularly important in this instance, with the soil's water retention capacity and effectively its unsaturated hydraulic conductivity having a major effect on the downward movement of water after a rainfall event. A water retention test was carried out on a specimen of soil from a depth of 20cm at the burnt forest site. The resulting curve is shown in Figure 3 and as can be seen, the sand had a very low air-entry value and exhibited an extremely rapid loss of moisture upon application of suctions greater than about 4kPa.

In an attempt to determine whether there was any obvious difference in the water repellency of the various profiles, small specimens from each of the test locations and depths at which permeabilities were measured in the field (ie analogous to Table 1) were subjected to a simple wettability test as outlined by Dekker and Ritsema (1994). The test consists of dripping a few drops of distilled water via a standard medicinal dropper onto a level surface of the soil. The

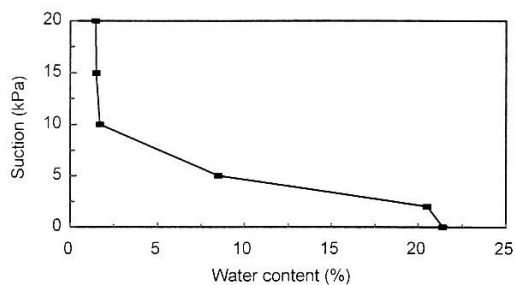


Figure 3: Water retention curve for sample of aeolian sand

time taken for the water drops to penetrate into the soil is measured. If this time is less than 5 seconds the soil is considered easily wettable. If the time is greater than 60 seconds it is strongly repellent. With only one exception, the time taken for the droplet to be absorbed was less than 2 seconds and all the sands

were thus highly wettable, with the one exception. This was the specimen from a depth of 59cm in the burnt forest area. The droplet absorbance time was about 20 seconds, indicating a relatively high degree of water repellency.

6 SIGNIFICANCE OF FINDINGS

There is insufficient data at this time to make categorical conclusions as to the effect of vegetation on the hydraulic characteristics of the sandy soil studied. It is desirable to carry out a much larger number of in-situ permeability tests, soil wettability tests and water retention tests, all on the same batch of specimens. In this way some of the apparent anomalies in the measured water content profiles during rainfall periods at various locations within the Tembe reserve may be resolved.

Changes in hydraulic characteristics of the soils at Tembe that result in changes to the vegetation distribution and density are extremely important to the ecological and conservation managers. However, as engineers it is perhaps the reverse that is of most interest, ie how vegetation may change the hydraulic characteristics of a particular soil. From the data presented in this paper, it is very clear that assuming that a number of sand specimens will all have the same water retention and hydraulic characteristics simply because they have a common origin and almost exactly similar particle size distribution curves is erroneous. At the Tembe site, as may occur at many sites where certain vegetation types are prevalent, the vegetation (and the burning of this vegetation which may occur frequently) does appear to have very significant impacts on the hydraulic characteristics of the near-surface soil.

It is clear from the literature that certain vegetation types exude organic substances, usually in an effort to discourage growth of other species. These substances have often been shown to alter the water repellency of the soil that comes into contact with the organic material, perhaps ultimately rendering it highly hydrophobic. Subsequent burning of the vegetation may have the effect of removing these coatings very close to the surface but also causing the organic material to penetrate deeper into the soil profile, often condensing in a localised layer which may be highly hydrophobic. These effects appear to be particularly pronounced in permeable, cohesionless soils, where penetration of the organic substances to relatively

significant depths is perhaps easier than in clayey soils.

Although this effect might be considered relatively subtle and of little interest to engineers, it is suggested that in certain circumstances it may in fact override all other considerations regarding appropriate testing and soil characterisation. Changes in field-saturated permeabilities were found to differ by over one order of magnitude (with only 12 tests being done) and it is likely that differences in unsaturated hydraulic conductivity (which would be closely linked to the water retention characteristics of the soil) might be even more pronounced.

Thus although the present study cannot lay claim to providing definitive quantification of the changes to hydraulic characteristics that occur as a consequence of vegetation 'activity', it has highlighted an area of investigation that has perhaps been ignored by geoenvironmental engineers.

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ANNEXURE 2

Van Rensburg, J.B, McGeoch, M.A., Matthews, W., Chown, S.L. & van Jaarsveld, A.S. 2000. Testing generalities in the shape of patch occupancy frequency distributions. *Ecology* 81: 3163–177.

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TESTING GENERALITIES IN THE SHAPE OF PATCH OCCUPANCY FREQUENCY DISTRIBUTIONS

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Abstract. Bimodal patch occupancy frequency distributions regularly appear in studies of a variety of taxa at a variety of spatial scales. Metapopulation models associated with the core–satellite hypothesis and a strong rescue effect predict the occurrence of this bimodality. However, there have been numerous other explanations, both artifactual and biological, of bimodality in patch occupancy frequency distributions. One approach to a better understanding of the phenomenon is to conduct studies on a variety of taxa and spatial scales. Here we examine patterns of patch occupancy frequency distributions for plants, dung beetles, and birds at four spatial scales in sand forest and mixed woodland in Tembe Elephant Park and Sileza Nature Reserve in South Africa. We then examine the predictions of each alternative mechanism proposed to explain bimodality with respect to the patterns found in this study. The incidence of bimodality was high. Little evidence was found for any of the artifactual or nonmetapopulation-based explanations of bimodality. Although there were no between-taxon differences in the shape of occupancy distributions, there was a clear trend of decreasing frequency of bimodality with an increase in the size of the area examined. The general shape of range-size frequency distributions in combination with an area effect is suggested as a mechanism underlying this pattern. Metapopulation dynamics associated with a strong rescue effect could also not be excluded as a possible mechanism playing a role in generating the bimodality found at the patch scale.

Key words: area effect; bimodality; community structure; core–satellite hypothesis; metapopulations; range size; rescue effect; South Africa.

INTRODUCTION

Hanski's (1982) core–satellite hypothesis focused much attention on the incidence of bimodality in the distribution of patch occupancy frequency distributions (occupancy distributions). The dynamic metapopulation models developed by Hanski (1982) and Hanski and Gyllenberg (1993) predict bimodal occupancy distributions. In other words, if the extent of occurrence (or range) of species in these distributions is divided into 10% occupancy classes, species occupying >90% of sites are termed core species, and species occupying <10% of sites are termed satellite species, and bimodal distributions with modes in these two classes are termed core–satellite distributions. The key mechanism underlying metapopulation models that predict core–satellite distributions is that these distributions are associated with a strong rescue effect (Hanski and Gyllenberg 1993). The bimodality thus arises as a result of two processes, i.e., an increase in the immigration rate with an increasing proportion of occupied sites and a decrease in the extinction rate with an increasing immigration rate (Hanski and Gyllenberg 1993). Han-

ski and Gyllenberg (1993) showed that over the long term, the distribution of occupancy frequencies resulting from these colonization–extinction properties of the rescue effect, and from interspecific variation in these extinction–colonization ratios, is bimodal. Therefore, when core–satellite distributions appear in empirical data for particular species assemblages, Hanski's (1982) and Hanski and Gyllenberg's (1993) interpretations suggest a metapopulation structure and the presence of a strong rescue effect in those assemblages.

There have, however, been many other, nonmetapopulation-based interpretations of core–satellite, or bimodal, patch occupancy frequency distributions (see also response to some of these by Hanski [1991]): (1) Bimodality is an artifact because occupancy is constrained to lie between zero and one (Raunkiaer 1934, Williams 1950). (2) Bimodality may arise from sampling biases when rare species are less likely to be observed or sampled (Nee et al. 1991). Problems associated with sampling rare species therefore result in an inflation of the satellite species mode. (3) The larger the number of sample sites, the greater the proportion of satellite species and the smaller the proportion of core species (Williams 1950, 1964). Therefore, the smaller the sample number used to generate the occupancy distribution, the greater the probability of find-

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ing bimodality. (4) The presence or absence of bimodality is sensitive to the spatial scale of observation (Williams 1964, Brown 1984). This phenomenon has also been termed “distance scaling” by Collins and Glenn (1997) and was first demonstrated by Williams (1950, 1964). Using maximum sample areas of 1.0 m² and plant data, he showed that as the size of the area sampled increases the percentages of satellite species decrease and core species increase. In contrast, Collins and Glenn (1997), at much larger scales of >10 km², show an increase in percentage of satellite and a decrease in percentage of core species with an increase in the size of the area sampled (see also Brown 1984). Collins and Glenn (1997) predicted that given an increase in environmental heterogeneity with increasing spatial scale, patterns of local species distribution will change accordingly with an increase in regionally rare species and a decrease in regionally abundant species with an increase in the size of an area sampled. (5) Bimodality is a direct consequence of underlying log-normal or logarithmic rank abundance curves (Preston 1948, Papp 1997). (6) Bimodal occupancy distributions result because species are either specialists or generalists and thus occupy either a few or most habitat patches (Brown 1984). (7) Occupancy distributions are determined by the productivity of landscapes and the degree of dominance of species in them, and bimodality is most likely to be found in lower productivity landscapes where a few species dominate resource use (Maurer 1990). (8) Tourist species bring about an inflation in the satellite mode (Nee et al. 1991). (9) Within a given area, better dispersing taxa will have more core species than poorly dispersing taxa, a trend referred to as “organismal scaling” (Collins and Glenn 1997).

In addition to all the above, bimodality has been the subject of debate because its very presence is statistically difficult to verify (Tokeshi 1992). Interpretation of the presence of bimodality in patch occupancy frequency distributions therefore faces problems associated not only with the quantification of bimodality, but also, and perhaps more importantly, with the identification of the mechanisms underlying that bimodality. That is, the pattern may have either an artificial (mechanisms 1–3 above) or biological origin, and if biological, the mechanism may or may not (mechanisms 4–9 above) involve a strong rescue effect associated with metapopulation dynamics (mechanism 10).

In an attempt to achieve some clarity on the mechanisms that generate patch occupancy frequency distributions, it is helpful to consider the closely related interspecific abundance–range–size relationship. It has been widely documented that abundant species commonly have wider ranges than locally rare species (although the proportion of variation explained is generally low) (Gaston et al. 1997). However, Gaston et al. (1997) showed that these positive relationships may be generated by any of eight principal mechanisms (in-

cluding both artificial and biological, of which one is metapopulation based). They also show that none of these mechanisms has unequivocal support and that each is likely to contribute to the relationship to different degrees under different circumstances. Although far less attention has been paid to understanding patch occupancy frequency distributions than has been the case for abundance–range–size relationships, it appears likely that occupancy distributions are likewise not generated by any single or simple combination of mechanisms.

Regardless of the mechanisms involved, bimodal patch occupancy frequency distributions regularly appear (although unimodality is more common) in studies of a variety of taxa at a variety of spatial scales (e.g., Gotelli and Simberloff 1987, Collins and Glenn 1990, 1997, Tokeshi 1992, Pirintsos et al. 1996). One approach to understanding the incidence of this bimodality is to conduct studies on a variety of taxa at a variety of spatial scales, quantifying and comparing the shapes of the occupancy distributions found. Should generalities in the incidence of core–satellite distributions be found from these studies, tests can then be conducted to investigate the mechanisms (be they biological, including metapopulation-based, or artificial) that generate them.

Here we present the findings of a study of modality patterns for three taxa (dung beetles, birds, and plants) in two habitat types and at four nested spatial scales. First we examine the relationship between distribution and abundance because positive interspecific abundance–range–size relationships are fundamental to most regional metapopulation models (Hanski 1982, 1991, Brown 1984, Kolasa 1989, Collins and Glenn 1997), and metapopulation dynamics is one of the mechanisms proposed to explain bimodality (mechanism 10 above). Next, with respect to the findings of this study, we test (mechanisms 1, 3–5, 9) and examine (mechanisms 2, 6–8, 10) the predictions of each alternative mechanism that has been proposed to explain bimodal occupancy distributions.

METHODS

Study area

Field work was undertaken in Tembe Elephant Park (27°01' S 32°24' E) and Sileza Nature Reserve (27°06' S 32°36' E), on the southern Mozambique Coastal Plain of Northern KwaZulu-Natal, South Africa. There are two distinct habitat types in these reserves, i.e., sand forest and mixed woodland, and the smaller patches of sand forest are embedded within a larger matrix of mixed woodland (van Wyk 1996; see Plate 1). Sand forest is characterized by tree species such as *Dialium schlechteri* and *Erythrophleum lasianthum* (Caesalpinioideae) (Moll 1977, van Wyk 1996) with a poorly developed understory. The surrounding, more open, mixed woodland is characterized by common, woody



PLATE 1. Photograph showing the two distinct, clearly bounded habitat types in the study areas on the southern Mozambique Coastal Plain of Northern KwaZulu-Natal, South Africa: sand forest (right) and mixed woodland (left). Photo credit: B. J. van Rensburg.

savanna species such as *Acacia burkei*, *Albizia versicolor*, and *A. adianthifolia* (Mimosoideae). It has a well-developed grass understory represented by *Aristida*, *Pogonarthria*, and *Perotis* species (Moll 1977, 1980). The soils in both study areas are homogeneous, grey, siliceous, aerolian sands which are highly leached (dystrophic) and relatively acidic (water pH \approx 6.1) (van Rensburg et al. 1999).

Sampling

Replicated sampling sites in these reserves were selected from within standardized vegetation communities (sand forest and mixed woodland; van Wyk 1996). Two sand forest sites and two mixed woodland sites were sampled in each reserve, i.e., eight sampling sites, grouped into four reserve-habitat combinations (Tembe sand forest, Tembe mixed woodland, Sileza sand forest, Sileza mixed woodland). Distances between sites and between the areas sampled in the two reserves were, respectively, 1.3–3.1 km and \sim 18 km.

Bird surveys

Each survey site was comprised of 16 randomly selected fixed survey points. The appropriate number of survey points for these assemblages was determined from a pilot study following the method advocated by Buckland et al. (1994). Distances between the 16 points within a site were at least 150 m. These distances minimized the probability of double detection, ensuring

data independence, and provided suitable replicates for the study. Because of terrain difficulties, particularly in the sand forest, sampling points were placed along game and elephant paths. Although this could potentially bias the results, this is unlikely where mobile animals such as birds are surveyed (S. T. Buckland, *personal communication*). Survey points were, however, identified without prior knowledge of bird distributions, and care was taken to ensure that sampling points did not follow more prominent natural features (e.g., forest edges; see Guthery 1988).

Visual and auditory bird surveys were conducted bimonthly between May 1995 and April 1996, at all four sites in a reserve (the two reserves were surveyed in alternate months), using point sampling (see Buckland et al. 1994). During one month, each of the four sites was surveyed four times. The 16 sampling points from a single site were surveyed in one morning (10 min per sampling point). Three minutes were spent at each survey point prior to data collection to allow the birds time to adjust to the disturbance caused by the observer. Survey periods were limited to reduce the risk of multiple detection resulting from birds moving out of and back into an observation area, which could lead to substantial density overestimation (Buckland et al. 1994). Thus a compromise between maximization of the probability that individuals in a survey point would be detected (e.g., interval-based bird calls) and minimization of the probability of multiple detection,

or of attracting curious species (e.g., Southern Boubou Shrike, *Laniarius ferrugineus*), was sought.

On initial detection, birds were placed into distance categories, demarcated by fixed markers placed at known distances from the observation point (0–4, 5–9, 10–15, 16–30, and 31–50 m) before the study commenced. Although determination of the exact distance at which each bird was detected would have been desirable, this was not practical when many birds were heard and not observed (Buckland et al. 1994). In addition, estimation of exact distances when large numbers of birds are seen over a short period may lead to observational difficulties and a reduction in survey accuracy (Bibby et al. 1985). The distance to a bird in the tree canopy was taken as the distance from the observer to a point directly below the bird on the ground. All birds within 50 m of the survey point, including birds involved in territorial displays, were recorded. Birds flying over the study area were excluded. Records were also categorized as reliable sightings or as bird call records. Unreliable sightings were not included in the database. The number of individuals of each species observed over the course of the study period were summed for each survey point within each site. Survey points within a site were reduced from 16 to 4 by randomly pooling sets of four data points. These four sets are henceforth referred to as “grids” for uniformity of reference with the dung beetle and plant sampling grids.

Beetle sampling

At each sampling site, 30 pitfall traps were set out in five grids of six pitfalls each, with the six pitfalls placed 2 m apart in a 2 × 4 m rectangle. Distances between the five grids within a site were 200 m. Beetles were sampled bimonthly between May 1995 and April 1996, at all four sites in a reserve (the two reserves were sampled in alternative months), using pitfall traps baited with 50 g elephant dung. During each sampling month the pitfalls were set once for 48 h, with rebaiting and the first collection taking place at 24 h, and the second collection at 48 h. Traps were then closed and left in situ until the following sampling month. Specimens were identified by comparing them to identified specimens in the collections of the South African National Insect Collection. The number of individuals of each species trapped over the course of the study period was summed for each sampling grid and each site.

Plant sampling

Twenty 100-m² sample grids (10 × 10 m) were distributed in a stratified manner throughout the sampling sites. Sampling was carried out from January to May 1993. The total floristic composition, as well as a cover-abundance value for each species, was recorded using the Braun-Blanquet cover-abundance scale as described by Mueller-Dombois and Ellenberg (1974): R = rare, + = <1%, 1 = 1–5%, 2A = >5–12%, 2B =

>12–25%, 3 = >25–50%, 4 = >50–75%, and 5 = >75% (see Matthews et al. 1999 and W. S. Matthews et al., *unpublished manuscript*, for further details of sampling and plant community dynamics at Tembe and Sileza).

Data analysis

Four spatial scales were considered in the analyses; patch (i.e., Tembe sand forest, Tembe mixed woodland, Sileza sand forest, and Sileza mixed woodland, each between 2 and 4.5 km² in extent), reserve (Tembe and Sileza: 4.5–6 km²), habitat (all sand forest and all mixed woodland sites, between 22 and 24 km²), and local (the full extent of the area sampled; i.e., all sampled sites, ~26 km²).

Species accumulation curves were compiled for each taxon to establish the degree of sampling representivity. Samples were randomly and sequentially selected without replacement from the full data sets for each taxon until all samples had been selected. This procedure was repeated five times and species accumulation curves compiled from the mean number of species across the five replicates for each sample number.

Ordinary least-squares linear regression was used to establish whether positive interspecific abundance-range size relationships existed, i.e., number of grids in which each species was present vs. their average abundance across those grids, for each of the higher taxa, at each of the four spatial scales sampled in the region.

Tokeshi's (1992) method of determining the exact probability of obtaining an observed frequency value (p_o) for the left- and rightmost classes under the null hypothesis of random occurrence of species in a region was used to quantify modality patterns (see also Collins and Glenn 1997). The probability of obtaining the observed frequency for the left- (p_l) or rightmost (p_r) class can also be calculated separately under the same null hypothesis (Tokeshi 1992): if $P < 0.05$ for both the left- and right-extreme frequency classes then the distribution is bimodal, whereas if $P < 0.05$ for only one of the classes then the distribution is unimodal. This method was used for each taxon at each spatial scale. In all cases the number of grids sampled, and in which species were recorded, was ≥ 10 , and the distribution could thus reasonably be expressed as the proportion of grids occupied by species in 10% grid occupation categories.

To test whether the occupancy distributions found were sample size independent, data from all grids within each habitat type, (1) all sand forest and (2) all mixed woodland grids, were used. Grids were then randomly selected from these data sets until new data sets with sample sizes representing 50% of the original sample size were reached. This procedure was repeated five times for each higher taxon in both sand forest and mixed woodland. The sample size of 50% of the original sample reduced sample sizes to levels equivalent

to the smallest sample sizes used in this study (patch scale). The occupancy distributions generated from the smaller randomly selected samples for each taxon were then compared with observed occupancy distributions compiled from similar sample sizes. These sample size reductions were carried out within habitat types only to remove possible habitat heterogeneity effects on the occupancy distributions generated, as far as possible.

Given the prediction that there will be an increase in regionally rare (satellite) species and a decrease in regionally abundant (core) species with an increase in the size of an area sampled (Collins and Glenn 1997), distance scaling was assessed by examining changes in the numbers of core and satellite species from the smallest to largest spatial scales for each taxon.

To test the prediction that bimodal occupancy distributions reflect underlying lognormal or logarithmic series distributions, truncated lognormal and logseries models were fitted to the rank abundance plots of each taxon at each spatial scale (Magurran 1988, Papp 1997).

Organismal scaling was tested by comparing the occupancy distributions of taxa, on the assumption that their rank-order dispersal ability is birds > dung beetles > plants. Here we predict, based on Collins and Glenn's (1997) rationale, that the better dispersing taxa (e.g., birds) will have more core species than the poorer dispersing taxa (e.g., plants). The occupancy distributions of each taxon within each spatial scale were also compared to each other using Kolmogorov-Smirnov two-sample tests (Siegel 1956). To further test Collins and Glenn's (1997) organismal scaling prediction of better dispersing taxa (i.e., those with larger ranges) in the core mode, we used the bird data collected here and examined the broader southern African distributions (percentage of 25-km² grid cells in which species has been recorded in southern Africa, extracted from Harrison et al. 1997) of those species in the core and satellite categories of the distributions generated by this study. The prediction here is, if core mode species are better dispersers they should be subregionally widespread, whereas if satellite species are poor dispersers they should have narrow subregional distributions.

RESULTS

The number of species recorded in each taxon across scales ranged between 65 and 112 for birds, 35 and 68 for dung beetles, and 95 and 501 for plants (Table 1). The species accumulation curves showed that the species richness of the dung beetle and bird assemblages reached an asymptote well within the sample size used in this study (Fig. 1). The plant assemblage required a far larger sample size before representivity was achieved; however, this assemblage also reached an asymptote within the sample size used (Fig. 1). All three assemblages sampled were thus highly representative of the area.

The relationship between number of sites occupied

and average abundance was positive for all and significant for 24 of the 27 taxon-spatial scale combinations (Table 1). The three nonsignificant relationships were all at the patch scale. Nonetheless, the metapopulation assumption (Hanski 1982), or prediction (Hanski and Gyllenberg 1993), of a positive relationship between distribution and abundance was largely met.

Significant bimodality was detected in just under 50% of the cases examined and was present in occupancy distributions of all three taxa (Fig. 2). However, there was a clear tendency for decreasing frequency of bimodality with increasing spatial scale (from Fig. 2A–D). Evidence of distance scaling was also stronger within, rather than across, habitat types (Fig. 2). When moving from a particular habitat at the patch scale (Fig. 2A) directly to the same habitat type at the larger, habitat scale (skipping the reserve scale) (Fig. 2C), the switch from bimodal to unimodal was clearer than when including the intermediate reserve scale (Fig. 2B) that combines data for both habitat types.

The reduction of sample sizes by 50% did not change largely the shape of the patch occupancy distributions (Table 2). At the habitat scale all observed occupancy distributions were unimodal (Fig. 2). Reducing these data sets to sample sizes equivalent to those used at the smallest (i.e., patch) spatial scale did not change the distributions from unimodal to bimodal (with the exception of two replicates of the mixed woodland dung beetle assemblage; Table 2). The presence of bimodality at the patch scale therefore could not be attributed to the smaller sample sizes used at this scale.

Within each of the three taxa examined there were fewer species in the core modes at the larger local and habitat scales than at the smaller patch and, in some cases, reserve scales (Fig. 2, Table 3). The number of satellite species, in contrast, increased from patch to local scales for dung beetles. The increase was less clear for birds, and neither an increase nor a decrease in the number of species with increasing spatial scale was evident for plants (Table 3). Distance scaling was thus clear for core, but not satellite, species in the three taxa tested. The bimodality detected at patch and reserve scales thus resulted from the presence of a core mode, and although there were some signs of an increase in the satellite mode with increasing spatial scale these did not contribute to the change in distribution from unimodal to bimodal.

Dung beetle assemblages fitted the logarithmic series distribution at all spatial scales (Table 4), regardless of the shape of the corresponding occupancy distribution (Fig. 2). Therefore logarithmic series were found to underlie both unimodal and bimodal occupancy distributions. Similar results were found for birds and plants, although only in some instances did the rank abundance distributions fit the logarithmic series (Table 4). However, those that did fit the series were never exclusively associated with bimodal occupancy distributions (Fig.

TABLE 1. Relationship between number of sites occupied (N) and average abundance for each taxon group at each spatial scale using least-squares linear regression (all were positive) in Tembe Elephant Park and Sileza Nature Reserve in South Africa.

Spatial scale	Taxon	S	N	R^2	P
Patch					
Tembe sand forest	Birds	65	15	0.81	<0.001
	Dung beetles	48	10	0.31	0.089
	Plants	95	10	0.87	<0.001
Sileza sand forest	Birds	63	16	0.75	<0.001
	Dung beetles	35	10	0.54	0.014
	Plants	107	10	0.77	0.053
Tembe mixed woodland	Birds	85	16	0.76	<0.001
	Dung beetles	54	10	0.45	0.035
	Plants	292	20	0.39	<0.01
Sileza mixed woodland	Birds	74	15	0.65	<0.001
	Dung beetles	63	10	0.34	0.074
	Plants	156	17	0.43	<0.01
Reserve					
Tembe	Birds	94	25	0.76	<0.001
	Dung beetles	65	20	0.35	<0.01
	Plants	230	28	0.59	<0.01
Sileza	Birds	90	27	0.71	<0.01
	Dung beetles	56	16	0.28	0.036
	Plants	197	20	0.56	<0.01
Habitat					
Sand forest	Birds	87	27	0.74	<0.001
	Dung beetles	52	15	0.41	0.0101
	Plants	159	14	0.48	<0.01
Mixed woodland	Birds	99	29	0.72	<0.001
	Dung beetles	68	20	0.30	0.0126
	Plants	343	40	0.47	0.0279
Local					
	Birds	112	43	0.70	<0.001
	Dung beetles	68	29	0.28	<0.01
	Plants	501	54	0.56	0.0122

Notes: Average abundances were calculated from the number of occupied sites rather than the total number of sites. S = number of species. Table-wide $\alpha = 0.05$ for birds, dung beetles, and plants using the sequential Bonferroni technique (Rice 1988).

2). The bird and plant assemblages were almost exclusively truncated lognormally (Table 4), again regardless of the shape of the corresponding occupancy distribution (Fig. 2).

Little evidence of organismal scaling (larger core modes for better dispersing taxa) according to the proposed rank dispersal ability of the three taxa examined (i.e., birds > dung beetles > plants) was found (Table 3). Dung beetles had the largest core mode percentages at all patch and reserve scales. Although at the larger habitat and local scales birds did have higher core percentages than the other two taxa (Table 3), none of these occupancy distributions were significantly different from each other (Table 5). The distributions of the three taxa were therefore almost exclusively similar within each scale examined (Table 5) (in spite of large differences in the species richness of the three assemblages; Fig. 2). These results therefore provide no support for the effect of organismal scaling on the shape of occupancy distributions.

In addition, bird species in each of the core and satellite categories in this study (Fig. 2A) included species with both narrow and wide ranges in southern

Africa (Fig. 3). This was true of core and satellite categories at patch, habitat, and local scales. For example, at the sand forest habitat scale, satellite species included species that occur in 0.04–70% of the grid cells in southern Africa, i.e., the satellite mode included both subregionally restricted and widespread species. Within the core category in the same habitat there were species that are found in 2.2–32.7% of the quarter-degree grid cells in southern Africa, i.e., the core category included species with narrow to moderately wide subregional distributions. Therefore, neither core nor satellite modes contained species with either exclusively narrow or wide distribution ranges in southern Africa.

DISCUSSION

After testing, and elsewhere less formally examining, the mechanisms that have been proposed to explain bimodality and the variability in its incidence (outlined in *Introduction*), a number appear invalid or inapplicable, whereas a few find support, in light of the results found here.

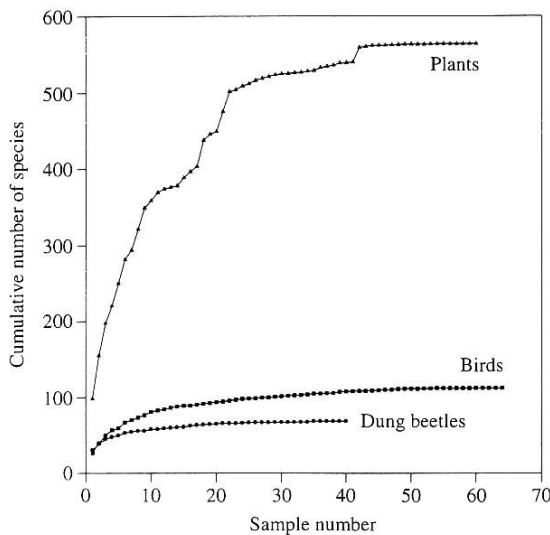


FIG. 1. Species accumulation curves for dung beetle, bird, and plant assemblages in Tembe Elephant Park and Sileza Nature Reserve in South Africa. Each point on the curve represents the mean of five randomly selected samples from the full data set for the higher taxon in question.

Artificial mechanisms

(1) If bimodality occurs because occupancy is constrained to lie between zero and one (Raunkiaer 1934, Williams 1950), then this mechanism should apply equally across all spatial scales. This was not the case here.

(2) Considering sampling representivity and the possible effect of undersampling rare species on occupancy distributions, the assemblages of the three taxa sampled in this study are based on data accumulated over 12 mo and were highly representative of the area (as compared to species lists for these areas and as evident from the species accumulation curves that were compiled). Although representative, it is possible that rare species in these assemblages were sampled at fewer sites than at which they actually occur, bringing about an inflation in satellite modes. The overwhelming majority of occupancy distributions, and indeed species abundance distributions, even in the most well-sampled assemblages, have a peak in the lowest abundance class, or are right skewed (Gaston and Lawton 1990). Although undersampling may inflate the satellite mode, the observed rare species mode in such distributions is so common that there can be little doubt as to its existence (Tokeshi 1992). Nonetheless, it is the disappearance of the core mode at larger scales, rather than any change in the satellite mode, that converted the occupancy distributions from bimodal at small scales to unimodal at larger scales in this study. To test the extent of this rare species effect on the satellite mode, it would be necessary to quantify the change in oc-

cupancy patterns of the rare species with increasing sample effort.

(3) The presence of bimodality in this study could not be attributed to Williams' (1964) demonstration that the fewer sites sampled, the higher the fraction of species present in the core mode, because random sample size reductions did, by and large, not produce bimodal distributions. Gotelli and Simberloff (1987) also showed that the predicted reduction in the proportion of core species across an increase of 100 sampled quadrates was only ~2–3%. The observed reduction in core species across the 100 quadrates, in contrast, was ~16% (see Gotelli and Simberloff 1987: Fig. 6). Similarly, in this study there was a reduction of 13–15% in core species between smallest to largest scales, with an average increase of only 40 sample sites (see Tables 1 and 4). The reduction in percentage of core species is therefore greater than may be expected to result purely from an increase in sample size.

Biological mechanisms

(4) We did find that patch occupancy frequency distributions were sensitive to the spatial scale of observation, and furthermore, that there appears to be a systematic pattern to this sensitivity, i.e., that there is some form of distance scaling. Occupancy distributions were bimodal at the smallest spatial scales examined here (2–4.5 km²), becoming unimodal at larger spatial scales. As found in similar empirical studies to date (e.g., Gotelli and Simberloff 1987, Collins and Glenn 1990, 1997, Pirentos et al. 1996), the incidence of bimodality in the frequency distributions in this study was high (50%) (although see Tokeshi 1992). However, unlike other studies, for all taxa we found a decreasing incidence of bimodality with an increase in the spatial extent covered. Although Collins and Glenn (1997) found a similar change across two scales, their small scale (36 km²) was somewhat larger than the largest, local scale (26 km²) in this study. In addition, the larger scale Collins and Glenn (1997) examined covered a different geographic area to the smaller scale they examined, with variable spatial extents for each taxon (they do not provide areas of coverage). Therefore, in their study within each taxon the species set at the smaller scale was not a geographic subset of the assemblage at the larger scale, and it is unclear to what extent, if any, the species composition of the assemblages at the two scales overlap. The study presented here, in contrast, examines true distance scaling where each smaller spatial scale is a geographic subset of the next larger one. Nonetheless we too find a decrease in the frequency of bimodality with increasing spatial extent, although across four rather than two spatial scales. Furthermore, we find that this pattern is stronger within (from almost exclusively bimodal at the habitat-patch scale [2–4 km²] to exclusively unimodal at the larger habitat scale [22–24 km²]), than across, habitat types (see also Raunkiaer 1934, Gotelli and Simberloff

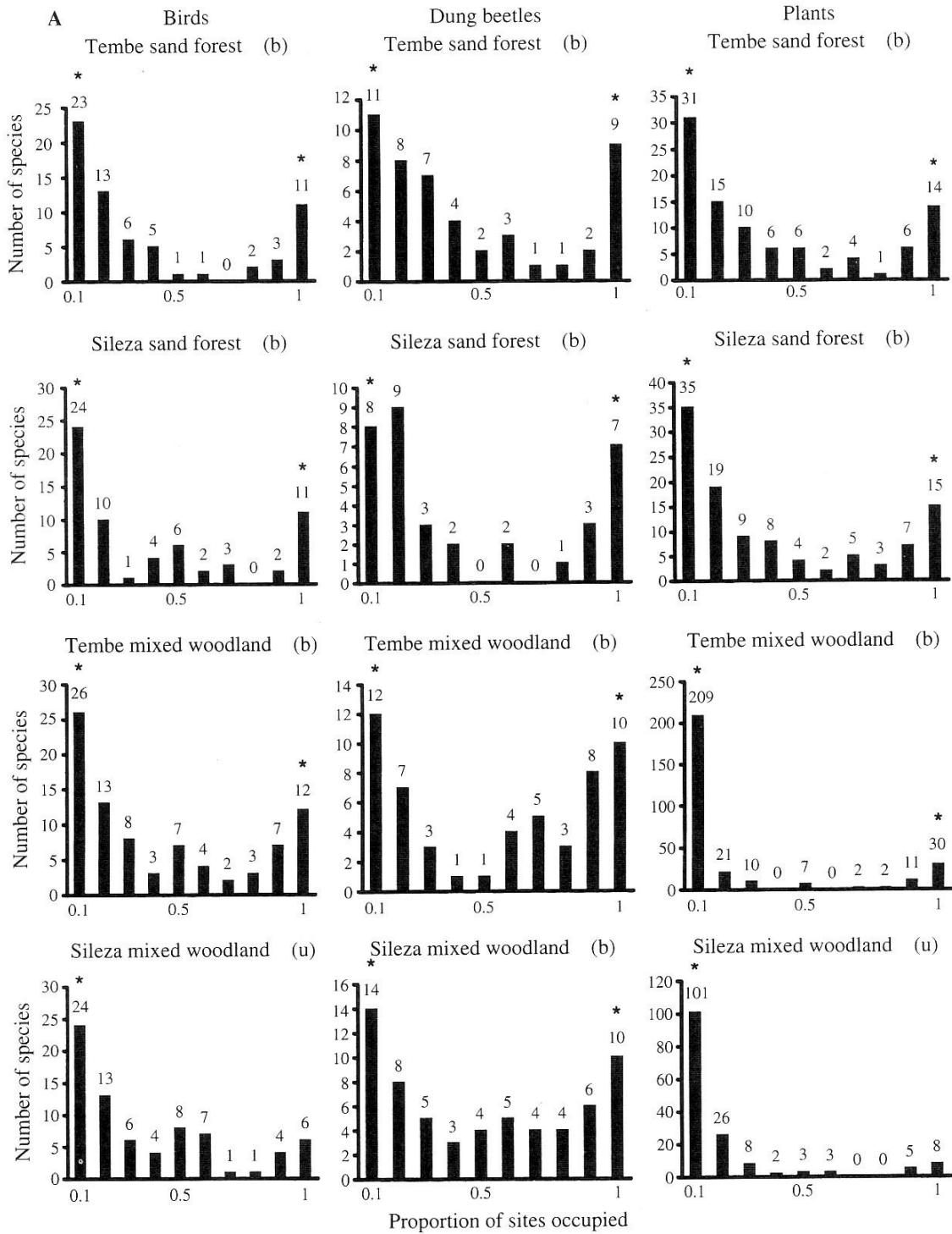


FIG. 2. Patch occupancy frequency distributions of the three taxa at (A) patch, (B) reserve, (C) habitat, and (D) local scales. All distributions were significantly different from random ($p_c < 0.001$); Stars (*) associated with core and satellite classes denote modes significant at $P < 0.005$; b = bimodal, u = unimodal distribution.

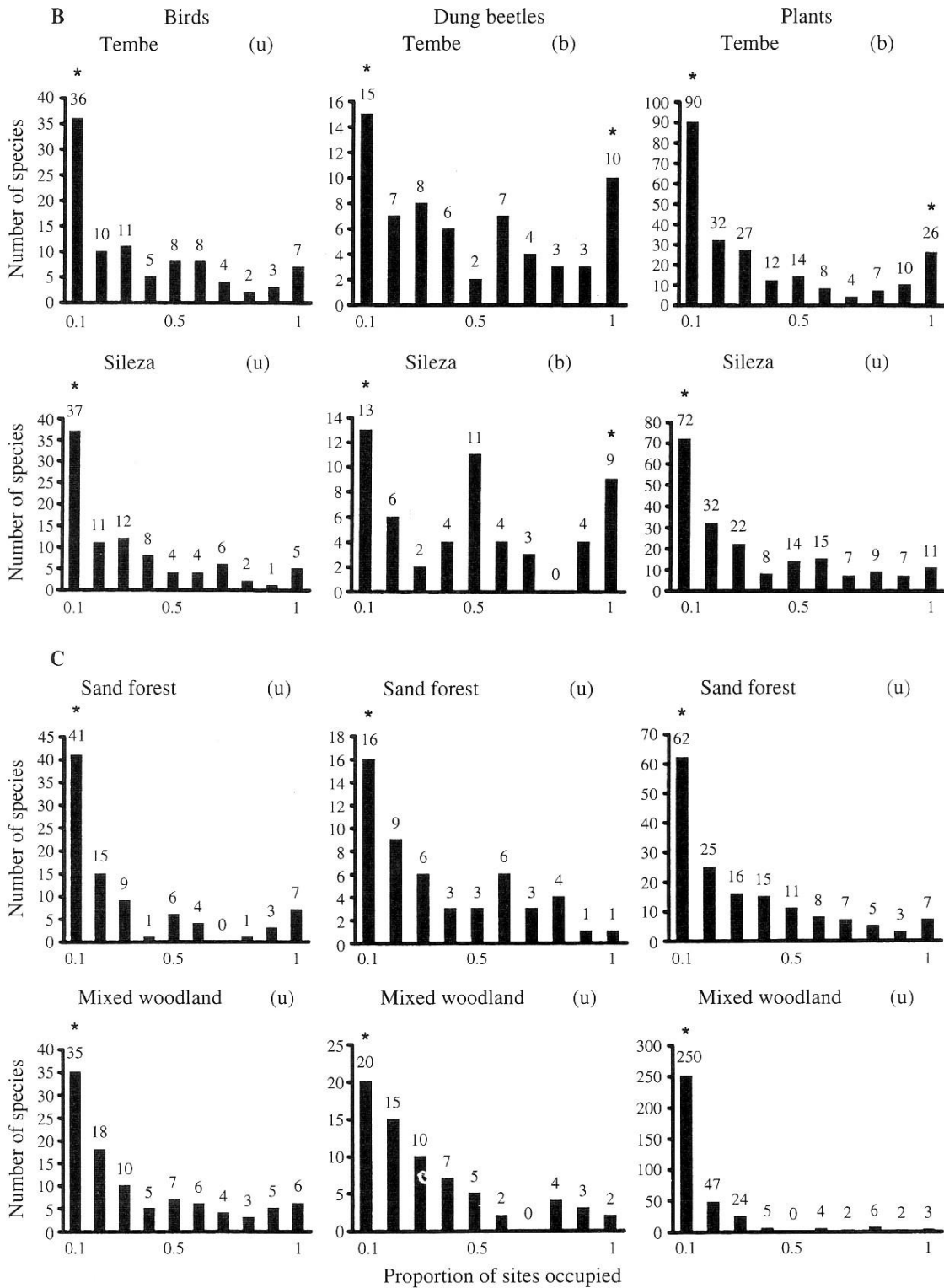


FIG. 2. Continued.

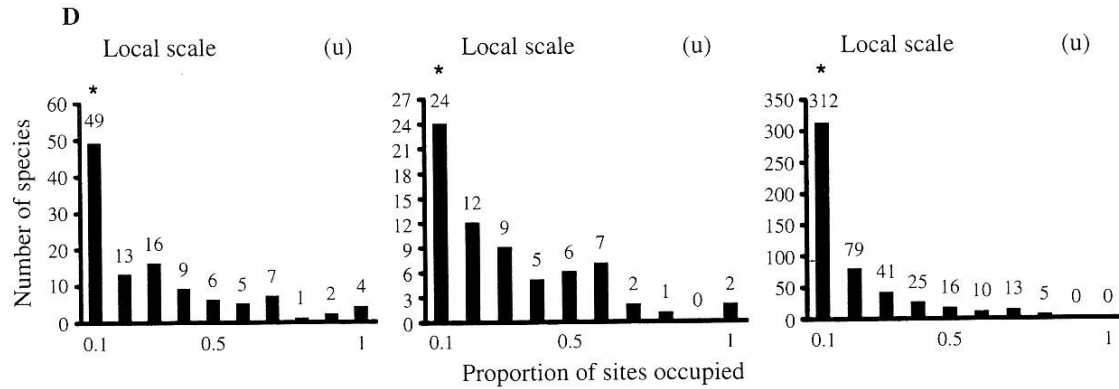


FIG. 2. Continued.

1987). Bimodal and unimodal distributions were equally frequent at the smaller (across habitat) reserve scale (4–6 km², including two habitat types) becoming unimodal at the local (26 km²) scale. Other studies of Tembe Elephant Park and Sileza Nature Reserve show significant differences in the bird (van Rensburg et al.

unpublished manuscript) and dung beetle (van Rensburg et al. 1999) assemblages of the two habitats (sand forest and mixed woodland). This may explain the incidence of unimodality at smaller, across habitat (i.e., reserve) scales, where inclusion of a new habitat type and different species assemblage leads to a more rapid

TABLE 2. Patch occupancy frequency distributions of samples of grids randomly selected from each habitat type.

Habitat/taxon	<i>N</i>	<i>N_r</i>	<i>R</i>	<i>p_c</i>	<i>p_l</i>	<i>p_r</i>	Diagnosis
Sand forest							
Birds	32	16	1	<0.0001	<0.0001	0.13	unimodal
			2	<0.0001	<0.0001	0.13	unimodal
			3	<0.0001	<0.0001	0.16	unimodal
			4	<0.0001	<0.0001	0.24	unimodal
			5	<0.0001	<0.0001	0.07	unimodal
Dung beetles	20	10	1	<0.0001	<0.0001	0.10	unimodal
			2	<0.0001	<0.0001	0.32	unimodal
			3	<0.0001	<0.0001	0.08	unimodal
			4	<0.0001	<0.0001	0.18	unimodal
			5	<0.0001	<0.0001	0.33	unimodal
Plants	20	10	1	<0.0001	<0.0001	0.22	unimodal
			2	<0.0001	<0.0001	0.21	unimodal
			3	<0.0001	<0.0001	0.23	unimodal
			4	<0.0001	<0.0001	0.20	unimodal
			5	<0.0001	<0.0001	0.21	unimodal
Mixed woodland							
Birds	32	16	1	<0.0001	<0.0001	0.33	unimodal
			2	<0.0001	<0.0001	0.27	unimodal
			3	<0.0001	<0.0001	0.37	unimodal
			4	<0.0001	<0.0001	0.26	unimodal
			5	<0.0001	<0.0001	0.33	unimodal
Dung beetles	20	10	1	<0.0029	<0.05	0.02	bimodal
			2	<0.002	<0.17	0.003	unimodal
			3	<0.014	<0.069	0.124	no mode
			4	<0.004	<0.014	0.119	unimodal
			5	<0.003	<0.032	0.031	bimodal
Plants	40	20	1	<0.0001	<0.0001	0.20	unimodal
			2	<0.0001	<0.0001	0.22	unimodal
			3	<0.0001	<0.0001	0.22	unimodal
			4	<0.0001	<0.0001	0.23	unimodal
			5	<0.0001	<0.0001	0.24	unimodal

Notes: The final sample size (*N_r*) used for each taxon represents a sample size reduction of 50% of the original sample size (*N*). *R* = replicate number; *p_c*, *p_l*, and *p_r* are the exact probabilities of obtaining the observed frequency value for the left- and rightmost classes combined, the leftmost class, and the rightmost class, respectively (see *Methods: Data analysis*).

TABLE 3. Percentage of species in the satellite and core modes (those species occupying between 1% and 10% and between 91% and 100% of grids, respectively) for each taxon (Pl = plants, Db = dung beetles, Bi = birds) at the different spatial scales.

Scale	Percentage of satellite species			Percentage of core species		
	Pl	Db	Bi	Pl	Db	Bi
Patch						
Tembe sand forest	32	22	35	15	18	17
Sileza sand forest	32	22	38	14	19	17
Tembe mixed woodland	71	22	30	10	18	14
Sileza mixed woodland	64	22	32	5	16	8
Reserve						
Sileza	36	23	41	6	16	5
Tembe	39	23	38	11	15	7
Habitat						
Sand forest	39	30	47	4	2	8
Mixed woodland	73	29	35	1	3	6
Local	62	35	44	0	3	4

Notes: Spatial scales are ranked from smallest to largest. Comparisons down columns for each taxon = distance scaling. Comparisons across taxa within rows = organismal scaling.

increase in species in the satellite mode, than would the addition of a patch of the original habitat type. Because the core-satellite hypothesis attempts to explain the distribution of species that can potentially occupy all sites (i.e., considers occupancy frequency distributions within homogenous sets of patches) (Hanski and Gyllenberg 1993), it is important to consider the possible effects of including different habitats on the shape of occupancy distributions (see also Raun-

TABLE 5. Differences in patch occupancy frequency distributions between taxa at each spatial scale based on pairwise Kolmogorov-Smirnov two-sample tests

Spatial scale/taxon group	Taxon group	
	Plants	Birds
Patch		
Tembe sand forest		
Birds	NS	
Dung beetles	NS	NS
Sileza sand forest		
Birds	NS	
Dung beetles	NS	NS
Tembe mixed woodland		
Birds	NS	
Dung beetles	<0.05	NS
Sileza mixed woodland		
Birds	NS	
Dung beetles	NS	NS
Reserve		
Tembe		
Birds	NS	
Dung beetles	NS	NS
Sileza		
Birds	NS	
Dung beetles	<0.05	NS
Habitat		
Sand forest		
Birds	NS	
Dung beetles	NS	NS
Mixed woodland		
Birds	NS	
Dung beetles	NS	NS
Local		
Birds	NS	
Dung beetles	NS	NS

Note: Table entities are P values.

TABLE 4. Logarithmic and truncated lognormal series chi-square goodness-of-fit tests of the rank abundance distributions of each taxon at each spatial scale.

Scale	Logseries									Truncated lognormal					
	Dung beetles			Birds			Plants			Dung beetles		Birds		Plants	
	χ^2	df	P	χ^2	df	P	χ^2	df	P	χ^2	P	χ^2	P	χ^2	P
Patch															
TSF	9.92	10	NS	3.40	8	NS	9.32	7	NS	23.75	**	8.39	NS	4.75	NS
SSF	10.29	10	NS	4.07	8	NS	13.96	6	*	20.05	*	8.52	NS	11.29	NS
TMW	16.70	10	NS	11.22	8	NS	6.29	8	NS	19.92	*	9.75	NS	4.76	NS
SMW	9.59	10	NS	7.81	7	NS	17.21	8	*	15.62	*	4.40	NS	6.77	NS
Reserve															
TEM	10.22	10	NS	17.26	9	*	9.38	8	NS	14.97	NS	12.85	NS	6.23	NS
SIL	6.38	10	NS	4.90	9	NS	45.67	8	***	14.74	NS	6.56	NS	14.45	NS
Habitat															
SF	13.81	10	NS	7.44	9	NS	19.75	7	**	23.16	**	16.72	*	3.16	NS
MW	10.12	10	NS	10.25	8	NS	52.02	8	***	10.09	NS	5.53	NS	42.16	**
Local	14.15	10	NS	12.85	10	NS	143.42	8	***	12.34	NS	8.52	NS	46.05	**

Note: TSF and SSF = Tembe and Sileza sand forests, TMW and SMW = Tembe and Sileza mixed woodlands, TEM = Tembe Elephant Park, SIL = Sileza Nature Reserve, SF = sand forest, MW = mixed woodland.

* P < 0.05, ** P < 0.01, *** P < 0.001; significant difference between the model and observed series. NS = no significant difference between the model and observed series.

† df = 10 throughout for truncated lognormal tests.

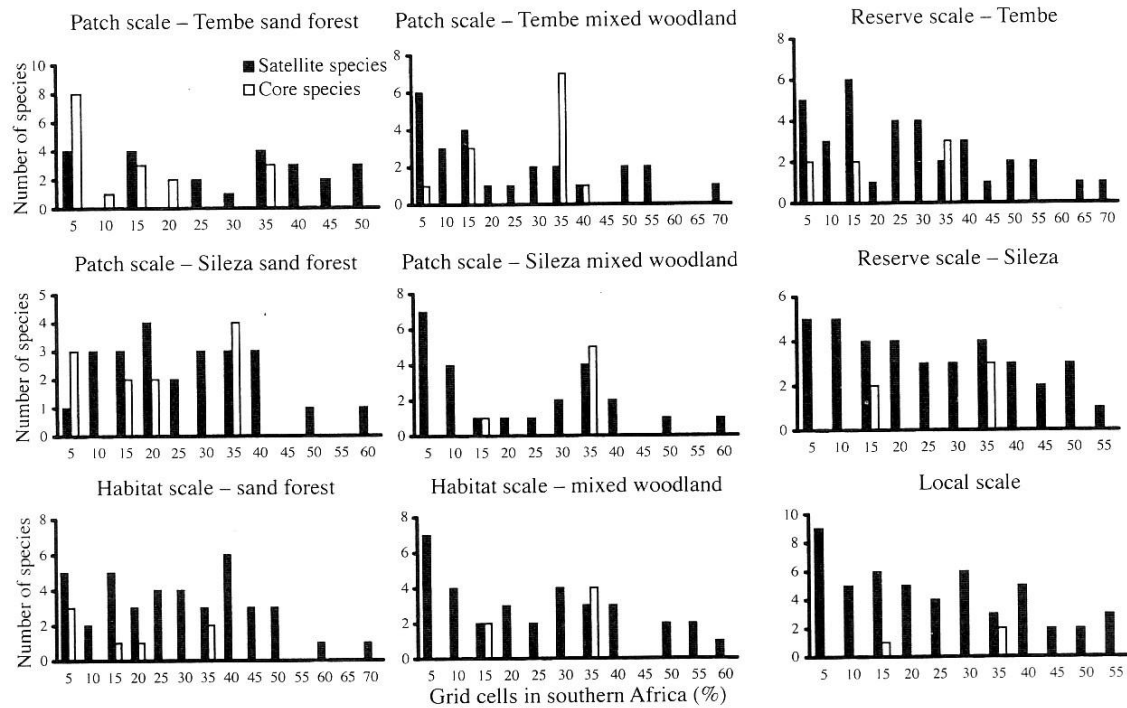


FIG. 3. Percentage of quarter degree (25 km²) grid cells in which the core and satellite bird species, identified at four spatial scales in the present study, are found in southern Africa.

kiær 1934, Gotelli and Simberloff 1987). It is thus critical to have information on the heterogeneity of an area before attempting to quantifying occupancy distributions. In spite of occupancy distributions being examined across habitat types for part of the analyses presented here, bimodality remained more frequent at smaller than at larger scales for this part of the analysis.

The distance scaling of occupancy distributions discussed above may be related to the nature of range-size frequency distributions, which are commonly unimodal and right skewed (Gaston 1998), and an associated area effect. Because the majority of species have small range sizes, as the size of an area sampled increases it will increasingly extend beyond the distribution ranges of species in the assemblage being sampled. Therefore, the larger the area sampled the fewer species one would expect to occupy >90% of the patches within it (see also Brown 1984). This would lead to the observed decrease in the size of the core mode with increasing spatial scale. At 50% the frequency of bimodality in this study was high (compared to studies in general; Tokeshi 1992). However, this may be expected considering the relatively small scale at which it was conducted (2–26 km²).

(5) Papp (1997) predicted that bimodal occupancy distributions arise from underlying lognormal or logarithmic series rank abundance distributions. Although Papp (1997) showed that these distributions generate bimodal occupancy distributions, he did not consider

possible alternative mechanisms that may also generate bimodality, nor did he suggest which form of rank abundance series underlies unimodal frequency distributions. Here we found no relationship between the presence of bimodality and either logseries or truncated lognormal distributions.

(6) As outlined by Hanski and Gyllenberg (1993), Brown's (1984) specialist–generalist explanation for bimodality does not hold within patches of similar habitat, because all species can potentially occupy all sites. In this study bimodality was found predominantly within homogenous sets of patches (i.e., at the patch scale) and the assumption that all species could occupy all areas within these patches appears sound. However, the assumptions of Brown's (1984) model may be violated at the restricted spatial scale examined in this study. It should perhaps rather be tested at scales more representative of the range sizes of the species in question and using assemblages where specialist and generalist species can be readily identified.

(7) Commenting on the core mode, Maurer (1990) predicted that bimodality is associated with high dominance in assemblages in low productivity habitats. Although we cannot comment on the productivity of the habitats sampled, at the patch scale the dung beetle and bird assemblages of Sileza sand forest had the highest percentage dominance (52%), and Tembe mixed woodland had the lowest dominance (28%) (van Rensburg et al. 1999; B. J. van Rensburg, *personal observations*).

In spite of this 24% difference in dominance between habitats, and comparatively low degree of assemblage dominance in both, the occupancy distributions for dung beetles and birds in both of these patches were bimodal. The degree of dominance of assemblages therefore did not explain the bimodality found here. To test Maurer's (1990) hypothesis comparisons should be made between matched assemblages in habitats with known, different productivity levels.

(8) Tourist species may indeed bring about an inflation in the satellite mode, but again it is the presence or absence of a core (see point 2 above), rather than a satellite, mode that identifies the occupancy distributions here as either bi- or unimodal. In addition, uniform distributions or unimodal distributions with the mode in the core category are generally uncommon (Tokeshi 1992). The identification of tourist species is controversial (Gaston 1994). However, if methods were developed by which they could be objectively designated (such as that suggested by McGeoch and Chown 1998), then their effect on the shape of occupancy distributions could be quantified.

(9) The prediction of higher proportions of core species for taxa with better dispersal abilities, based on the assumption that birds are better dispersers than dung beetles and dung beetles better than plants, was not realized in this study. Little evidence of an organismal effect on the shape of occupancy distributions was thus found (similar to the findings of Collins and Glenn 1997), and such an effect is unlikely in this type of study (i.e., partial analyses, sensu Gaston and Blackburn 1996, and a snapshot of species distributions that have accumulated over time). On further consideration it appears unlikely that any conclusions can be made about the dispersal abilities of species in core and satellite modes when sampling is conducted as it was in both this study and that of Collins and Glenn (1997). When representative samples are taken of an assemblage from a patch, habitat, or local area (as was the case here), the occurrence of a species at a certain number of sites represents the distribution of that species in the area sampled. Given that over evolutionary time most species have had the opportunity to colonize and occupy all suitable patches (and this is a reasonable assumption in the areas sampled here and areas of a similarly small size), then the occupancy distributions represent snapshots of accumulated distributions over evolutionary time. In this instance better dispersers may not necessarily be expected to occur at more sites than poorly dispersing species. However, if the actual colonization of an area, particularly an island, is being monitored over time (such as is the case in the study by Nieminen and Hanski 1998), it is likely that better dispersing species will shift more rapidly from the satellite to core mode of occupancy distributions than species with poorer dispersal abilities. Of course, this may also be true of highly fragmented or very patchy habitats (With and Crist 1995). Given sufficient time in

comparatively unfragmented habitats, however, the core-satellite distribution will again represent only those species that are either patchily or locally rare or abundant, without encompassing any information on the dispersal abilities of the species concerned. This argument is supported by the occurrence of both widely and narrowly distributed bird species in southern Africa in each of the core and satellite modes of the occupancy distributions generated by sampling sand forest and mixed woodland in Tembe and Sileza. Assumptions of the relative dispersal abilities of higher level taxonomic groups is also problematic. For example, it has recently been shown that the rate of spread of tree species may be far more rapid than previously thought (Clark 1998). It is thus clear that the species in core categories do not exclusively demonstrate greater "dispersal abilities," if one uses, as suggested by Collins and Glenn (1997), the number of sites at which a species is present as an indication of its dispersal ability.

The final mechanism (10) proposed to explain bimodality is of course a strong rescue effect associated with metapopulation dynamics. With no information on the population structure and dynamics of any of the species in the three assemblages examined, we were unable to test this hypothesis. However, the shape of empirically derived occupancy distributions is commonly used as an indirect indication of the possible presence of metapopulation dynamics (Gotelli and Simberloff 1987, Gaston and Lawton 1989, Collins and Glenn 1990, 1997). If there is no bimodality there should be no strong rescue effect. We could therefore predict, based on the findings of this study, that metapopulation dynamic processes are not generating the occupancy distributions at larger scales (22–26 km²) for the three taxa we examined. Bimodality at the patch level on the other hand was pervasive. Therefore, the presence of a strong, metapopulation dynamics-associated rescue effect for dung beetles, birds, and plants within scales of 2–4.5 km² in Tembe and Sileza cannot be ruled out without having quantified the immigration and extinction dynamics of these taxa. Very little evidence exists in the literature in support of plant or vertebrates exhibiting metapopulation dynamics (Pfister 1988, Gotelli and Kelley 1993, Harrison et al. 1995, Gaston et al. 1997, Scheiner and Rey-Benayas 1997), and only some evidence has been found for insect species (e.g., Harrison et al. 1988, Kindvall and Ahlén 1992, Hanski 1994, but see Gaston and Lawton 1989). Birds, for e.g., appear unlikely to exhibit metapopulation dynamics because the dispersal ranges of the vast majority of species are so large (Blackburn et al. 1997). Nonetheless, both bird and dung beetle assemblages are known to differ significantly between mixed woodland and sand forest habitats (van Rensburg et al. 1999; B. J. van Rensburg, S. L. Chown, A. S. van Jaarsveld, and M. A. McGeoch, *unpublished manuscript*), and sand forest characteristically exists as distinct patches of varying sizes within a matrix of mixed woodland

(van Wyk 1996, van Rensburg et al. 1999). At the patch scale bimodality was found for all sand forest assemblages, whereas the two unimodal occupancy distributions at this scale were associated with mixed woodland. The natural patchiness of the mixed woodland-sand forest system may therefore contribute to the bimodality found, and metapopulation dynamics cannot be ruled out as a possible mechanism at this scale.

The results presented here relate to mechanisms responsible for the presence or absence of bimodality in occupancy distributions within and across comparatively small spatial scales. However, processes affecting patch occupancy patterns may change as the sampling extent incorporates increasingly larger spatial scales, until the point where the geographic ranges of species are encompassed by the sample area. Therefore, some of the mechanisms that were found to contribute to the shape of occupancy distributions in this study may change as larger spatial scales are examined. However, the approach to testing the mechanisms used here can similarly be applied at and across any combination of spatial scales.

Conclusion

Although undersampling of rare species may play a role in other studies where the satellite mode is responsible for generating the bimodality, unimodal and left-skewed distributions are uncommon and right-skewed occupancy distributions (such as those in this study) are pervasive (Tokeshi 1992). It was certainly the behavior of the core mode within and across taxa and spatial scales, rather than the satellite mode, that was of interest across the relatively small extent of the sample area examined here. Therefore, two of the ten mechanisms said to account for bimodality were identified as possible and/or likely candidates explaining the bimodal occupancy distributions found at this scale. Of these, right-skewed range-size frequency distributions and an area effect, explaining the decrease in the size of the core mode from small to large scales, appear most likely. Finally, metapopulation dynamics associated with a strong rescue effect remains a possibility, and this study highlights the importance of considering habitat heterogeneity and area effects when testing metapopulation models.

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ANNEXURE 3

Table showing the volumes removed by elephant, preference index and densities per ha for each woody species in each habitat type in Tembe Elephant Park.. The species are grouped (thick dashed line) in terms of the volume utilized and the volume available, and then in terms of selection in all habitats combined (see text). Abbreviations are: SF – Sand Forest, Th – Thicket, ThC – Thicket on Clay, CW – Closed Woodland, OW- Open Woodland, OWA – Open Woodland with high *A. adianthifolia* densities, SW – Sparse Woodland, AHC – All Habitats Combined, VPD – Volume in Cubic Metres/Preference/Density per ha, CLS – Utilization Class. For the volumes removed H – High, M – Moderate, L – Low, T – Trace. For the Preferences S – Selected, N – Neutral Use, R – Rejected. For the Densities Available H – High Densities, M – Moderate, L – Low, R – Rare. * indicates samples of less than 3 individuals. # indicates those species where the All Habitats Combined data result in a classification which is different to that for most of the separate habitats. The figures surrounded by a light dotted line indicate where the utilisation of a particular species in a particular habitat type differs substantially from the intensity of use in other habitats types.

Species	SF	Th	ThC	CW	OW	OWA	SW	AHC	VPD	CLS
<i>Albizia adianthifolia</i>	258 / 4.2/6.4	121 / 2.5/0.4*	20 / 2.4/0.8*	171 / 2/0.3*	3752 / 2.1/2.1	15365 / 1.5/11.5	//	19688 / 2.1/3.1	HSL	i
<i>Albizia versicolor</i>	//	95 / 2.5/4.3*	343 / 2/9.9	1168 / 2/3	1670 / 1.9/6.8	6081 / 1.5/13	226 / 1.7/4.7	9583 / 1.9/6	HSL	i
<i>Sclerocarya birrea sub. caffra</i>	145 / 2.4/26.3	975 / 1.9/10.2	1265 / 2/7.1	518 / 1.8/26.3	2294 / 1.9/3.5	755 / 1.2/3.5	619 / 1.5/2.2	6571 / 1.8/11.3	HSM	i
<i>Terminalia sericea</i>	44 / 4.2/8.1*	560 / 2.1/38.6	1051 / 1.5/67	1372 / 1.6/127.9	4368 / 1.6/42.5	5841 / 1.2/59.2	1103 / 1.4/87.2	14340 / 1.6/61.5	HSH	i
<hr/>										
<i>Acacia burkei</i>	304 / 1.4/19	2898 / 1.4/85.9	790 / 1/104.4	992 / 0.9/62.5	2051 / 0.6/46.5	447 / 0.7/9.9	435 / 0.7/17.7	7916 / 0.8/49.4	HNH	ii
<hr/>										
<i>Acacia robusta sub. clavigera</i>	39 / 2.8/24.5	29 / 2.5/0.4*	1354 / 2.1/14.5	101 / 2/0.9	//	1104 / 0.8/1	//	2627 / 1.7/5.9	MSL	iii
<i>Azelia quanzensis</i>	38 / 1.4/9.9	189 / 1.9/1.7	382 / 1.9/6.6	439 / 0.9/29.3	429 / 1.8/1.9	1278 / 1.3/2.8	48 / 2/0.1*	2804 / 1.4/7.5	MSL#	iii
<i>Trichilia emetica</i>	98 / 4.2/5.2*	//	25 / 1.2/3*	353 / 1.4/2	1509 / 2.1/3.2	//	98 / 2/0.3*	2084 / 2/2	MSL	iii
<hr/>										
<i>Combretum molle</i>	0 / 0/5.2*	288 / 1.3/60.4	249 / 1.7/9.1	781 / 1.1/145.3	212 / 1/14.9	1643 / 1/21.2	14 / 1.2/11.4	3187 / 1.2/38.2	MNM	iv
<i>Dialium schlechteri</i>	639 / 1.7/46.2	1087 / 1.3/93.8	10 / 1.6/6.5	429 / 0.5/20.4	646 / 0.9/6.9	1584 / 1/6.8	0 / 0/18.3	4395 / 0.9/28.4	MNM	iv
<i>Strychnos madagascariensis</i>	6 / 2.1/5.2*	662 / 2.1/141.3	28 / 1.4/11.7	173 / 1.3/58.3	710 / 0.9/65.5	1417 / 1.1/110.2	322 / 1.2/71.7	3317 / 1.3/66.3	MNH#	iv
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<i>Galpinia transvaalica</i>	2 / 4.2/10.3*	//	330 / 2.4/0.2*	//	//	//	//	332 / 2.1/1.5	LSL	v
<i>Garcinia livingstonei</i>	//	//	3 / 2.4/2.2*	73 / 2/2	145 / 1.3/3	265 / 1/7.4	13 / 2/0.2*	499 / 1.5/2.1	LSL	v
<i>Antidesma venosum</i>	//	//	26 / 0.8/5.3	47 / 1.2/14.4	31 / 1.8/2.9	241 / 1.3/6.5	//	344 / 1.6/4.2	LSL	v
<i>Manilkara discolor</i>	201 / 1.8/42.1	//	0 / 2.4/5.6*	//	//	//	//	201 / 1/6.8	LSL*	v

<i>Newtonia hildebrandtii</i>	638 / 2.6/9.3	//	//	//	//	//	//	638 / 1.3/1.3	LSL	v
<i>Wrightia natalensis</i>	192 / 1.4/3.5	//	//	//	//	//	//	192 / 0.7/0.5	LSL	v
<i>Ficus stuhlmannii</i>	//	//	//	//	147 / 2.1/0.2*	//	//	147 / 2.1/0	LSR	v
<i>Syzygium cordatum</i>	//	//	145 / 0.8/1	143 / 1.2/2	118 / 1.8/1.1	37 / 1.6/0.1*	22 / 2/0.1*	464 / 1.4/0.6	LSR	v
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<i>Erythrophleum lasianthum</i>	60 / 0.7/7	//	//	//	//	51 / 1.6/1.8	//	111 / 0.9/1.3	LNL	vi
<i>Sapium integerrimum</i>	17 / 2.1/5.2*	0 / 0/7.6*	//	37 / 1.1/15.9	93 / 0.9/5.7	234 / 0.9/12.6	//	380 / 1.1/6.7	LNL	vi
<i>Ziziphus mucronata</i>	//	0 / 0/0.4*	362 / 1.3/10.4	11 / 2/0.7*	8 / 0.7/6.6	93 / 0.7/3.8	0 / 0/3.7*	475 / 0.9/3.7	LNL	vi
<i>Balanites maughamii</i>	0 / 0/9.9	372 / 2/2.1	0 / 0/1*	0 / 0/0.6*	34 / 2.1/0.1*	312 / 0.5/1.6	//	717 / 0.7/2.2	LNL	vi
<i>Commiphora neglecta</i>	0 / 0/38.6*	95 / 1.4/42.5	16 / 1.8/15.6	0 / 0/54.9	14 / 1.1/2.1*	//	//	125 / 0.8/22	LNM [#]	vi
<i>Psyrax fragrantissima</i>	264 / 1.7/106.1	//	//	//	//	//	//	264 / 0.9/15.2	LNM	vi
<i>Pteleopsis myrtifolia</i>	411 / 2.4/102.4	12 / 0.8/21.6	//	//	//	0 / 0/1.2*	//	423 / 1.1/17.9	LNM [#]	vi
<i>Spirostachys africana</i>	212 / 2.8/3.5	29 / 1.7/18.8	1110 / 0.9/33.7	62 / 0.8/15.5	255 / 1.2/3	17 / 0.3/2.9	84 / 0.7/0.2	1769 / 0.9/11.1	LNM [#]	vi
<i>Strychnos spinosa</i>	0 / 2.1/38.6*	66 / 1.2/114	8 / 0.5/38.8	25 / 0.6/29.9	134 / 0.9/23.7	95 / 0.8/14.4	12 / 1/7.7	341 / 0.9/38.1	LNM [#]	vi
<i>Cordia caffra</i>	//	//	166 / 2.4/0.2*	0 / 0/1.7*	//	//	//	166 / 1.1/0.3	LNR	vi
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<i>Cleistanthus schlechteri v. schlechteri</i>	29 / 0.3/39.6	//	//	//	//	301 / 1.1/2.7	//	331 / 0.6/6.1	LRL	vii
<i>Acacia senegal v. rostrata</i>	//	//	152 / 0.7/22.8	//	//	//	//	152 / 0.6/3.3	LRM	vii
<i>Psyrax locuples</i>	70 / 2.8/18.4	59 / 0.7/249.6	7 / 0.2/36.2	53 / 1.8/17.2	0 / 1.1/2.1*	12 / 0.8/1.5*	//	201 / 0.8/46.4	LRM [#]	vii
<i>Tabernaemontana elegans</i>	19 / 0.8/48	1 / 0.5/50.7	0 / 0/13.4	47 / 1.5/9	27 / 0.6/7.6	22 / 0.5/7.4	//	116 / 0.7/19.4	LRM [#]	vii
<i>Dichrostachys cinerea</i>	21 / 2.8/97.8	20 / 1.5/84.6	5 / 0.3/43.5	4 / 2/10.6*	26 / 0.6/15.8	49 / 0.6/8.3	0 / 0/91.7	124 / 0.5/50.3	LRM [#]	vii
<i>Euclea natalensis</i>	0 / 0/59.2	20 / 0.6/87.4	154 / 0.5/38.1	0 / 0/39.6	6 / 0.1/13.2	0 / 0/4.5	0 / 0/3.7*	180 / 0.2/35.1	LRM	vii
<i>Hymenocardia ulmoides</i>	1218 / 1/166.7	57 / 1/46.7	//	//	//	11 / 0.2/13.6	0 / 0/3.7	1286 / 0.5/33	LRM	vii
<i>Vepris lanceolata</i>	142 / 0.7/33.7	379 / 0.3/139.8	0 / 0/8.6	15 / 0.7/22.5	//	0 / 0/1.2*	//	537 / 0.3/29.4	LRM	vii
<i>Drypetes arguta</i>	109 / 0.3/403.4	0 / 0/42.4	//	//	//	//	//	109 / 0.1/63.7	LRH	vii
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<i>Hyperacanthus microphyllus</i>	//	4 / 2.5/14*	//	//	//	//	//	4 / 2.1/2	TSL*	viii
<i>Warneckea sousae</i>	2 / 1.4/24.6*	//	//	//	//	//	//	2 / 0.7/3.5	TSL*	viii
<i>Tricalysia junodii var. junodii</i>	2 / 2.1/19.3*	//	//	//	//	//	//	2 / 1.1/2.8	TSL*	viii
<i>Elaeodendron transvaalensis</i>	//	//	72 / 2.4/1.8*	//	//	//	//	72 / 2.1/0.3	TSR*	viii
<i>Euphorbia tirucalli</i>	//	//	60 / 2.4/0.2*	//	//	//	//	60 / 2.1/0	TSR*	viii
<i>Kigelia africana</i>	//	//	//	9 / 2/0.7*	7 / 2.1/0.2*	//	//	16 / 2.1/0.1	TSR*	viii
<i>Phyllanthus reticulatus</i>	//	//	//	2 / 2/1.7*	//	//	//	2 / 2.1/0.2	TSR*	viii

<i>Boscia foetida</i> sub. <i>rehmanniana</i>	//	6 / 1/37	7 / 2.4/0.8*	//	//	//	//	12 / 1.1/5.4	TNL*	ix
<i>Canthium setiflorum</i> sub. <i>setiflorum</i>	//	0 / 0/14*	//	12 / 1/7	//	//	0 / 0/3.7*	12 / 0.7/3.5	TNL*	ix
<i>Euclea divinorum</i>	//	12 / 0.8/12.9	30 / 1.6/8.6	//	//	//	//	42 / 1.1/3.1	TNL#	ix
<i>Mimusops caffra</i>	65 / 2.4/16.8	//	//	0 / 0/12.9	//	//	//	65 / 0.7/4.2	TNL#	ix
<i>Rothmannia fisheri</i> sub. <i>moramballae</i>	2 / 1.4/48.9	//	//	//	//	//	//	2 / 0.7/7	TNL	ix
<i>Sideroxylon inerme</i>	//	//	48 / 1/18.2	//	//	//	//	48 / 0.9/2.6	TNL	ix
<i>Tricalysia delagoensis</i>	0 / 0/29.6*	//	//	0 / 2/8.9*	//	//	//	0 / 1.1/5.5	TNL*	ix
<i>Drypetes natalensis</i>	22 / 1.7/41.7	//	//	//	//	//	//	22 / 0.9/6	TNL	ix
<i>Bridelia cathartica</i>	5 / 1.4/39.9	0 / 0/7.2*	4 / 0.8/16.7	12 / 0.9/50.2	24 / 0.9/4.3	1 / 0.5/6.6	//	45 / 0.8/17.8	TNM	ix
<i>Lagynias lasiantha</i>	10 / 1.4/88.8	//	//	//	//	//	//	10 / 0.7/12.7	TNM	ix
<i>Rhus gueinzii</i>	55 / 2.8/18.4	0 / 0/28.1*	0 / 0.6/22.3	28 / 1.5/14.1	10 / 0.8/3.1	0 / 0/2.9	//	94 / 0.8/12.7	TNM#	ix
<i>Acacia nilotica</i> sub. <i>kraussiana</i>	0 / 0/4*	//	4 / 0.9/17.9	55 / 1/1.3*	//	23 / 1.6/2	//	83 / 1.2/3.6	TNR	ix
<i>Berchemia zeyheri</i>	//	//	91 / 1.2/3*	//	//	//	//	91 / 1.1/0.4	TNR	ix
<i>Combretum mkuzense</i>	//	//	//	//	//	33 / 1/2.7	//	33 / 1.3/0.4	TNR	ix
<i>Ekebergia capensis</i>	//	//	38 / 2.4/0.2*	0 / 0/1.7*	//	//	//	38 / 1.1/0.3	TNR*	ix
<i>Schotia brachypetala</i>	//	//	34 / 1.2/0.3*	37 / 2/0.3*	//	0 / 0/0.1*	//	71 / 1.1/0.1	TNR	ix
<hr/>										
<i>Canthium inerme</i>	0 / 0/48.9	//	0 / 0/7.8*	22 / 2/12.3	0 / 0/0.4*	//	//	22 / 0.7/9.9	TRL#	x
<i>Monodora junodii</i>	0 / 0/50.7	0 / 2.5/14*	//	//	//	//	//	0 / 0.4/9.3	TRL	x
<i>Acalypha glabrata</i>	4 / 2.1/38.6*	1 / 0/28.1*	//	//	//	//	//	4 / 0.5/9.5	TRL	x
<i>Acridocarpus natalitius</i> v. <i>linearifolius</i>	0 / 0/19.3*	//	//	//	1 / 0/4.3	0 / 0.5/3.6	//	0 / 0.3/3.9	TRL	x
<i>Ancylanthos monteiroi</i>	//	1 / 0/21.6	//	//	1 / 1.1/0.6*	//	//	1 / 0.4/3.2	TRL	x
<i>Dovyalis longispina</i>	0 / 0/19.3*	//	0 / 0/5.6*	2 / 1/10.6*	//	//	//	2 / 0.5/5.1	TRL	x
<i>Erythroxylum delagoense</i>	11 / 2.1/20.6*	//	//	0 / 0/26.6	0 / 0/0.4*	18 / 1.6/0.3*	//	28 / 0.6/6.8	TRL	x
<i>Grewia microthyrsa</i>	//	0 / 0/42.4	14 / 2.4/7.8*	//	3 / 0.5/3.6	0 / 0/3.6	//	18 / 0.5/8.2	TRL	x
<i>Margaritaria discoidea</i>	//	0 / 0/28.1*	//	2 / 1/10.6*	0 / 0/1.1*	//	//	2 / 0.4/5.7	TRL	x
<i>Maytenus senegalensis</i>	//	12 / 2.5/7.2*	0 / 0/33.5	0 / 0/8.9*	1 / 0.5/4.3	0 / 0/2.4*	//	13 / 0.3/8	TRL	x
<i>Ozoroa engleri</i>	//	//	//	0 / 0/8.9*	47 / 0.2/8.9	8 / 0.3/7.3	0 / 0/14.7	54 / 0.2/5.7	TRL	x
<i>Pavetta catophylla</i>	//	0 / 0/14*	1 / 1.2/11.2*	//	//	0 / 0/2.4*	//	1 / 0.4/3.9	TRL	x
<i>Phoenix reclinata</i>	0 / 0/10.3*	//	23 / 0.4/31.3	1 / 2/8.9*	//	//	//	23 / 0.5/7.2	TRL	x
<i>Ptaeroxylum obliquum</i>	0 / 0/68.4	0 / 0/18.3*	11 / 0.6/5.4	3 / 2/1.7*	//	0 / 0/0.3*	//	15 / 0.3/13.5	TRL	x
<i>Vangueria esculenta</i>	0 / 0/10.3*	//	0 / 0/2.2*	//	1 / 0.4/4	0 / 0/1.7*	3 / 2/0.2*	18 / 0.4/2.6	TRL	x
<i>Xylothea kraussiana</i>	0 / 0/29.6*	0 / 0/14*	0 / 0/5.6*	2 / 2/8.9*	//	0 / 0/2.4*	//	2 / 0.3/8.6	TRL	x
<i>Zanthoxylum capense</i>	0 / 0/10.3*	7 / 1.7/21.6	17 / 2.4/0.8*	3 / 0.7/4.2	0 / 0/3.1	0 / 0/0.8*	//	27 / 0.6/5.8	TRL	x
<i>Acacia borleae</i>	//	//	0 / 0/33.5	//	//	//	//	0 / 0/4.8	TRL	x
<i>Grewia caffra</i>	23 / 2.1/28.6	3 / 0.5/56.5	0 / 0/11.2*	//	0 / 0/1.1*	0 / 0/4.1	//	26 / 0.4/14.5	TRM#	x
<i>Hyphaene coriacea</i>	3 / 0.6/53.3	//	0 / 0/92.6	3 / 0.5/44.1	0 / 0/3.7	0 / 1.6/1.2	11 / 0.7/8.1	18 / 0.3/29	TRM#	x

<i>Salacia leptoclada</i>	5 / 0.4/115.2	//	//	//	//	//	//	5 / 0.2/16.5	TRM	x
<i>Strychnos decussata</i>	39 / 1.4/24.6	18 / 0.5/44.9	2 / 0.8/3.8	//	0 / 0/1.1*	//	//	60 / 0.5/10.6	TRM [#]	x
<i>Teclea gerrardii</i>	9 / 0.4/108.4	0 / 0/70.9	0 / 0/5.6*	0 / 0/3.1	//	0 / 0/2.2	//	9 / 0.1/27.2	TRM	x
<i>Todallioopsis bremekampii</i>	7 / 0.6/195.8	//	//	//	//	//	//	7 / 0.3/28	TRM	x
<i>Tricalysia capensis</i>	0 / 0/52.9	9 / 1/46.7	2 / 1.2/7.8*	0 / 0/8.9*	//	0 / 0/2.4*	//	12 / 0.5/17	TRM	x
<i>Vangueria infausta sub. infausta</i>	0 / 0/19.3*	5 / 0.6/56.1	17 / 1.9/17.9	22 / 1/17.6	13 / 0.4/28.8	7 / 0.2/13.6	1 / 0.5/11.2	66 / 0.5/23.5	TRM [#]	x
<i>Catunaregam spinosa sub. spinosa</i>	4 / 1.2/117.1	0 / 0/77.4	0 / 0/7.8*	3 / 0.3/175.2	0 / 0/11.4	0 / 0/3.6	0 / 0/14.7	8 / 0.2/58.2	TRH [#]	x
<i>Cola greenwayi</i>	27 / 0.3/498.5	1 / 0/7.2*	//	//	//	//	//	27 / 0.1/72.2	TRH [#]	x
<i>Brachylaena huillensis</i>	13 / 0.4/337.8	2 / 0.4/84.2	0 / 0/11.2*	0 / 0/26.6	0 / 0/5.3	1 / 0.2/10.2	0 / 0/66	16 / 0.1/77.3	TRH [#]	x
<i>Croton pseudopulchellus</i>	16 / 0.4/581.6	0 / 0/28.1*	0 / 0/5.6*	//	//	//	//	16 / 0.2/87.9	TRH [#]	x

<i>Clausena anisata</i>	0 / 0/29.6*	0 / 0/28.1*	0 / 0/5.6*	0 / 0/53.1	0 / 0/3.2	0 / 0/7.8	//	0 / 0/18.2	CM	xii
<i>Coddia rudis</i>	0 / 0/19.3*	0 / 0/56.1	0 / 0/39.1	0 / 0/8.9*	0 / 0/1.1*	0 / 0/1.7*	//	0 / 0/18	CM	xii
<i>Plectroniella armata</i>	0 / 0/23.3*	//	0 / 0/13.4	0 / 0/35.4	//	0 / 0/1.2*	//	0 / 0/10.5	CM	xii

<i>Coffea racemosa</i>	//	//	0 / 0/11.2*	//	//	//	//	0 / 0/1.6	CL*	xii
<i>Diospyros inhacaensis</i>	0 / 0/19.3*	//	//	0 / 0/8.9*	//	//	//	0 / 0/4.6	CL*	xii
<i>Ehretia rigida</i>	//	0 / 0/14*	0 / 0/5.6*	//	//	//	//	0 / 0/2.8	CL*	xii
<i>Euphorbia ingens</i>	//	0 / 0/8.9	0 / 0/0.3*	0 / 0/0.7*	0 / 0/0.1*	0 / 0/0.1*	//	0 / 0/1.4	CL	xii
<i>Gardenia volkensii</i>	//	//	0 / 0/5.6*	//	//	//	1 / 0/3.7	0 / 0/1.3	CL*	xii
<i>Haplocoelum gallense</i>	0 / 0/3.5	0 / 0/14*	//	//	//	//	//	0 / 0/2.5	CL*	xii
<i>Hyperacanthus amoenus</i>	0 / 0/24.6	//	//	//	//	//	//	0 / 0/3.5	CL*	xii
<i>Mundulia sericea</i>	//	//	//	0 / 0/35.4	0 / 0/12.8	0 / 0/8.7	0 / 0/3.7*	0 / 0/8.7	CL	xii
<i>Ochna arborea var. arborea</i>	0 / 0/4*	0 / 0/7.2*	//	//	//	//	//	0 / 0/1.6	CL*	xii
<i>Ochna barbosae</i>	0 / 0/38.6*	//	//	//	//	0 / 0/1.2*	//	0 / 0/5.7	CL	xii
<i>Ochna natalitia</i>	//	0 / 0/14*	0 / 0/16.7	0 / 0/17.7*	0 / 0/2.1*	0 / 0/3.6	//	0 / 0/7.7	CL	xii
<i>Oxyanthus latifolius</i>	0 / 0/10.3*	//	//	//	//	//	//	0 / 0/1.5	CL*	xii
<i>Strychnos henningsii</i>	0 / 0/27.4	//	//	//	0 / 0/1.1*	//	//	0 / 0/4.1	CL	xii
<i>Suregada zanzibariensis</i>	0 / 0/19.3*	//	//	//	//	//	//	0 / 0/2.8	CL*	xii
<i>Tarenna junodii</i>	0 / 0/19.3*	//	//	//	//	//	//	0 / 0/2.8	CL*	xii
<i>Vitex amboniensis</i>	0 / 0/18.4	//	//	//	0 / 0/1.1*	0 / 0/2.4*	//	0 / 0/3.1	CL	xii
<i>Acacia karroo</i>	//	//	0 / 0/4.5*	//	//	//	//	0 / 0/0.6	CR*	xii
<i>Albizia forbesii</i>	//	0 / 0/0.8	//	//	//	//	//	0 / 0/0.1	CR*	xii
<i>Casearia gladiiformis</i>	//	//	//	0 / 0/1.7*	//	//	//	0 / 0/0.2	CR*	xii
<i>Cassipourea mossambicensis</i>	0 / 0/5.2*	//	//	//	//	//	//	0 / 0/0.7	CR*	xii
<i>Combretum celastroides sub. orientale</i>	0 / 0/5.2*	//	//	//	//	//	//	0 / 0/0.7	CR*	xii

<i>Erythroxylum emarginatum</i>	//	//	0 / 0/5.6*	//	//	//	//	0 / 0/0.8	CR*	xii
<i>Euclea schimperi</i>	//	//	//	//	//	0 / 0/0.3*	//	0 / 0/0	CR*	xii
<i>Eugenia natalitia</i>	//	0 / 0/7.2*	//	//	//	//	//	0 / 0/1	CR*	xii
<i>Euphorbia grandidens</i>	//	//	//	0 / 0/0.7*	//	//	//	0 / 0/0.1	CR*	xii
<i>Lansea antiscorbutica</i>	0 / 0/2.3*	//	//	//	//	//	//	0 / 0/0.3	CR*	xii
<i>Manilkara concolor</i>	//	//	//	0 / 0/0.3*	//	//	//	0 / 0/0	CR*	xii
<i>Maytenus undata</i>	//	//	//	0 / 0/1.7*	//	0 / 0/1.2*	//	0 / 0/0.4	CR*	xii
<i>Premna mooiensis</i>	//	//	//	//	//	0 / 0/1.2*	//	0 / 0/0.2	CR*	xii
<i>Pseudobersama mossambicensis</i>	0 / 0/19.3*	//	//	//	//	//	//	0 / 0/2.8	CR*	xii
<i>Thespesia acutiloba</i>	//	//	0 / 0/6.4*	//	//	//	//	0 / 0/0.9	CR*	xii
Totals	5501 / /4479.3	8095 / /2290.2	8477 / /1029.3	7231 / /1352.4	18786 / /396.1	37347 / /436.8	3012 / /450.2	88465 / /1490.6		