

The floristics of Sand Forest in northern KwaZulu-Natal, South Africa

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ABSTRACT

We use multivariate analyses (ordination and classification) to assess both the floristic uniqueness of the woody vegetation of Sand Forest in relation to a range of other forest types in the region, and the range of variation within Sand Forest. Two broad Sand Forest subtypes and related Ecotonal Forests are described and grouped under the term Tropical Dry Forest, distinct from all evergreen forests in South Africa. Sand Forest, a dry semi-deciduous type in northeastern KwaZulu-Natal is defined by the presence of the canopy dominant *Cleistanthus schlechteri* as well as *Hymenocardia ulmoides*, *Psyrax fragrantissima*, *Croton pseudopulchellus* and *Drypetes arguta*. Sand Forests form a cohesive group in both DCA and TWINSpan analyses, with similar composition of canopy dominants at sampled sites. This implies that ecological functioning is similar across the geographical range in northeastern KwaZulu-Natal. However, turnover of subdominant species between recognisable Sand Forest types emphasizes the need to conserve the full range of extant forests.

INTRODUCTION

Maputaland, the northeastern tip of KwaZulu-Natal (Figure 1), forms the narrow southern portion of a large coastal plain extending up the east coast of Africa as far north as Somalia (Watkeys *et al.* 1993). Maputaland is bordered by Mozambique in the north, the Indian Ocean to the east and the Lebombo Mountains to the west (Moll 1978; Bruton & Cooper 1980). The southern boundary can be drawn from the southern end of the Lebombo Range to the mouth of the St Lucia Estuary (Watkeys *et al.* 1993). The vegetation is a complex mosaic of forest, thicket, savanna and grassland, with a high proportion of endemics (perhaps 40% of woody species) and abrupt local changes in response to soils and climate (Moll 1980).

Despite this botanical importance, the area has only recently been scientifically explored. Bayer, in a 1938 study encompassing the coastbelt and midlands of Zululand, stated: '...there is no doubt that throughout the coastbelt proper, evergreen sub-tropical forest ... is a true climatic climax.' However, moist, evergreen forest is certainly not the only forest type in the region. References to dry forest with a unique complement of species first appear in the literature in the mid-1960's (e.g. Vahrmeijer 1966; Tinley 1967). Moll (1968, 1978, 1980) and Moll & White (1978) used the local term 'Sand Forest' to describe this dry deciduous or semideciduous forest occurring on sandy soils. They list a variety of common and widespread tree species, including *Newtonia hildebrandtii*, *Cleistanthus schlechteri*, *Hymenocardia ulmoides*, *Balanites maughamii*, *Ptaeroxylon obliquum* and others. The term Sand Forest has since passed into general (e.g. Goodman 1990; Midgley *et al.* 1997) and popular use (e.g. Pooley 1993; Craib 1995). In South Africa, it refers to dense forests with numerous trees and shrubs (De Moor *et al.* 1977; Moll & White 1978; Moll 1978, 1980) with a relatively short canopy

(6 m or higher: De Moor *et al.* 1977, 10–25 m: Moll & White 1978; Moll 1978, 1980, 5–13 m with emergents above 15 m: Ward 1981), occurring in dry conditions (600–1 000 mm: Tinley 1967, 700–900 mm: Moll & White 1978) on white to deep red sandy soils (Vahrmeijer 1966; Tinley 1967; De Moor *et al.* 1977; Moll &

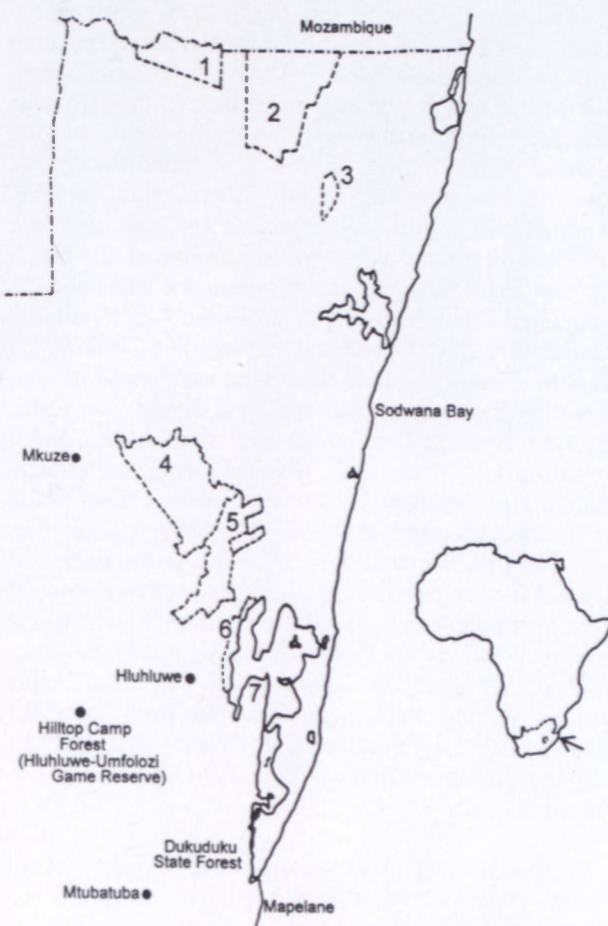


FIGURE 1.—Map of northeastern KwaZulu-Natal showing sampled sites and boundaries of reserves containing Sand Forest. 1, Ndumu Game Reserve; 2, Tembe Elephant Park; 3, Sileza Forest Reserve; 4, Mkuze Game Reserve; 5, Phinda Resource Reserve; 6, False Bay Park; 7, Hell's Gate.

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White 1978; Moll 1978, 1980; Ward 1981). These forests tend to be patchily distributed in characteristic north-south oriented strips (Vahrmeijer 1966; Moll 1978, 1980; Moll & White 1978; Ward 1981).

Although this forest type is a conspicuous feature in Maputaland (Moll 1978, 1980; pers. obs.), descriptions have been cursory (e.g. Vahrmeijer 1966; Tinley 1967; Moll 1978, 1980; Moll & White 1978) or very local (e.g. De Moor *et al.* 1977; Ward 1981; Goodman 1990). There is confusion regarding the definition of Sand Forest and which plant species are representative and characteristic (e.g. Moll & White 1978 cf. McKenzie 1996). The published literature describing Sand Forest is confined to a few paragraphs. Species lists associated with this forest type appear to be derived largely from casual observation, and feature conspicuous canopy emergents such as *Newtonia hildebrandtii* and *Balanites maughamii* which may be associated with other vegetation types (pers. obs.). Only one study, based on a regional data set and using quantitative methods, defines Sand Forest types in terms of characteristic tree species (MacDevette *et al.* 1989). However, that work is presented only as a preliminary classification of the KwaZulu-Natal indigenous forests, and is based on species checklists of varying reliability, with whole forests as the basic sample unit.

It is also unclear how closely Sand Forest is related to other forests in the region. Moll (1978, 1980) simply treats Sand Forest as one of thirteen or fifteen vegetation types in Maputaland. Moll & White (1978), in a description of the Indian Ocean Coastal Belt (a floristic zone stretching from just south of Somalia to the Cape), include Sand Forest in the Tongaland-Pondoland Regional Mosaic with four other forest types. Midgley *et al.* (1997) follow this approach and that of White (1983) which emphasizes the separation of the South African forest flora into the Afrotropical types and the Tongaland-Pondoland Regional Mosaic which includes Sand Forest. MacDevette *et al.* (1989), in a TWINSPLAN classification of the KwaZulu-Natal indigenous forests, group an Eastern and Western Sand Forest type under the title Tropical Dry Forest with four other Coastal Forest types. Their main division separates Coastal Forests from Interior Forests in a similar manner to the treatments described above. Tinley (1967, 1977), however, regards Tropical Dry Semideciduous Forest in South Africa as part of a much larger Southern Tropical Sand Forest Domain, completely separate from all moist evergreen forests (including evergreen coastal forests). Moll & White (1978) list a variety of Sand Forest species linking the Pondoland-Tongaland Regional Mosaic with Dry Forests in the Zanzibar-Inhambane Regional Mosaic, which would seem to support Tinley's approach.

Despite the lack of any comprehensive study of Sand Forest, its conservation in South Africa is considered important for a number of reasons. Sand Forest covers a small total area (McKenzie 1996) and is heavily impacted outside of reserves (Moll 1978; Geldenhuys & MacDevette 1989; McKenzie 1996; pers. obs.). It is rich in woody species (Moll & White 1978) and the habitat of a number of unusual or rare animals, such as the Suni,

Neotragus moschatus (Lawson 1986), the African broadbill, *Smithornis capensis*, and Neergaard's sunbird, *Nectarinia neergaardi*, which is largely confined to the Sand Forest (Harrison *et al.* 1997). It is a drawcard for tourists (Macfarlane 1993; Craib 1995) and an important local resource, providing a range of building materials, traditional medicines and some food plants (Cunningham 1985).

At present, there is little information available for conservation planning, or for the delimitation of sensible ecological units for management and research into the dynamics of this little known forest type. Human pressure on the natural environment is increasingly severe as improved infrastructure leads to a rapidly increasing rural population. This description is important in ascertaining the conservation worthiness of the forest type as a whole and how well the range of floristic variation is presently conserved. In addition it serves as a basis for further ecological work.

Our aims are: to determine how similar Sand Forest in northern KwaZulu-Natal is to other South African forests, especially the moist evergreen Coastal Forests of KwaZulu-Natal; to define Sand Forest in terms of its woody species composition; and to describe any variation within the Sand Forest type.

STUDY SITE

Maputaland in South Africa is a low coastal plain covering approximately 5 700 km² (Watkeys *et al.* 1993). The climate is moist subtropical along the coast where rainfall is over 1 000 mm per annum becoming dry subtropical inland with less than 600 mm per annum. Rainfall increases again to over 800 mm per annum along the crest of the Lebombo Mountains (Maud 1980; Watkeys *et al.* 1993). The highest monthly precipitation falls between September and April resulting in hot, humid summers and cool, dry winters.

The soils of Maputaland are complex, although most of the area is covered by infertile, sandy Tertiary and Quaternary deposits (Watkeys *et al.* 1993). Marine transgressions and regressions since the end of the Cretaceous have formed these deposits into dune ridges oriented in a north-south direction (Goodman 1990), parallel to the present-day coastline. These dune cordons decrease in age from west to east, and the oldest, most westerly dune cordon may date from the Plio-Pleistocene (Davies 1976, cited by Goodman 1990). These oldest palaeo-dunes are not well preserved and are deep red in colour due to advanced mineral diagenesis. The soils on younger, more easterly dunes are generally poorly developed, yellow to orange arenosols. Sand Forest occurs on the full range of these inland dunes. The tall coastal dune cordon is composed of dystrophic pallid sands, with steep slopes stabilised by dune forest and scrub. Between the dune ridges, the coastal plain is flat to gently undulating, and may be covered with loose dystrophic sands (Goodman 1990; Watkeys *et al.* 1993).

METHODS

Data collection

Analyses were based on two data sets, a 'Sand Forest' data subset, sampled specifically for this study, was combined with a regional Northeastern KwaZulu-Natal data set, to allow comparisons among a range of forest types. Sampling was confined to woody vegetation for a number of reasons. Non-woody understorey vegetation is temporally and spatially variable in these seasonally dry forests, and our short-term sampling program could not adequately assess this component. From a practical point of view, we are attempting to delimit ecological units, and it is the trees that most affect the forest environment. In Sand Forest the non-woody component is particularly sparse and contributes little to total biomass. Also, trees, shrubs and lianes are easier to find and identify than grasses and herbs, and we hope this study will be accessible to nonspecialists.

'Sand Forest' Data Set

Forests growing on or near sandy soils in Maputaland (excluding dune forests) were sampled to represent all the so-called Sand or Tropical Dry Forest types mentioned by De Moor *et al.* (1977), Moll (1978, 1980), Moll & White (1978), Ward (1981), MacDevette *et al.* (1989) and Goodman (1990). Sampled sites include the KwaZulu-Natal Nature Conservation Services reserves; False Bay Park, Mkuzi Game Reserve, Tembe Elephant Park, Ndumu Game Reserve and Sileza Forest Reserve, the privately owned Phinda Resource Reserve (hereafter referred to as False Bay, Mkuzi, Tembe, Ndumu, Sileza and Phinda respectively) and relatively undisturbed nearby areas which will be referred to by the same locality names. Protected areas were preferred for this survey as unprotected forests are usually heavily disturbed, complicating the recognition and definition of sand forest types.

At each locality, areas of forest (closed canopy, woody communities, > 5 m, MacDevette *et al.* 1989; Midgley *et al.* 1997) were chosen subjectively to represent the range of variation in structure and species composition. Within these areas, quadrats were randomly located, with the proviso that they be at least 50 m from any previous quadrats and the forest edge. The number of quadrats located at each locality was subjectively determined. Sampling was halted when the variation in species composition was adequately represented. Due to the naturally patchy and discontinuous nature of Sand Forest, which is further fragmented outside of protected areas, a more structured approach was considered impractical.

Samples consisted of circular 400 m² quadrats. This is a suitable size for short forest communities (Kent & Coker 1992), representing the approximate point of inflection of a species/area curve within a homogenous area of sand forest (Goodman 1990; D. Kirkwood unpubl. data) and is compatible with samples collected by other workers in the region. Species abundance values in each quadrat are total diameter at breast height (DBH), calculated from the sum of area at breast height of all individ-

uals. DBH of all woody individuals taller than 2 m, rooted within the quadrat was measured. Height of trees shorter than 2 m was measured, and converted to an estimate of diameter from a linear regression of height vs DBH for all trees between 2 and 3 m high at a site. Shrubs (largest individuals usually < 2 m), woody lianes and creepers were assigned an arbitrary total DBH of 2 cm. Tree species names follow Van Wyk & Van Wyk (1997).

Northeastern KwaZulu-Natal Data Set

Data from circular 400 m² quadrats sampled in a range of northeastern KwaZulu-Natal forests (see Figure 1) were used. Sites were chosen to represent Coastal and Inland Forest types (*sensu* MacDevette *et al.* 1989): Mapelane (35 quadrats) and Sodwana (34 quadrats) from the coastal dune cordon and Dukuduku Forest (20 quadrats) correspond to Undifferentiated Coastal Forest (*sensu* MacDevette *et al.* 1989) (Undifferentiated Lowland Forest *sensu* Moll & White 1978 or Coastal Forest *sensu* Lubke & McKenzie 1996) (R. van Wyk, D.R. MacDevette, D. Everard and I. Gordon, unpubl. data). Coast Scarp Forest (*sensu* MacDevette *et al.* 1989) (Lebombo Forest *sensu* Moll 1978, 1980), sampled in 1996 around Hluhluwe Game Reserve Hilltop Camp (21 quadrats: A. West, D. Kirkwood & J.J. Midgley unpubl. data), represents the Inland Forests.

These quadrats from coastal and inland types were combined with the 135 quadrats sampled for this study from as wide a range as possible of 'Sand Forest' and related types in Maputaland. This includes 16 quadrats sampled in Hell's Gate, just south of False Bay Park (D. Kirkwood unpubl. data), an area administered by the S.A. National Defence Force. The Hell's Gate quadrats are only included in the regional data set as the forest was substantially different floristically from other Sand Forest/Tropical Dry Forest types.

In this regional data set, abundance values were simplified to presence/absence of species, and small shrub, liane and creeper species were excluded, in order to overcome compatibility problems. While this reduces the information content of the data, it allows the robustness of results from analysis of the 'Sand Forest' data subset to be assessed.

Multivariate analysis

Our classification and definition of forest types, as well as the ordinations of samples are derived from indirect gradient analyses, utilising only floristic data. The most meaningful results were obtained using two well-known, robust and complementary techniques (Gauch 1982; Kent & Coker 1992): Two-Way Indicator Species Analysis (TWINSPAN, Hill 1979), a polythetic, divisive program and the Detrended Correspondence Analysis (DCA) option in the package CANOCO (Ter Braak 1991). These quantitative multivariate techniques were used to analyse the two data sets.

For all TWINSPAN analyses the following defaults were used: 10 indicator species per division and a minimum group size for division of five quadrats. Three lev-

els of division were adequate to separate the regional data set into groups consisting of quadrats largely from one locality. Four levels of division resulted in meaningful final groups used for the detailed classification of the Sand Forest data subset, which has a higher information content. Pseudospecies cut levels for the Sand Forest analysis were set at 0, 2.5, 10, 20 and 40 cm total DBH.

Analyses of the regional data set utilised all quadrats and only presence/absence abundance values were used. For the Sand Forest Data, two outlier plots significantly changed the relationships amongst the remaining plots. These were found to be quadrats in woodland clumps on the margin of sand forest patches in Tembe and Mkuzi and were thus eliminated from the final analysis. Our final classification of Sand Forest and related types is based on TWINSpan analyses of both the regional and Sand Forest data sets. TWINSpan, which is based on a reciprocal averaging algorithm, successively divides groups of samples utilising the differential presence or absence of species (Gauch 1982; Kent & Coker 1992). The program identifies indicator species for each division; 'characteristic species' are those which consistently occur in only one of the two groups of samples under consideration; 'preferential species' occur in a greater proportion of samples in one group than in the other.

All quadrats were used in the DCA of the regional data set. Similarly, although the related Hell's Gate Forests were not incorporated, all other Sand Forest/Tropical Dry Forest type quadrats were used in

the DCA analyses of the 'Sand Forest' data set. Two separate DCA analyses of the 'Sand Forest' data set were performed. The first uses species abundance values of total DBH. The subsequent analysis uses only presence/absence values to reduce the influence of dominant species.

Dominance

In order to evaluate the relative influence of dominant species on the grouping of Sand Forest quadrats by the DCA, dominance diversity curves were constructed for the six sites sampled. Importance values for these curves were calculated as the average of a species' relative dominance value (species total DBH/locality total DBH) and its relative density (no. plants/total no. plants) over all quadrats sampled in an area, excluding those shown to be outliers in the DCA ordinations. Quadrats sampled from the same area are grouped together by all analyses, with very few exceptions, indicating that forests are locally uniform, and sites can be used as natural units.

RESULTS

Affinities

The first two ordination axes of the detrended correspondence analysis of the northeastern KwaZulu-Natal forests (Figure 2) reveal that the majority of 'Sand Forest' quadrats are more widely separated from Coastal Forest types in Maputaland (Mapelane, Sodwana and Duku-

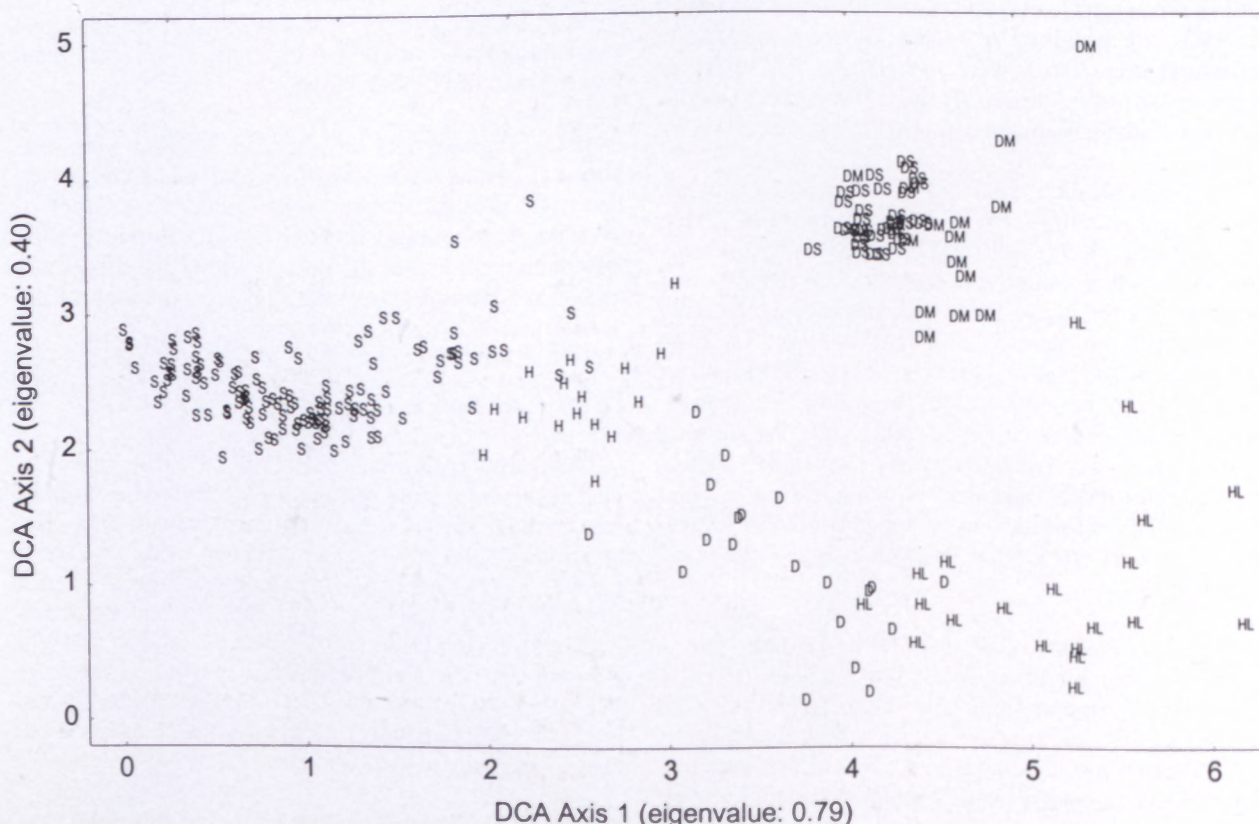


FIGURE 2.—Detrended correspondence analysis ordination of quadrats from a range of northeastern KwaZulu-Natal forests. S, 'Sand Forest' types; H, Hell's Gate; D, Dukuduku Forest; DS, Sodwana Dune Forest; DM, Mapelane Dune Forest; HL, forest around Hluhluwe Hilltop Camp.

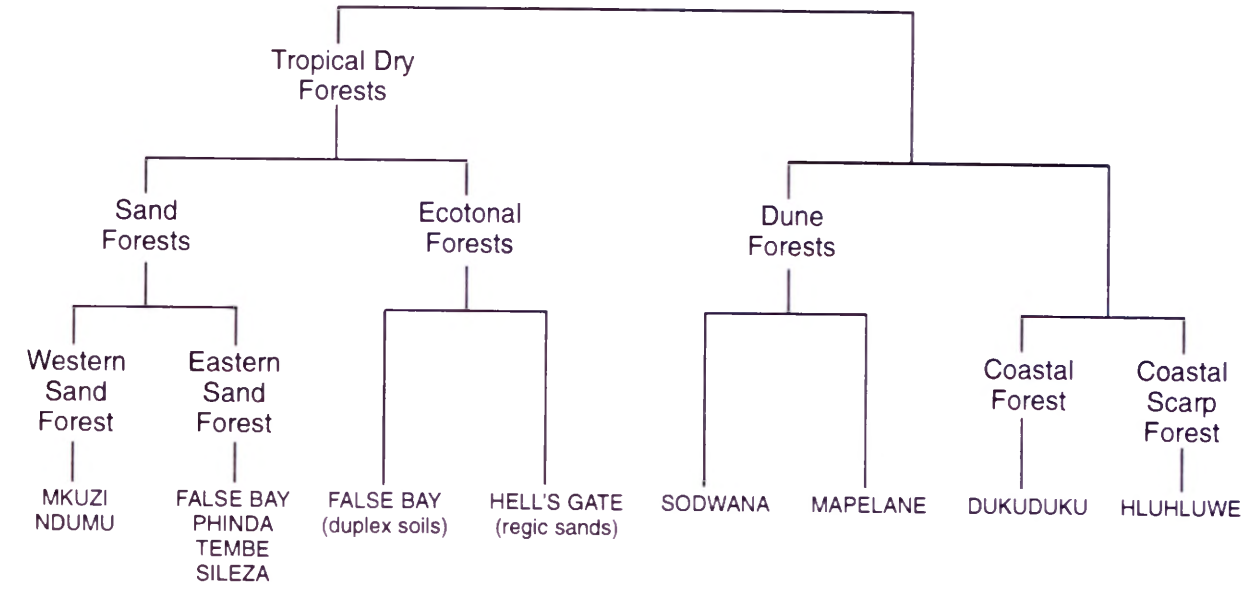


FIGURE 3.—TWINSpan classification of the northeastern KwaZulu-Natal data set. For clarity, final groups are presented only as locality names, as quadrats from the same locality are consistently grouped together (only 7 exceptions from 234 quadrats).

duku), than these Coastal Forest types are from an Inland Forest type represented by the Hluhluwe Game Reserve locality. Most of the quadrats sampled to represent 'Sand Forest' types form a tight group. Quadrats sampled at Hell's Gate forest and some 'Sand Forest' quadrats are however not closely allied to the other Sand Forest samples, and although distinct, are not widely separated from the Undifferentiated Coastal Forests of Dukuduku.

The TWINSpan classification of the same data set (Figure 3) emphasizes the separation of samples of 'Sand Forest' and it's allies from those of the moist evergreen

Coastal and Interior Forests in the first division (eigenvalue: 0.749).

Classification

In classifying the Sand Forest types we follow the terminology of MacDevette *et al.* (1989), whose group names are sensible and easily remembered. However, it is important to note that the groups are substantially modified and many of our characteristic and representative species differ.

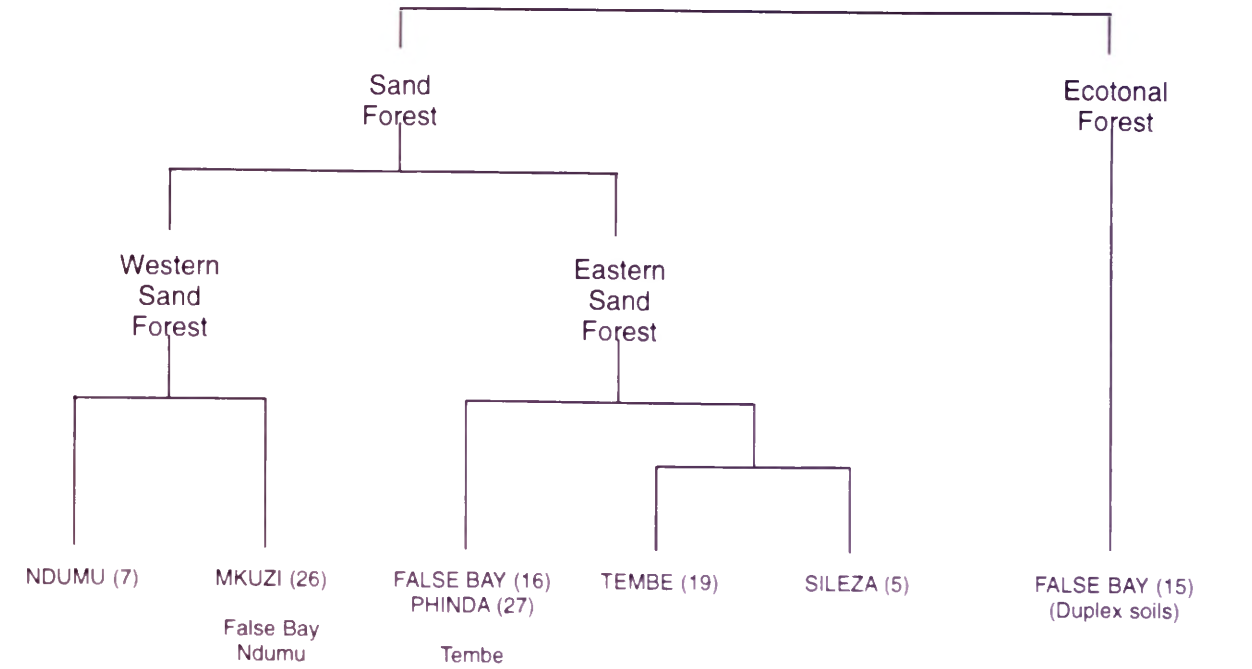


FIGURE 4 —TWINSpan classification of the Sand Forest data set. The number of quadrats from each area occurring in a final group are indicated in parentheses behind locality names. Lower case place names indicate that one quadrat from that locality occurs in the final group.

TWINSPAN analyses of the regional data set (Figure 3) and the Sand Forest data set (Figure 4) produce completely congruous classifications. Characteristic and preferential species based on divisions 1 and 2 of the regional analysis and divisions 2, 3 and 4 of the Sand Forest analysis are presented in our classification.

We suggest that the term 'Tropical Dry Forest' be used in South Africa to encompass both Sand Forest and allied dry semideciduous forests. Although these forests are strictly subtropical, it seems likely that they are floristically allied and ecologically similar to other Tropical Dry Forests in Africa.

Tropical Dry Forest

This forest type is defined by the presence of the characteristic tree species *Hymenocardia ulmoides*, *Wrightia natalensis*, *Pteleopsis myrtifolia*, *Cleistanthus schlechteri*, *Newtonia hildebrandtii* and *Drypetes arguta*. Preferential tree species are *Cola greenwayi*, *Hyperacanthus amoenus*, *Boscia foetida*, *Brachylaena huillensis*, *Combretum mkuzense*, *Dialium schlechteri*, *Grewia microthyrsa*, *Haplocoelum gallense*, *Monodora junodii*, *Psydrax fragrantissima*, *Ptaeroxylon obliquum*, *Strychnos henningsii*, *Toddaliopsis bremekampii* and *Tricalysia lanceolata*.

Although we have comprehensively sampled Tropical Dry Forest, only a small range of KwaZulu-Natal forests is used for comparison here. While the tree species characterising Tropical Dry Forest at this level of classification are representative, they may not be definitive when used in comparison with forests not included in this analysis.

Tropical Dry Forest is divided into two subtypes: Sand Forest and Ecotonal Forest (eigenvalue: 0.326).

Ecotonal Forest

These samples, while clearly allied to Sand Forest, are floristically diverse and occur on a variety of soils. Quadrats sampled in False Bay Park on duplex soils and soils with a high clay content fall into this group, as do quadrats on grey regic sands from the Hell's Gate area. Due to the variable species composition of quadrats in this group, we will not define subtypes within this group.

Characteristic tree species are *Strychnos usambarensis* and *Catunaregam spinosa* subsp. *spinosa*. Preferential tree species are *Chaetacme aristata*, *Diospyros inhacaensis*, *Drypetes natalensis*, *Manilkara concolor* and *Strychnos madagascariensis*.

Sand Forest

This type includes the majority of Tropical Dry Forest samples (103 of 143) and forms a cohesive group in the

DCA of the regional data set (Figure 2). Most samples occur on base-rich aeolian sands.

Characteristic tree species are *Cleistanthus schlechteri*, *Hymenocardia ulmoides*, *Toddaliopsis bremekampii*, *Psydrax fragrantissima*, *Pteleopsis myrtifolia* and *Haplocoelum gallense*. Preferential tree species are *Boscia foetida*, *Combretum mkuzense*, *Croton gratissimus*, *Hyperacanthus microphyllus*, *Monodora junodii* and *Vitex ferruginea* subsp. *amboniensis*.

For further divisions, the results of the TWINSPAN analysis of the Sand Forest data subset are presented. Shrubs and lianes, as well as abundance values for all woody species are recorded in this subset of quadrats. Where a species name is marked with an asterisk or double asterisk, this denotes that a characteristic or preferential species of a group is abundant—total diameter at breast height (DBH) > 20 cm; or very abundant—total DBH > 40 cm. Despite the increased information content of this data set, the TWINSPAN classification of Sand Forest samples (Figure 4) corresponds exactly with the divisions produced using the regional data set (Figure 3).

Sand Forest can be subdivided into two broad types, Western and Eastern Sand Forest (eigenvalue: 0.216).

Western Sand Forest

This type is represented by the Sand Forests from Mkuzi and Ndumu Game Reserves.

Characteristic species are the trees *Croton gratissimus* and *Brachylaena huillensis*. Preferential species include the trees *Brachylaena huillensis**, *Combretum mkuzense**, *Commiphora neglecta*, *Craibia zimmermanii*, *Croton gratissimus**, *Gardenia comuta*, *Rhus gueinzii* and *Strychnos spinosa*¹, as well as the lianes and creepers *Combretum* sp.² and *Grewia caffra*.

Eastern Sand Forest

Eastern Sand Forest includes the samples from False Bay Park, Phinda, Tembe and Sileza.

Characteristic species are the subcanopy trees *Cola greenwayi*, *Drypetes arguta* and *Tricalysia lanceolata*. Preferential species include the trees: *Balanites maughanii*, *Cola greenwayi***, *Dialium schlechteri*, *Dovyalis zeyheri*, *Drypetes arguta**, *Erythrophleum lasianthum*, *Grewia microthyrsa*, *Haplocoelum gallense**, *Hyperacanthus amoenus*, *Leptactina delagoensis*, *Manilkara discolor*, *Ochna arborea*, *O. natalitia*, *Oxyanthus latifolius*, *Psydrax locuples*, *P. fragrantissima**, *Ptaeroxylon obliquum*, *Strychnos henningsii*, *Suregada zanzibariensis*, *Toddaliopsis bremekampii* and *Vitex ferruginea* subsp. *amboniensis*. Other preferential species are the lianes and creepers *Acacia kraussiana*, *Dalbergia obovata*, *Landolphia kirkii*, *Monanthes caffra* and *Synaptolepis kirkii*.

The third level of division in the TWINSPAN classification of the Sand Forest data set (Figure 4) essentially subdivides both the Western (eigenvalue: 0.207) and

¹ Forest growth form, known locally as umHlalakolotshe.

² *Combretum* cf. *celastroides*, an unidentified but common climber in these forests.

* abundant, total DBH > 20 cm.

** very abundant, total DBH > 40 cm.

the Eastern (eigenvalue: 0.260) Sand Forest types into groups of samples that reflect species turnover between geographically separate sites. Only quadrats from Phinda and those on sandy soil at False Bay are grouped together. In the fourth and final level of division (not illustrated) it is notable that both the Mkuzi quadrats (Western Sand Forest), and the Phinda/False Bay quadrats (Eastern Sand Forest) are subdivided into groups characterised by the presence or absence of *Newtonia hildebrandtii*. Localised stands dominated by this tree, a large, spreading canopy emergent, are a conspicuous feature of these forests (pers. obs.; Moll & White 1978).

Species turnover and dominance in Sand Forest samples

In a DCA ordination of the same Sand Forest data subset (Figure 5), with species abundance values of total DBH, quadrats are not separated into the groups described above. Samples from False Bay, Mkuzi, Phinda, Tembe and Ndumu are grouped together, with a high degree of overlap within a range of two half changes (each DCA unit or average standard deviation of species turnover is approximately equivalent to a 50% change in species composition of samples, Gauch 1982). Only quadrats from Ecotonal Forest on duplex soils at False Bay and the Sileza samples are clearly separated from the main group. However, when species abundance values are reduced to presence/absence values, the resulting DCA ordination plot (Figure 6), groups quadrats in an identical manner to the final level of the

TWINSPAN classification illustrated in Figure 4. This result confirms the validity of the classification. In addition, ground-truthing using this classification outside of sampled areas indicated that we have adequately covered the range of variation of Sand Forest in Maputaland.

Separation of Sand Forest subtypes in the DCA ordination presented in Figure 6 results from reducing the influence of dominant species. This implies that within the Sand Forest type, forests have similar dominant species, but there is significant turnover of the less common species between groups. Dominance-diversity curves at each locality (Figure 7) indicate that this is the case. *Cleistanthus schlechteri* and *Newtonia hildebrandtii* rank consistently high. Note the disparity between the importance values of the one or two most dominant species and the other species at most sites.

Although the division between Western and Eastern Sand Forest is justified and convenient, it seems that the most natural grouping of forests is into three groups: the Mkuzi/Ndumu Group, separated from all other samples on the first and third DCA axes in Figure 6, and the Phinda/False Bay Group separated from the Tembe/Sileza Group on the second axis. These groups may represent a soil gradient, from the oldest red sands of Western Mkuzi/Ndumu Group, through orange to yellow sands of Sand Forests at Phinda and False Bay Park, to the predominantly yellow to white sands of Tembe and Sileza. The samples at Sileza, an isolated forest occurring on dystrophic white sands and surrounded by *Hyphaene natalensis* Palm Veld, although included in Eastern Sand

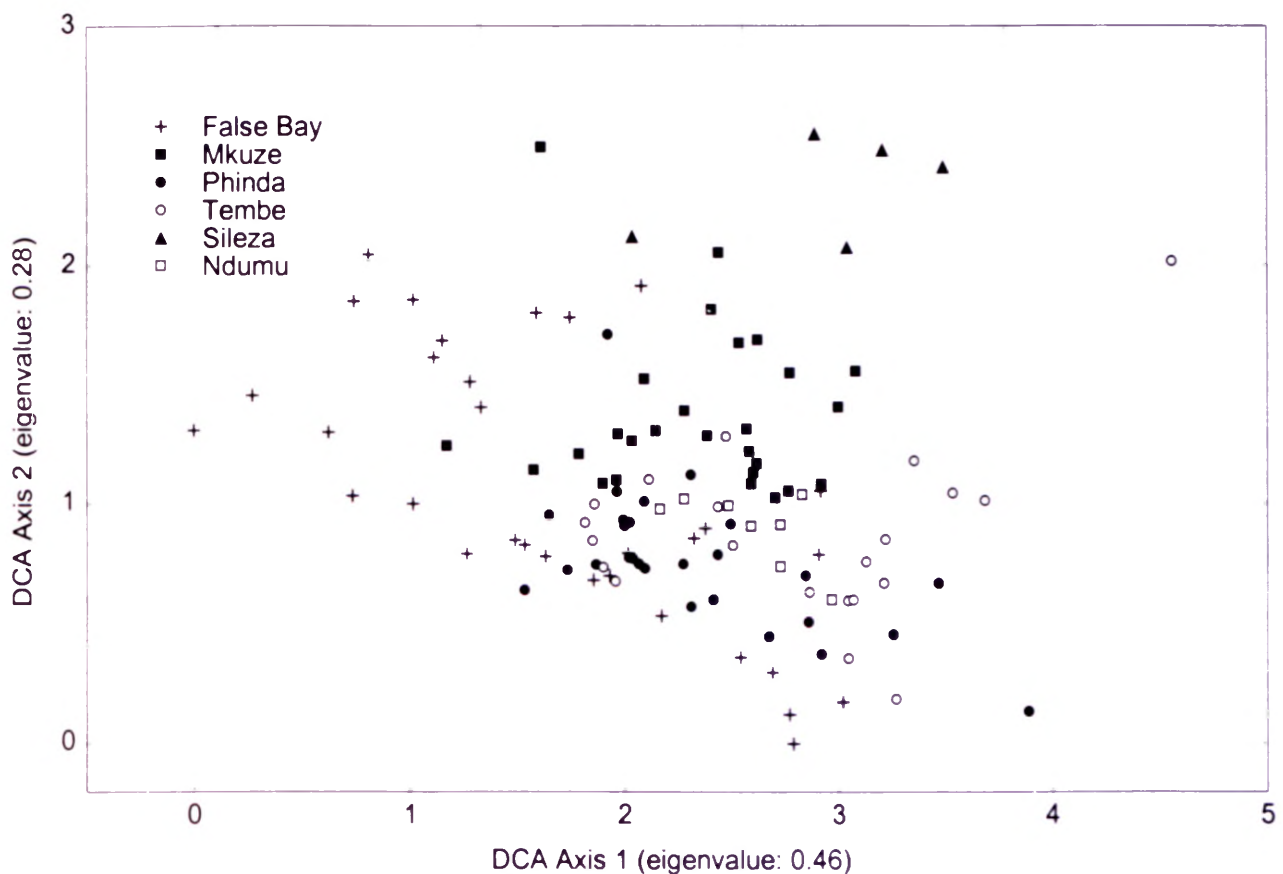


FIGURE 5.—Detrended correspondence analysis ordination of Sand Forest and associated quadrats utilising species abundance values of total diameter at breast height (DBH). Further axes do not reveal identifiable groups.

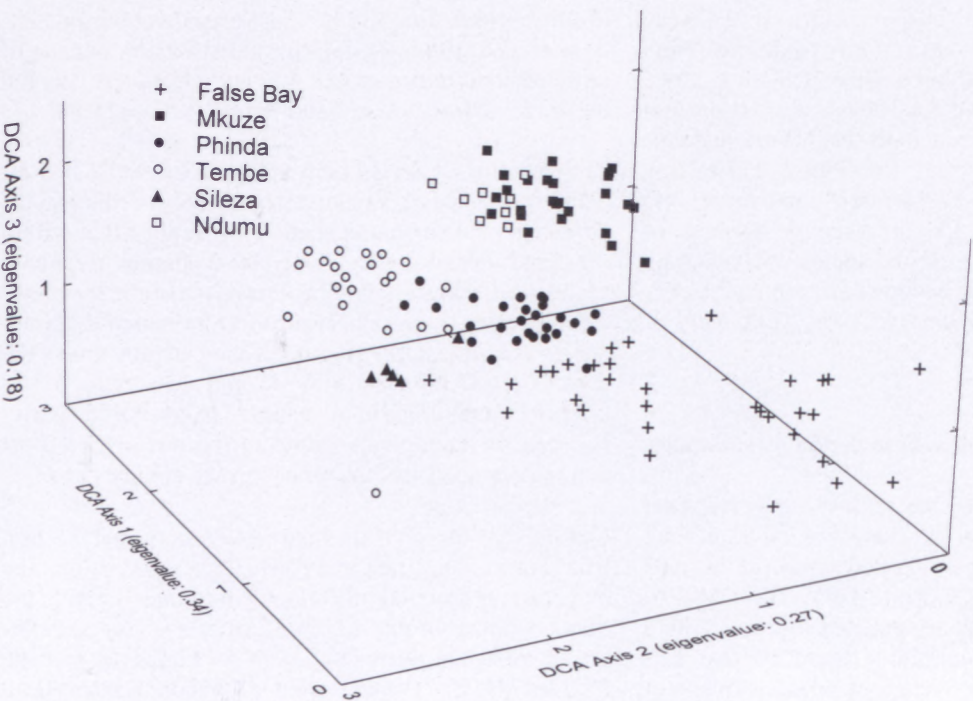


FIGURE 6.—Detrended correspondence analysis ordination of Sand Forest and associated quadrats utilising only species presence or absence (cf. Figure 5).

Forest, are separated from other Sand Forests by all DCAs and should not be considered typical.

A sample by species table of the Sand Forest data set is presented in Table 1 with a complete species list for all

the localities sampled. Importance value classes in the table matrix represent total stem diameter at breast height for a species: 1 = 0–2.5 cm DBH, 2 = 2.5–10 cm DBH, 3 = 10–20 cm DBH, 4 = 20–40 cm DBH, 5 = > 40 cm DBH.

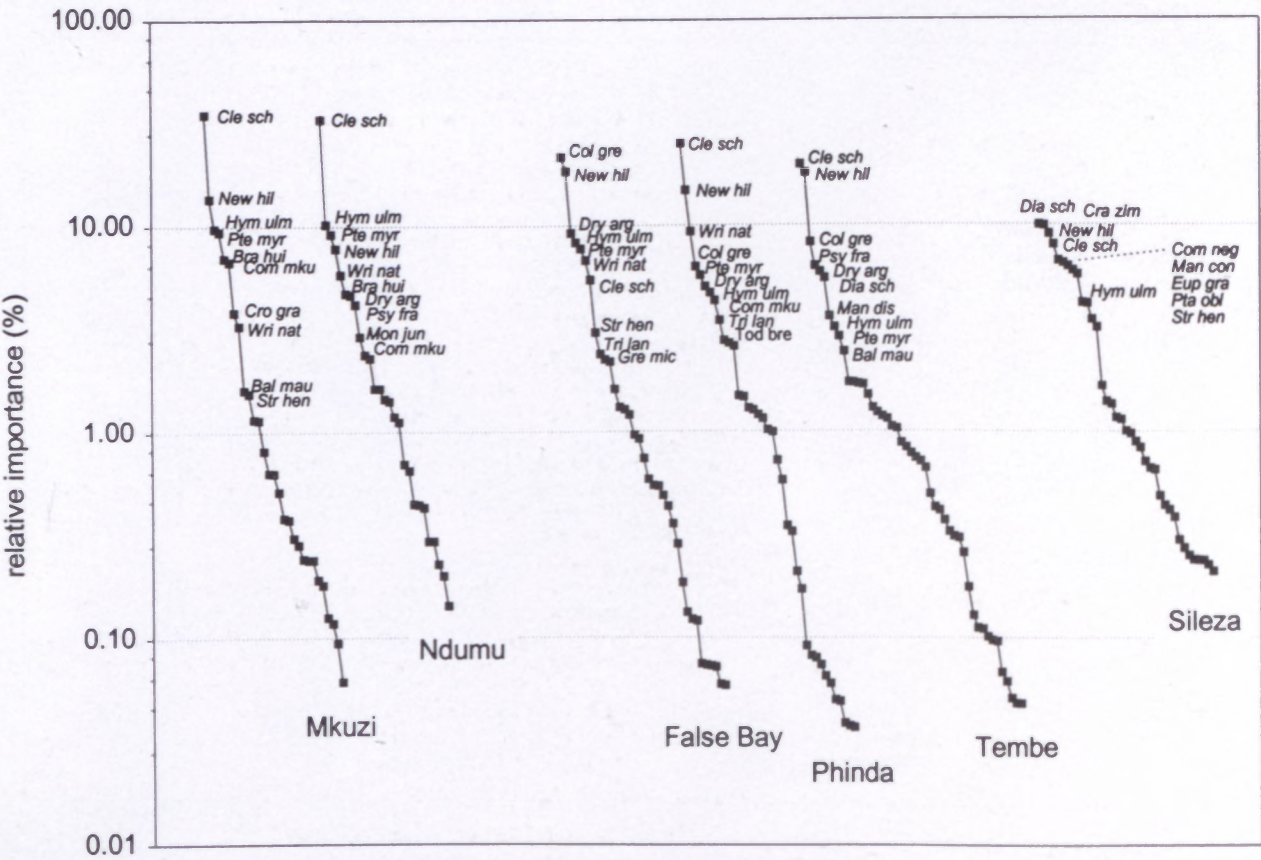


FIGURE 7.—Dominance diversity curves of Sand Forests at sampled sites. Importance values for these curves were calculated as the average of a species' relative dominance (species total DBH/locality total DBH) and its relative density (no. plants/total no. plants) over all quadrats sampled in an area, excluding those shown to be outliers in the DCAs. See Table 1 for full species names.

DISCUSSION AND CONCLUSION

In KwaZulu-Natal, Tropical Dry Forest, including Sand Forest and Ecotonal types, is clearly distinct from both coastal forests and an interior forest. This would tend to support Tinley's (1967, 1977) approach emphasizing the separation of Tropical Dry Forests from all evergreen forests, rather than the more widely accepted approach, grouping Sand Forest and related types with the Coastal Forests (*sensu* MacDevette *et al.* 1989). Clarification of this issue would require objective comparison of Tropical Dry Forest with a broader range of forests in southern Africa, especially Afromontane types.

In the sampled range of Tropical Dry Forests in KwaZulu-Natal, Sand Forest samples form a natural and cohesive group, with most sites dominated by a similar range of species, primarily *Cleistanthus schlechteri* and *Newtonia hildebrandtii*. Sand Forest is however characterised by the presence of *Cleistanthus schlechteri*, *Hymenocardia ulmoides*, *Toddaliopsis bremekampii*, *Psydrax fragrantissima*, *Pteleopsis myrtifolia* and *Haplocoelum gallense*.

In the most comprehensive floristic study of KwaZulu-Natal forests to date, MacDevette *et al.* (1989) classify the indigenous forests of KwaZulu-Natal using species lists (of varying reliability) from 105 sites. Tropical Dry Forests, characterised by the presence of *Cleistanthus schlechteri*, are classified as a subtype of the Coastal Forests with *Pteleopsis myrtifolia*, *Suregada zanzibariensis*, *Monodora junodii*, *Salacia leptoclada* and *Croton pseudopulchellus* as preferential species. Tropical Dry Forests are further divided into Western and Eastern Sand Forests. Western Sand Forests include forests in Ndumu Game Reserve, Mkuzi Game Reserve, False Bay Park and the area now included in Phinda Resource Reserve and have *Brachylaena huillense*, *Boscia foetida*, *Cadaba natalensis*, *Newtonia hildebrandtii*, *Haplocoelum gallense*, *Wrightia natalensis* and *Strychnos usambarensis* as preferential species. Eastern Sand Forests (Manguzi Forest, Sileza Forest and forests in Tembe Elephant Park and Sodwana State Forest) are said to occur from Cape Vidal northwards with *Canthium setiflorum*, *Coffea racemosa*, *Tarenna supra-axillaris* subsp. *barbetonensis*, *Inhambanella henriquesii*, *Ephippiocarpa orientalis*, *Cavacoa aurea* and *Apodytes dimidiata* as preferential species. Their study provides a useful framework for comparison, although discrimination at fine scales is probably poor due to the use of whole forests as individual sample units, with only presence/absence of species noted. We support MacDevette *et al.* (1989) in dividing Sand Forest into convenient Western and Eastern types, although our groups do differ.

The similarity in terms of dominant tree species across the range of Sand Forests indicates that these forests can be treated as functionally uniform. This is important, as it allows us to extrapolate the results of ecological research and apply similar management practices throughout. Significant turnover of plant species does occur however, and since many species appear to be confined to these forests (*pers. obs.*), conservation of the range of variation is crucial. Fortunately, although Sand Forest covers a smaller area than any other vegetation

type in South Africa, it is well conserved (Low & Rebelo 1996). Our survey of woody plants indicates that the full range of variation in South Africa is represented in conserved areas. Forests in Mkuzi and Ndumu Game Reserves represent the Western Sand Forest, while forests in False Bay Park, Phinda Resource Reserve, Tembe Elephant Park and Sileza Forest Reserve adequately represent the more variable Eastern Sand Forest. The non-woody understorey component of these forests deserves further study. Turnover of herbaceous plants and grasses between sites appears to be high and these plants may include a high proportion of endemics. The naturally patchy nature of these forests suggests that the fragmentation associated with conservation in non-contiguous reserves is unlikely to be important.

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[illegible]

Matrix values correspond to total DBH of all stems: 1 = 0-2.5 cm, 2 = 2.5-10 cm, 3 = 10-20 cm, 4 = 20-40 cm, 5 >40 cm

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